1991

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Catherine Cae Maynard
The University of Montana

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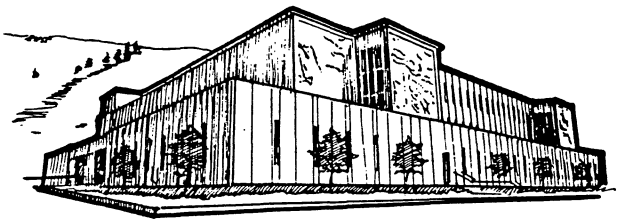


DISTRIBUTION OF DAMAGE BY ARMILLARIA ROOT DISEASE IN THE DOUGLAS-FIR SERIES OF THE LOLO NATIONAL FOREST, MONTANA

by

Catherine Cae Lee Maynard

B.S. Utah State University, 1977

Presented in partial fulfillment of the requirements

for the degree of

Master of Science

UNIVERSITY OF MONTANA

1991

Approved by,

Chairman, Examination Committee

Dean, Graduate School

June 12, 1991

Date

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

ACKNOWLEDGEMENTS

Funding for the field portion of this project was provided by grants from the Northern Montana Forestry Association, the Blackfoot Forest Protective Association, and the Marie Lucas Resource Analysis Award.

Thanks are due to Dr. Ronald Wakimoto for his encouragement and enthusiasm, to Dr. James Byler for generous technical assistance, to Dr. Vicki Watson and Dr. Tom Nimlos for serving on the committee, and to my many instructors and friends for their knowledge, help and support.

I would like to give special thanks to my wonderful husband, Philip and to my children, Mars and Indigo, whose love and sacrifice have made the completion of this work possible. I offer also a special tribute to my late father, Walker Keith Lee, whose love of knowledge and thoroughness instilled in me the fundamentals of scientific investigation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

INTRODUCTION

This study took place in western Montana, where the extent of forested acres occupied primarily by Douglas-fir (Pseudotsuga menzesii var. glauca (Beissn.) Franco has continually increased over the past several decades. Within the boundaries of the Lolo National Forest, 250,460 ha. are currently occupied by stands supporting, or having the potential to support, Douglas-fir as a climax species (U.S.D.A. Timber Stand Data Base, Lolo N.F., 1989). Historically, in much of the northern Rockies, Douglas-fir was less abundant. It occurred as a stand component with ponderosa pine (Pinus ponderosa Dougl.) on warm dry sites at lower elevations, and under cooler, moister conditions with lodgepole pine (Pinus contorta Dougl.) and western larch (Larix occidentalis Nutt.).

Several factors have contributed to the gradual increase in numbers and distribution of Douglas-fir. The selective cutting of pine and other high value species certainly played a role, however the most influential factor has been the suppression of wildfires (Wellner 1984). Natural wildfires occurred with varying frequency in most of the Northern Rockies prior to 1930, when organized fire control efforts became widespread and for the most part successful (Arno 1980). Although all of the above mentioned conifers are adapted to wildfire, only Douglas-fir continues to

regenerate in the absence of disturbance (Cooper and Pfister 1984; Arno et al. 1985). This characteristic has given the species a competitive advantage, primarily responsible for its present dominance throughout the region.

For most of this century the increases in Douglas-fir populations were encouraged by silviculturists, due to the economic importance of the species. In the mid 1970's, however, forest pathologists in the Northwest began compiling inventory results of acreages with tree mortality caused by root disease. It then became apparent that the populations of several species of root pathogens were being stimulated by the increase in numbers and distribution of this susceptible host and associated management practices (James et al.1984; Smith 1984; Byler 1982). Douglas-fir is a primary host for several species of root pathogens, including: Armillaria ostoyae (Romagna) Herick; Phellinus weirii (Murr.)Gilb; Ceratocystis wageneri Goheen and Cobb; Fomes annosus (Fr.)Che.; and Phaeolus schweinitzii (Fr.)Pat.

Throughout the Pacific Northwest, and in portions of the northern Rockies, alarmingly high estimates of infected acreage and losses of timber volume were found. In 1984 R.S. Smith calculated that 113,000 cubic meters (3.9 million cubic ft.), of timber volume is being lost annually in northern Idaho and western Montana, where 1.4 million ha. of commercial forest land are known to have tree mortality caused by root pathogens. In northern Idaho, near the

southern border of the Lolo National Forest, U.S.F.S. pathologist, Geral McDonald, has described the root disease situation as "a full blown epidemic, with infection on the rise and estimates of 50 percent loss of site productivity in some areas" (Close, 1988).

Simply defined, an epidemic is an increase in the population of a pathogen (Van der Plank 1963). Once present in the system, disease may increase exponentially, or at a rate proportional to the amount already accumulated. To describe this phenomenon epidemiologists have applied what is known as the 'compound interest equation for disease':

$x=x_o e^{rt}$

> where x is the amount of accumulated disease at time t (i.e. the amount after it has accumulated for t days, years or whatever the units of time may be); x_o is the initial amount of disease (i.e. the amount at zero time); r is the rate of infection (which does not necessarily remain constant); and e is 2.718 (Van der Plank 1961).

Given an environment where the population of a susceptible host is plentiful, constraints on the exponential growth of the pathogen, as implied by this equation, are then limited to environmental or biological factors that must be identified for the unique species of pathogen being studied.

Most population ecologists accept that species density is naturally regulated by a complex of factors pertaining to the population system and its environment as a whole. At any particular time, one or several factors may be playing the decisive role in limiting population growth (Berryman

1981). It was recognized by both Malthus and Darwin that spontaneous competition for limited resources is the most likely mechanism for regulation of population density among crowded individuals. In tree species the resources most often limiting are water and nutrients. Inadequate intake of these essentials may result in physiological stress, a factor commonly associated with increased susceptibility to root disease (Boyce 1961; Agrios 1978; Blanchard and Tattar 1981; Manion 1981).

A population's influence on the properties of its environment either through pollution, overexploitation of its resources or the buildup of natural enemies, produces effects that will usually be transmitted, with a time delay to future populations (Berryman 1981). The relationship between species density and frequency of occurrence is logarithmic, not linear; therefore once a species is well established, the potential exists for a dramatic increase in its population numbers. This increase will impact not only its own future population, but populations of co-occurring species and communities (Greig-Smith 1957). These principles of population dynamics are active in the interactions occurring between the subjects of this study, the coniferous host (Pseudotsuga menzesii), and its fungal pathogen,(Armillaria ostoyae).

Armillaria is a member of the Basidiomycetes class of higher fungi and has worldwide distribution in forest

ecosystems. Globally there are more than 55 named species of Armillaria, of which 10 are unique to North America (Anderson and Ullrich 1979). Some species and clones of this genera function as nonpathogenic, saprophytic decomposers of lignin, while others are primary or secondary pathogens (Anderson et al. 1979; Rishbeth 1982; Kile 1983; Wargo and Shaw 1985). Surveys have confirmed that members of the genus Armillaria are among the most damaging of the pathogenic microflora in western coniferous stands (James et al. 1984; McDonald et al. 1987b).

The degree of management that a stand undergoes tends to substantially increase the severity of root disease caused by Armillaria (McDonald et al. 1987b; Hagle and Goheen 1988). Woody debris that accumulates in the soil from partial cutting, slash piles, and stumps from thinning operations have all been identified as contributing to the food base available for the fungus and thus stimulating Armillaria populations (Garrett 1960; Rabbe and Trujillo 1963; Filip 1977; Redfern 1978; Shaw 1980; Filip and Goheen 1982). Researchers have also concluded that specific combinations of stand development history and habitat type influence pathogenic behavior in Armillaria species (Shaw et al. 1976; Morrison 1985; Bloomberg and Beale 1985; Hagle and Goheen 1988; McDonald et al. 1987a). On the Coeur d' Alene National Forest in Idaho, Williams and Marsden (1982) found that root disease patches were associated with stand

and site characteristics and were not randomly located. However, the dynamics between site, stand, and pathogenicity in any given location are still poorly understood. In the case of Armillaria root disease, the parameters of site, regardless of disturbance, have not yet been fully defined.

The intent of this study was to identify more fully the characteristics of the locations where pathogenic Armillaria was known to be causing mortality in Douglas-fir, by using the habitat type site classification system.

USE OF THE HABITAT TYPE SYSTEM

Two significant advantages of using the habitat-type vegetation classification system in identifying sites with a high potential to support pathogenic *Armillaria* are:

1) The habitat type classification system is in widespread use by forest management personnel throughout the United States, so any relationship established between root disease and habitat type may allow management considerations pertinent to root disease to be conveyed using this site identifier.

2) A complex of site characteristics (i.e. soils, elevation, temperature and precipitation regimes) are incorporated and expressed via the present or potential plant communities (Daubenmire 1974; Pfister et al. 1977).

The habitat-type system distinguishes sites on the basis of potential climax vegetation. Dominant tree species in the climax community determine habitat *series*. Temperature and moisture gradients from warm/dry to cool/moist are recognized by delineations known as *types* within each of the series. The Douglas-fir series contains fifteen such habitat types (Pfister et al. 1977). Each type represents a range of conditions over which Douglas-fir can be expected to occur as the existing or potential climax tree species. The five more widely distributed Douglas-fir habitat types exhibit *phase* expressions that allow the type to be further

delineated by more specific environmental conditions and coverage classes of dominant vegetation.

BACKGROUND STUDIES

Beginning in 1987, a disease survey of the Lolo National Forest was undertaken by U.S.F.S. pathologists. Using techniques developed by Williams and Leaphart (1978), aerial photos of the forest were scanned for locations exhibiting distinguishable characteristics of root disease. The plotted locations were then ground checked to verify the disease and calculate infected acreage more accurately. Of all the commercial forest land on the Lolo N.F. 18.8%, (123,255 ha.) contained root disease patches or scattered mortality caused by root pathogens (Byler et al. 1990).

From this initial inventory, 579 stands were further evaluated by Byler et al. (1990), in an attempt to develop a prediction tool for identifying stands with the greatest probability of exhibiting root disease mortality. Using presence or absence of tree mortality due to root disease as the dependent variable, a variety of tree, site and stand characteristics were tested for association. Regressions performed indicated the most strongly correlated independent variable tested was habitat type series. Within the Douglas-fir series, mortality was most commonly caused by Armillaria sp. probably ostoyae. The existence of both secondary and primary pathogens among Armillaria species and clones has been suggested however, it is currently accepted to treat the pathogenic species throughout this region as

Armillaria ostoyae (Morrison 1985).

Stands with greater than 40% basal area in Douglas-fir were identified as being highly susceptible to Armillaria. Survey analysis also suggested that stands in the Douglas-fir series on southerly aspects had a higher incidence of root disease than those on northerly aspects.

On both pristine and disturbed sites in Idaho, McDonald et al.(1987a), reported that the incidence of pathogenic Armillaria tended to decrease as site productivity of habitat type increased, and observed no disease in the warm/dry habitat types. Their findings suggested that populations of pathogenic Armillaria were restricted to cool/moist locations, and that Armillaria distribution and damage is constrained by habitat type (Harvey et al. 1986). Byler et al.(1990), found high probabilities of disease in the productive grand fir, Douglas-fir, and western hemlock series, and also reported Armillaria caused mortality in some warm/dry habitat types. These conflicting results indicated a need for further investigation of conditions at sites of disease occurrence.

The previously referenced work of Byler et al. (1990). relied upon the Lolo National Forest timber stand database for pertinent stand information used in their analysis. Because of the sampling method by which these data were collected the features of habitat type and aspect applied only to generalized locations within the land units

inventoried for root disease, but were not specific to verified root disease centers. Thus, mortality may have occurred in stands assigned one habitat type but originated at a location within the stand of another habitat type. Consequently, estimations of disease in the warm/dry habitat types may have been inaccurate. Therefore, a need existed for field verification of habitat type at disease centers. This study was undertaken to provide more information about the possible relationship between root disease and habitat-type. The primary tasks of this project were:

1) To sample from the locations included in the original root disease inventory of the Lolo National Forest;
2) Record the presence or absence of Armillaria root disease;
3) Identify the habitat type to the phase level.

The objective of these tasks was to determine if significant differences existed in the proportions of diseased versus non-diseased plots within each habitat type and phase of the Douglas-fir series represented by this sample.

PHYSICAL DESCRIPTION OF SAMPLING AREAS

The Lolo National Forest is located in the northern Rocky Mountains and encompasses 840,000 ha. in west central Montana. The southwest boundary of the Forest follows the Bitterroot Divide. It also includes the Coeur d' Alene, Rattlesnake, Swan and south Mission mountain ranges. The Clark Fork river bisects the Forest from east to west, with the major tributaries of the Clark Fork being the Blackfoot, Bitterroot, Flathead, St.Regis, and Thompson rivers. It is generally favored by a modified Maritime climate, with mean annual summer and winter temperatures of 19 C. and -5 C. respectively.

The Forest is predominately mountainous forest land dissected by large valleys such as the Missoula, Swan, Bitterroot and Potomac, which create strong orographic effects. Precipitation ranges from 36 cm. annually in the Missoula valley (at 945 m. elevation) to 240 cm. annually on mountain peaks of 2700 m. elevation. The western and northeastern portion of the Forest receive a higher proportion of annual precipitation as snow, while in the southeastern portion a higher proportion of the annual precipitation falls in the form of rain. The Forest contains a broad range of elevations, from 900 meters in the valleys to peaks of over 2500 meters (Sasich 1988).

Within the sampling locations, landforms are predominately

steep to moderate relief mountain slopes (30-55%), or moderately steep stream breaklands. A lesser component of plots was located on broad, convex ridges or stream terraces. Parent materials most frequently encountered were weak to moderately weathered metasedimentary argillites, quartzites, and siltites. Soils found in the sampling locations were predominately Inceptisols of the Ochrept suborder. These soils are characterized as weakly developed mineral soils. Varying soil moisture regimes among locations were indicated by the presence of the Ustochrept and Xerochrept great groups. Some Cryochrepts were included at higher elevations. A subsurface accumulation of volcanic ash was common throughout many of the sampling locations, as indicated by a predominance of map units in the Andic subgroup. Soil textures were commonly loams and silt loams with 15-25% coarse rock fragments.

Maps of the ten sampling locations are found in Appendix I and can be referenced by the following coordinates:

SUBCOMPARTMENT NAME	QUADRANGLE	TOWNSHIP,RANGE,SECTION
Camp Creek	Camp Creek	40N,21W,S1,7,18
Gilbert	Cleveland Mt. N.E.	10N,16W,S28 10N,17W,S30
Little Joe	Illinois Peak N.W.	17N,28W,S8,18
McCabe Creek	Ovando Mt.	15N,11W,S26,34
Miller Creek	Spread Mt. S.E. Missoula	11N,18W,S6,32
Russian Bill	Superior S.W.	15N,26W,S17,20
Schwartz Creek	Cleveland Mtn. N.E.	11N,17W,S10,11,13
Sixmile	Alberton S.E.	15N,21W,S5,32
Twelvemile	St.Regis N.W.	20N,29W,S1,12
Yellowjacket	Dunham Point	16N,11W,S4 16N,12W,S8

A description of the vegetation characteristics of the sampling locations can be found in Appendix II. This includes the abbreviations used hereafter in referencing habitat types and phases.

METHODS

Prior to field sampling, an initial stratification was undertaken to determine potential sampling locations that covered the range of site characteristics over which both habitat types of the Douglas-fir series, and pathogenic Armillaria occurred. An effort was made to sample from locations where site characteristics encompassed most of the variability of the Douglas-fir habitat types as they occur on the Lolo National Forest. This was accomplished by examining existing maps, and Forest Service timber stand database information pertaining to the original 60 subcompartments identified with root disease mortality from the aerial inventory. I then examined the field reconniassance notes of the pathologists who ground checked the stands for root disease, plotted on maps of the forest the locations of verified Armillaria centers that were within the Douglas-fir series and selected ten sampling locations with diverse habitat type features that seemed to incorporate the range of variability within the identified disease centers.

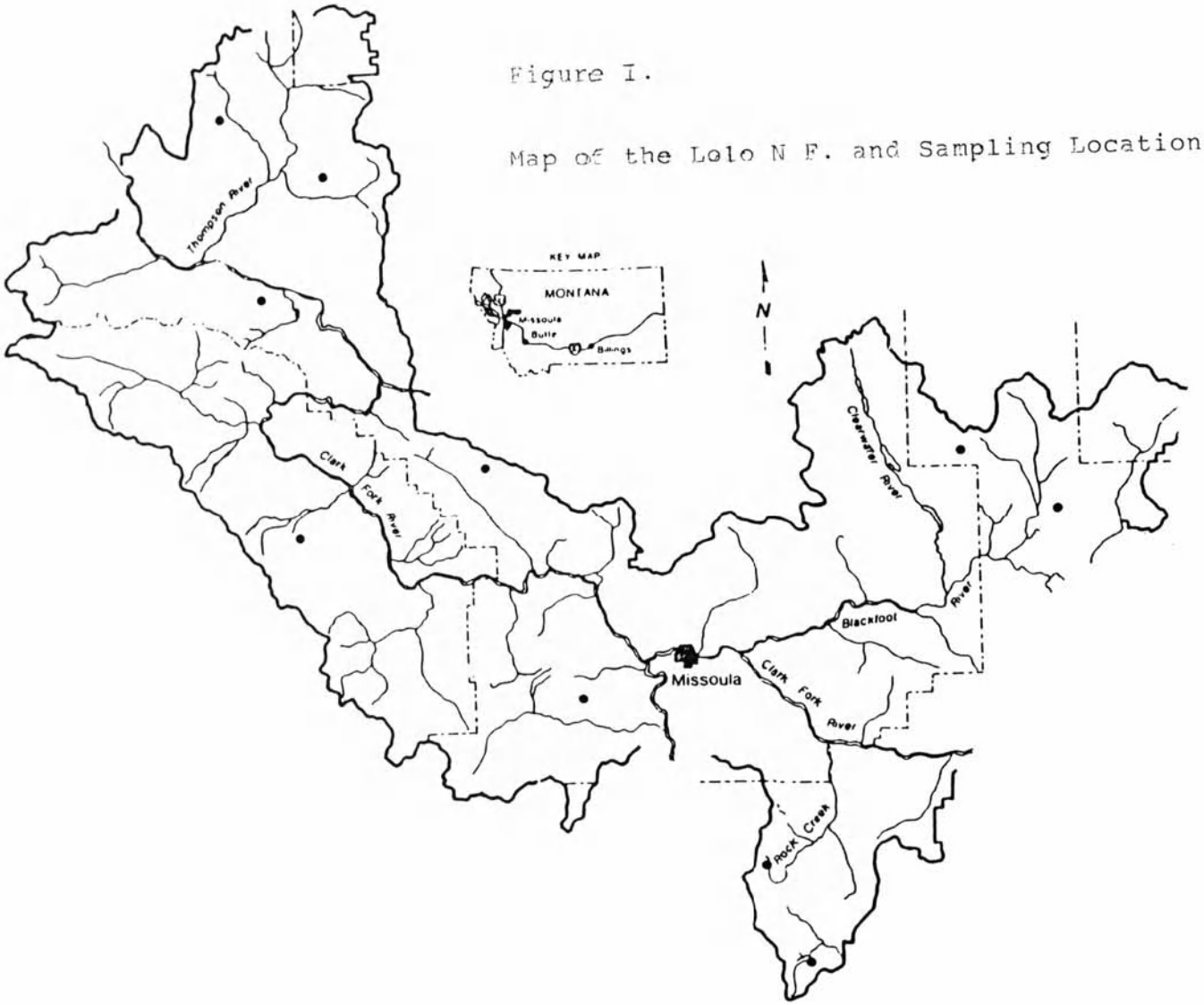
Trees with Armillaria are not scattered uniformly over the landscape, but rather they tend to occur in foci or areas of abnormally high concentrations of disease. In the case of Armillaria these are expressed as disease 'centers' (Van der Plank, 1963). Hereafter I use the term 'disease centers'

to refer to both concentrated groups and scattered individual tree mortality. After examining aerial photos of the infected locations, I estimated that a sampling area of approximately 500 ha. (2 sections), per location would be needed to encompass the variability in topography and elevation over which the disease centers occurred and changes in habitat type would be evident. Assuming uniform distribution over this size of an area, and using six plots per 250 ha. as the standard, a distance of 265 m. between plots was required. At each location the first plot was located by generating a random number, the first three digits of which were used as the azimuth of the direction toward the plot center; 265 m. from the plot center in the next randomly selected direction was the center for the second plot, and so forth. This method was used to assure that the orientation of each plot had equal probability of being included in the sample. If the random azimuth that was generated caused the plot to be located in a non Douglas-fir series habitat type, a new azimuth was generated and the process repeated. The plots were located in ten land units selected from the 60 original subcompartments identified in the Lolo disease inventory mentioned earlier (see Figure 1).

At each of the ten locations, twelve plots were randomly located, habitat type to the phase level was identified, and presence or absence of Armillaria root disease was recorded. A total of 120 plots were evaluated and used in the

Figure I.

Map of the Lolo N F. and Sampling Locations



analysis. For purposes of feasibility, locations at extreme distances from Missoula (>300 km.) or those inacessible by roads, or greater than a 10 km. hike were excluded from consideration.

Identification of habitat-type and phase was done according to the procedure established by Pfister et al. (1977) that is, temporary 375 m.sq. (one-tenth acre) circular plots were marked and ocular estimates of vegetation coverage classes were made. Standard habitat type field forms were used to record plot information (see Appendix III). Habitat type and phase identifications were based on distribution of indicator species in the coverage classes. Refer to Pfister et al.(1977) for further discussion of habitat typing procedures.

Plots were recorded as having no disease if the plot did not contain trees with visible aboveground root disease symptoms and if no mortality caused by root disease was present. Decline or mortality by agents other than Armillaria were not included. Plots were recorded as 'diseased' when visible symptoms of root disease induced decline were evident in one or more of the trees present on the plot, or mortality of one or more trees on the plot could be attributed to Armillaria. Basal resinosus, loss of needles from the stem out, thinning of crowns, and other aboveground symptoms were used as evidence of Armillaria root disease (Blanchard and Tattar 1981; Hagle et al. 1987).

In living trees showing symptoms of infection, the bark at the root collar was removed with a pulaski, and if a thick, fan-shaped mat of mycelium was evident in the cambium of the roots and root collar, or if black rhizomorphs were evident on the outside of infected roots, positive identification of Armillaria was assumed. Dead trees with active mycelial fans no longer evident were examined for properties of the decayed wood or fan impressions in the root collar bark. If the rotting wood was characteristically spongy or stringy and white to yellow in color, or if black zone lines were obvious, the mortality was attributed to Armillaria. At each of the ten locations a sample of fungal tissue was taken from one or more of the infected trees. This sample was later cultured to verify the species of the pathogen. See Appendix IV for the procedure used in the culture and identification of the inoculum.

The data collected were tabulated according to habitat type and phase, presence or absence of disease and plot aspect. Proportions of diseased plots on north and south aspects, and proportions of diseased plots in each habitat type and phase were compared for significant differences. The SYSTAT statistical software program was used throughout the analysis (Wilkinson 1986).

RESULTS

The results of this study support the conclusion that Armillaria root disease commonly occurs and causes mortality in Douglas-fir habitat types on southerly aspects. The overall frequency of plots that occurred on combined southerly aspects (SO.,SW.,SE.) was less than the frequency of plots on northerly aspects (NO.,NW.,NE.), n=45 vs. n=57. However, southerly aspects accounted for 60% of the diseased plots. A test of the hypothesis that a difference due to aspect existed in proportions of diseased plots revealed that the proportion of diseased plots on southerly aspects was significantly greater than the proportion of diseased plots on northerly aspects at $P<0.01$ using a z-test for proportions with pooled variances.

A histogram of the percentages of plots with root disease by aspect is displayed in Figure 2, while Table 1 reports the the distribution of diseased plots by aspect.

Of the fifteen possible Pseudotsuga habitat types, seven were represented by sample plots. Three dominant types (PSME/PHMA, PSME/VAGL, and PSME/CARU) accounted for 85% of the plots. The remaining 15% of sample plots were located in PSME/LIBO (6%), PSME/VACA (4%), PSME/SYAL (2.5), and PSME/FESC (1.5%) habitat types. Of the seven habitat types represented all but two contained plots with evidence of root disease. No disease was observed in plots of the PSME/LIBO and PSME/SYAL types.

Of the entire sample, 43% of the plots were observed to contain tree mortality or symptoms of decline caused by Armillaria (n=52). Of the three major habitat types in the sample population, the largest proportion of diseased plots occurred in the PSME/CARU type, where 14 of the 21 plots contained Armillaria root disease (see Fig. 3). Types and phases were compared by testing the hypothesis that the difference in proportions of plots with disease was due to habitat type. Although the overall frequency of plots was greatest in the PSME/PHMA h.t. (n=47), the proportion of diseased plots in this group was less than in PSME/CARU (P=0.0336). Similarly, plots in the PSME/VAGL type also occurred with greater frequency (n=34) than those of PSME/CARU, yet contained a significantly smaller proportion of diseased plots (P=0.0136). Proportions of diseased plots between the PSME/PHMA and PSME/VAGL types were not different at the <.10 probability level (P=.2574). The overall frequency with which each habitat type was represented and the proportions of diseased plots in each category is displayed in Table 2.

Frequency and proportions of disease in the phase expressions of the habitat types sampled are presented in Table 3. As can be seen, VAGL/XETE was the most frequently observed phase (n=28), closely followed by PHMA/CARU (n=26) and PHMA/PHMA (n=21). Figure 4 presents a histogram of the total numbers of plots and diseased plots in each of the

phases sampled.

Testing between the phases of each habitat type required the use of the Bonferroni procedure, which reduces the level of probability by factoring the number of related categories. The differences between phases of any one type were not found to be statistically significant at the <.10 probability level. Results of the z-test calculations are shown for types and phases in Tables 4 and 5 respectively. Under the normal approximation to the binomial distribution, categories with less than ten observations could not be accurately tested. However significant differences may have occurred, such as in the PSME/VACA h.t., where four of the five plots observed contained root disease.

Statistically, the most significant phase distinction observed was that between CARU-CARU and PHMA-PHMA, which indicated a greater proportion of diseased plots occurred in the drier type and phase (P=.0084). The results of testing for differences in proportions of diseased plots between VAGL/XETE and PHMA/CARU showed PHMA/CARU to contain a greater proportion of diseased plots (P=0.0985). Differences between the drier PSME/PHMA phase,(PHMA-CARU) and the PSME/CARU-CARU phase were not large enough to be statistically significant at the <.01 level (P=.1423). The differences in proportions of diseased plots between the PHMA-PHMA and VAGL-XETE and the PHMA-CARU and PHMA-PHMA phases were not signifcant at the <.10 probability level.

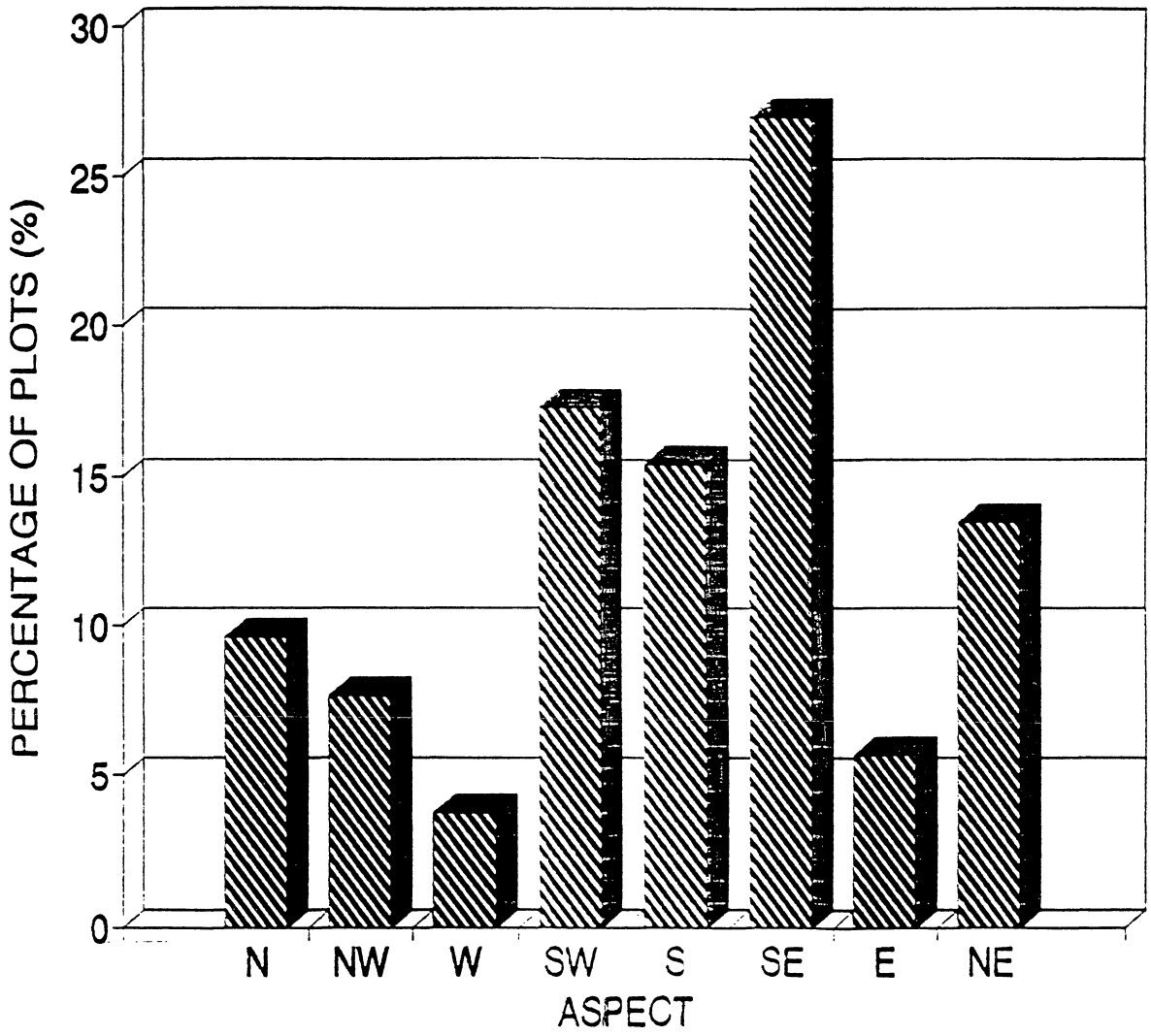


Figure 2. Histogram of Percentages of Diseased Plots by Aspect.

Table 1. Distribution of Diseased Plots by Aspect

Aspect	n	% disease present
North	5	9.6
N.West	4	7.7
West	2	3.8
S.West	9	17.3
South	8	15.4
S.East	14	27.0
East	3	5.7
N.East	7	13.5
	52	
COMBINED ASPECTS		
SO.+ SW.+ SE.	31	59.6
NO.+ NW.+ NE.	16	30.7

Table 2. Habitat Types Represented and Frequency of Disease

Habitat Type	Total Plots	Diseased Plots	Proportion with Armillaria damage
PHMA	47	20	.4255
VAGL	34	12	.3529
CARU	21	14	.6666
LIBO	8	0	-
VACA	5	4	.8888
SYAL	3	0	-
FESC	2	2	1.0000
	120	52	

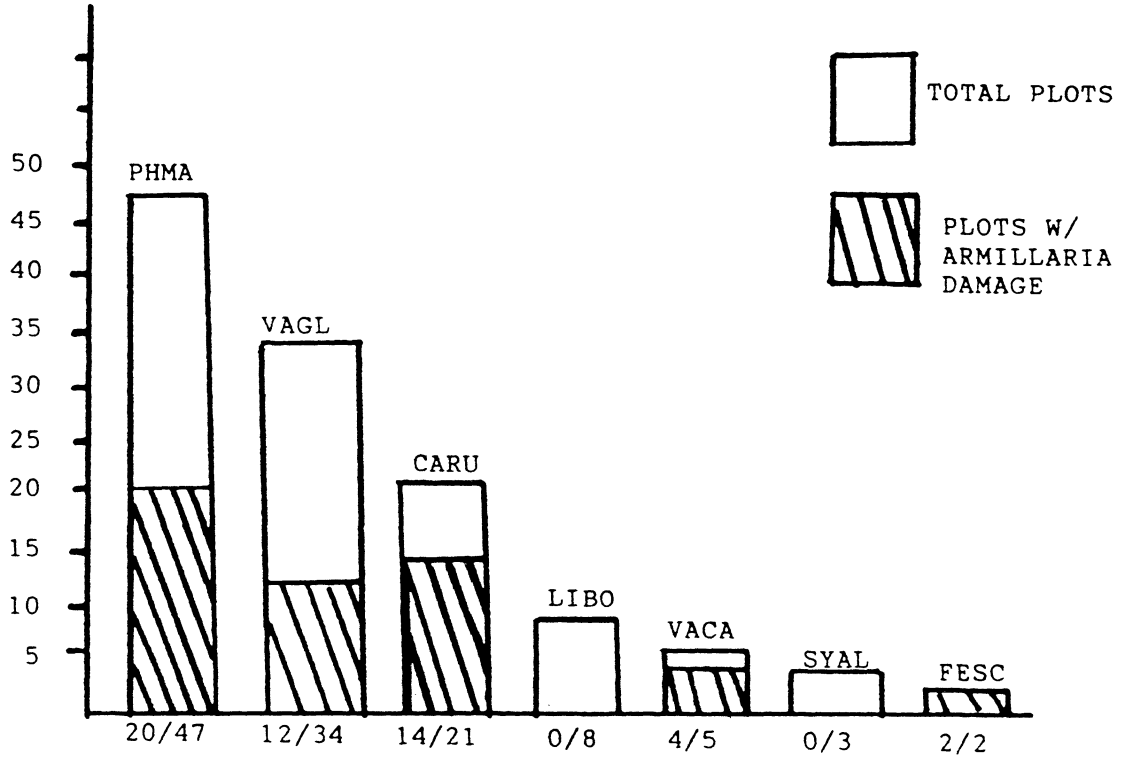


Figure 3. Histogram of Total and Diseased Plots by Habitat Types.

Table 3. Phases Represented and Frequency of Disease

HABITAT PHASES	TOTAL PLOTS	DISEASED PLOTS	PROPORTION WITH ARMILLARIA DAMAGE
PSME/PHMA	47	20	.4255
PHMA-PHMA	21	6	.2857
PHMA-CARU	26	14	.5384
PHMA/VAGL	34	12	.3529
VAGL-XETE	28	10	.3571
VAGL-VAGL	6	2	.3333
PSME/CARU	21	14	.6666
CARU-CARU	11	8	.7272
CARU-ARUV	10	6	.6000
PSME/VACA	5	4	.8000
PSME/FESC	2	2	1.0000
	120	52	

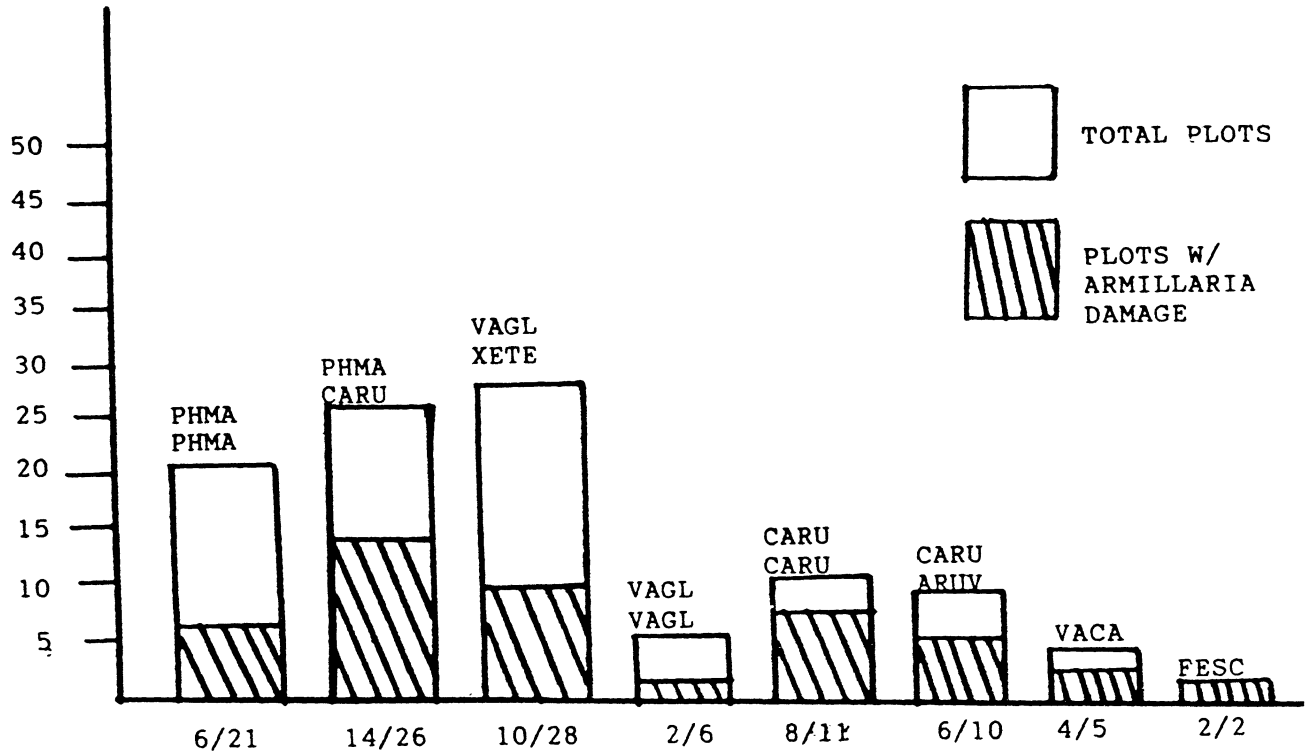


Figure 4. Histogram of Total and Diseased Plots by Phases.

Table 4. Results of z-test for Differences in Proportions of Three Major Habitat Types.

Habitat type	z-value	P.
PSME/CARU > PSME/VAGL	2.218	.0136
PSME/CARU > PSME/PHMA	1.832	.0336
PSME/PHMA > PSME/VAGL	.653	.2574

Table 5. Results of z-test for Differences in Proportions of Disease by Habitat Phases. (n>10)

Habitat phase	z value	P.
CARU-CARU > PHMA-PHMA	2.399	.0084
CARU-CARU > VAGL-XETE	2.095	.0183
PHMA-CARU > VAGL-XETE	1.293	.0985
CARU-CARU > PHMA-CARU	1.072	.1423
PHMA-PHMA > VAGL-XETE	.527	.3015
PHMA-CARU > PHMA-PHMA	1.742	.5204

DISCUSSION

In this study, pathogenic Armillaria was found in stands of the Douglas-fir series on a variety of exposures, topographic positions and temperature/moisture regimes. In keeping with the results of Byler et al. (1990), the predominance of mortality caused by Armillaria on southerly aspects was clearly verified. However, the limitation of Armillaria distribution to cool/moist habitat types, as implied by McDonald et al. (1987a), was not supported by these findings. Rather, the results of this study supply field verification to the suggestion of Armillaria mortality in warm/dry habitat types reported by Byler et al. (1990).

Overall, the distribution of the sample plots among the various types of the Douglas-fir series were reasonably consistent with the relative percentages of the types as they occur on the Lolo National Forest (see Table 7). In this regard the sample population appears to have successfully incorporated the variability of these types and the range of conditions over which pathogenic Armillaria occurs throughout the Forest. As indicated by the results, the types and phases with statistically larger proportions of disease were the Pseudotsuga/Calamagrostis rubescens type, Calamagrostis rubescens phase; and the Pseudotsuga /Physocarpus malvaceus type, Calamagrostis rubescens phase; and there was not a significant difference between the

Table 6. Percentages of Douglas-fir Habitat Types on the Lolo N.F. and in the Sample.

HABITAT TYPE	SAMPLE %	LOLO N.F. %
PSME/PHMA	39.16	52.47
PSME/VAGL	28.33	20.93
PSME/CARU	17.50	11.59
PSME/LIBO	6.6	2.87
PSME/SYAL	2.50	4.32
PSME/VACA	4.10	1.05
PSME/FESC	1.60	3.24

proportions of diseased plots of these phases.

Although the level of significant differences in proportions of plots with disease between habitat types and phases reported here may be an artifact of the sampling method employed, or the sample size; the fact remains that Armillaria caused mortality was observed in stands of the Douglas-fir series with warm/dry microclimates.

As stated earlier, the overall intent of this study was to identify more fully the characteristics of the physical locations where pathogenic Armillaria was known to be causing mortality in Douglas-fir by using the habitat type classification system. In keeping with this objective, the list of habitat types supporting pathogenic Armillaria noted by Byler et al.(1990) as being PSME/PHMA, PSME/VAGL, and PSME/CARU can be expanded to include the phases PHMA-PHMA, PHMA-CARU; VAGL-VAGL, VAGL-XETE; CARU-CARU and CARU-ARUV. Furthermore, the habitat types PSME/VACA and PSME/FESC may be added to the list of sites where pathogenic Armillaria has been observed.

Unfortunately, the objective of providing more information about the possible relationship between root disease and habitat type has been met only insomuch as that additional questions have been raised. Such as, why is Armillaria root disease found throughout habitat types and phases of varying temperature/moisture regimes from cold/moist to warm/dry? Perhaps the combined feature of temperature/

moisture gradient, as incorporated into habitat type and phase is not a reliable indicator of the parameters that affect the pathogen's distribution. Another interpretation is that the level of disturbance may take precedent over habitat type. However, this study sampled from locations not stratified by type or level of disturbance. Before the relationship between habitat type and Armillaria root disease can be fully understood, a more extensive sampling of disease locations stratified by habitat type and disturbance history would be required.

In spite of this, habitat type may still be a useful point of reference when evaluating the potential of a site to support pathogenic Armillaria if it is used in conjunction with other characteristics and history of the site and stand. According to Arno (1980), in most areas where the Douglas-fir series commonly occurs, historically the mean fire free intervals ranged from 15 to 30 years. For many centuries the low to medium intensity ground fires that were common in this series maintained stands composed of a greater variety of species and structures than are presently found (Houston 1973; Loppe and Gruell 1973; Arno 1976). In the PSME/CARU type, open stands with ponderosa pine as a dominant overstory component were widespread in western Montana. Similarly, stands in the PSME/PHMA type were also maintained in a more open condition. Quite possibly the trend in many locations toward more climax conditions with

high population densities of Douglas-fir may be supporting pathogenic Armillaria where historically the temperature/ moisture relations that occurred in stands of a more seral condition may indeed have played a limiting role in the pathogen's distribution.

In addition to the direct effect the absence of fire has had on stand structure and species composition, there is the indirect influence it has had on nutrient cycling and the species composition of microflora communities.

Low intensity fires contribute to the mineralization of nitrogen, calcium, magnesium and potassium, and may influence the amounts of these essential nutrients available to vegetation (Algren 1974; DeBell and Ralston 1979; Grier 1975). Low and medium intensity burning lowers the C/N ratio and increases the structural accessibility of litter to soil organisms, favoring microbial activity and subsequent nitrogen transformations (Mroz et al. 1980; Waring and Schlesinger 1985). Alteration of the soil and litter pH by burning also influences nutrient availability.

Due to seasonal limitations of temperature and moisture on microbial activity, in the Douglas-fir series of western Montana, dry matter accumulates faster than it decays. Historically, wildfires played an important role in regulating the accumulation of dry matter and contributing to long term soil quality and stability by producing humus, decayed wood and charcoal (Harvey et al. 1978). Research

done on beneficial ectomycorrhizae has shown that charcoal serves as an important substrate for the species of mycorrhizae common to Douglas-fir (Harvey et al. 1976). Mycorrhizae are known to increase the effective surface area of roots and thus enhance the tree's ability to absorb both water and nutrients. Conifers growing without the symbiotic association of beneficial mycorrhizae exhibit significantly slower growth rates and reduced amounts of essential elements in their tissue. Such factors could easily translate into stress and increased susceptibility to disease (Manion 1981; Kimmins 1987).

Research by Matson and Boone (1984) in Oregon suggests that there is a strong correlation between both nutrient availability, light limitation, and infection by Phellinus weirii (a root pathogen which often co-occurs with, and has characteristics similar to Armillaria) (Matson and Waring 1984). Their experiments revealed that trees with very low nitrogen reserves were more susceptible to infection. Were studies of this nature to be conducted on Douglas-fir and its susceptibility to infection by Armillaria, the specific nature of site conditions favoring development of the disease in a stand might be further illuminated. Further understanding of the cause and effect properties associated with infection by pathogenic Armillaria would give more meaning to correlations between disease occurrence and habitat types.

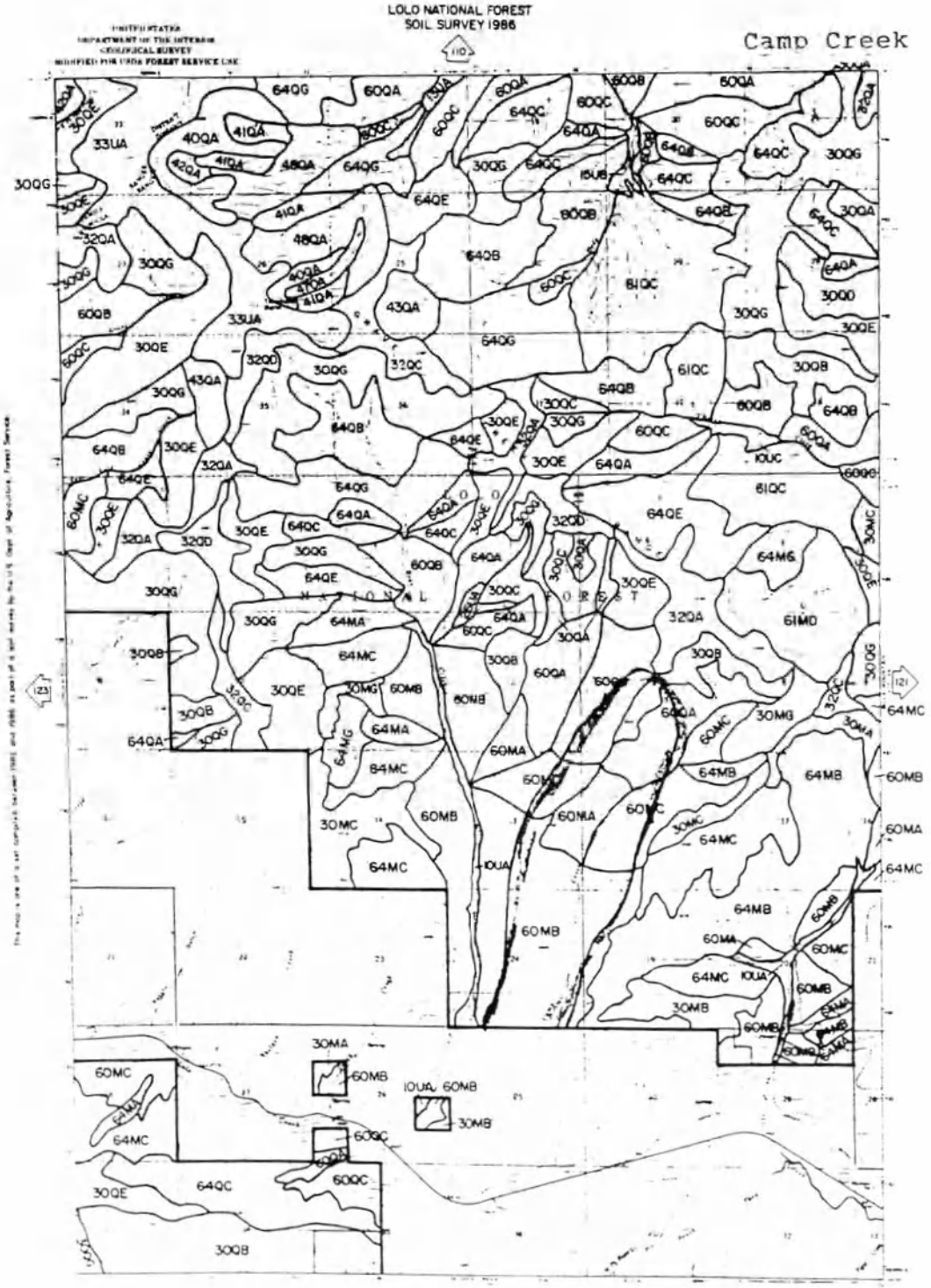
The classification of sites by habitat type is undoubtedly a useful system, however the temperature/moisture parameters of habitat type and phase may not be directly correlated to micro-climate limitations on the development of Armillaria root disease in the Douglas-fir series. Thus it becomes necessary to consider the host of other variables influencing the distribution of the pathogen. Certainly fire is an important ecosystem component, and it's role in the cycling of nutrients both by directly altering the chemistry and structure of litter and duff, and by impacting microbial composition and activity may have direct bearing on the potential of a stand to support Armillaria root disease. Likewise, the type and extent of other types of disturbance must be considered. A thorough and extensive study of disease locations stratified by stand characteristics, disturbance and fire histories, and habitat type would be likely to yield more conclusive results than have been reported here.

CONCLUSION

Given the results of this study, it is apparent that Armillaria root disease may occur in any of the three major Douglas-fir habitat types common in western Montana (PSME/PHMA, PSME/VACA, PSME/CARU). The ability of the pathogen to survive over the range of site conditions associated with these habitat types suggests that site limitations on the pathogen's distribution are less stringent than previously thought, and presents a difficult scenario for land managers.

Knowing that the potential exists for the increasingly widespread distribution of Armillaria root disease places additional responsibility for the control of its spread into the realm of creative silviculture, or what has been recently coined 'New Forestry'. An integrated, ecosystem approach to stand management that allows fire to fulfill its essential functions of maintaining species diversity and enhancing nutrient cycling is a major recommendation to those participating in the process of controlling the spread and severity of the disease.

Appendix I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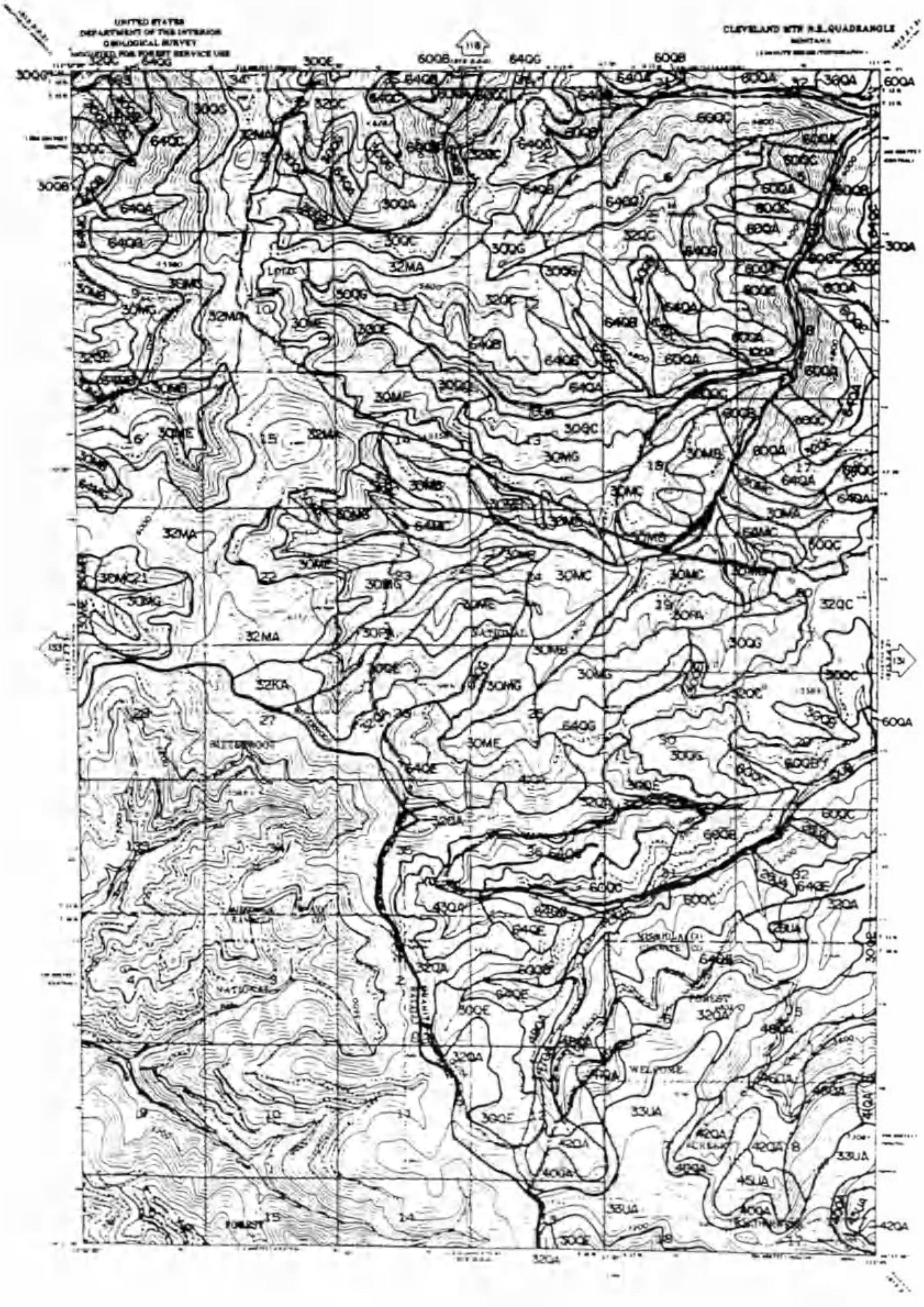
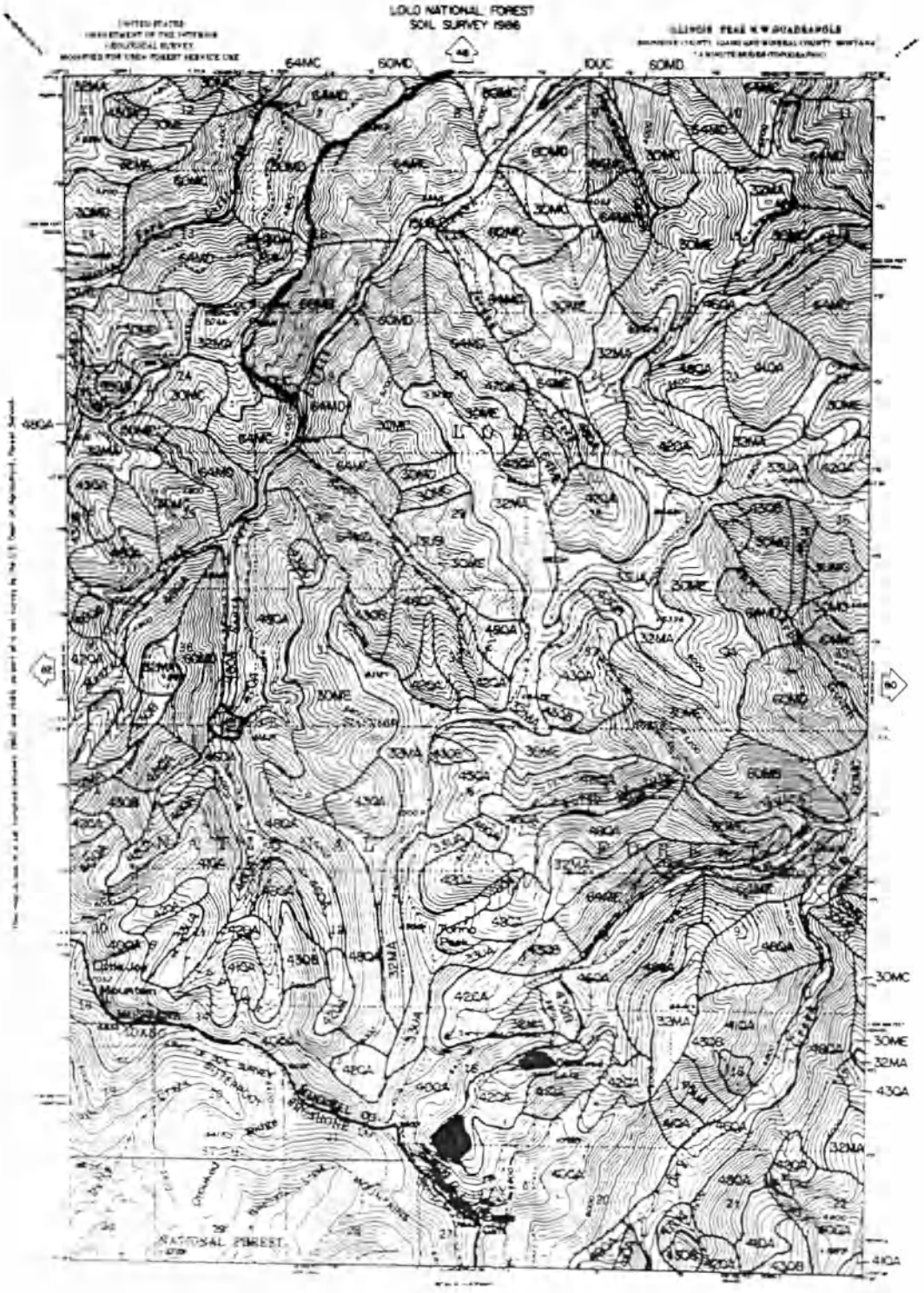
SOIL SURVEY 1986
Camp Creek
NATIONAL FOREST


UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
CLEVELAND MTN N.E. QUADRANGLE
MONTANA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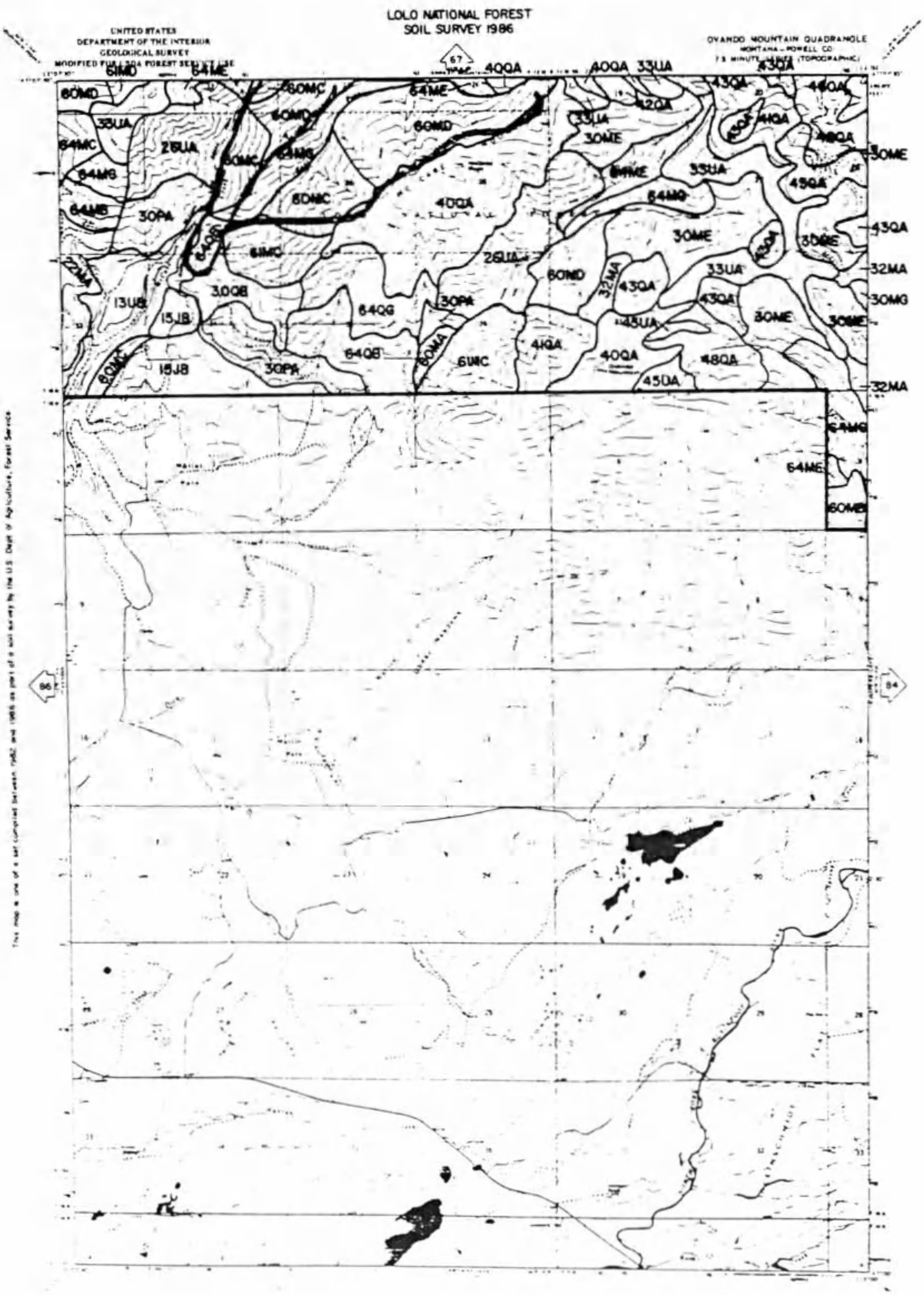
SOIL SURVEY 1986
ILLINOIS PEAK N W QUADRANGLE
64MC
60MD
IDUC
60MD
NATIONAL FOREST


LOLO NATIONAL FOREST
SOIL SURVEY 1986
UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
OVANDO MOUNTAIN QUADRANGLE
MONTANA – POWELL CO.
67
86
84
60MD
61MD
64ME
60MC
33UA
64MC
26UA
64MG
64MB
30PA
60MD
60MC
61MC
40QA
30QB
13UB
15JB
64QG
64QB
30PA
60MA
61MC
41QA
40QA
45UA
48QA
45DA
33UA
30ME
42QA
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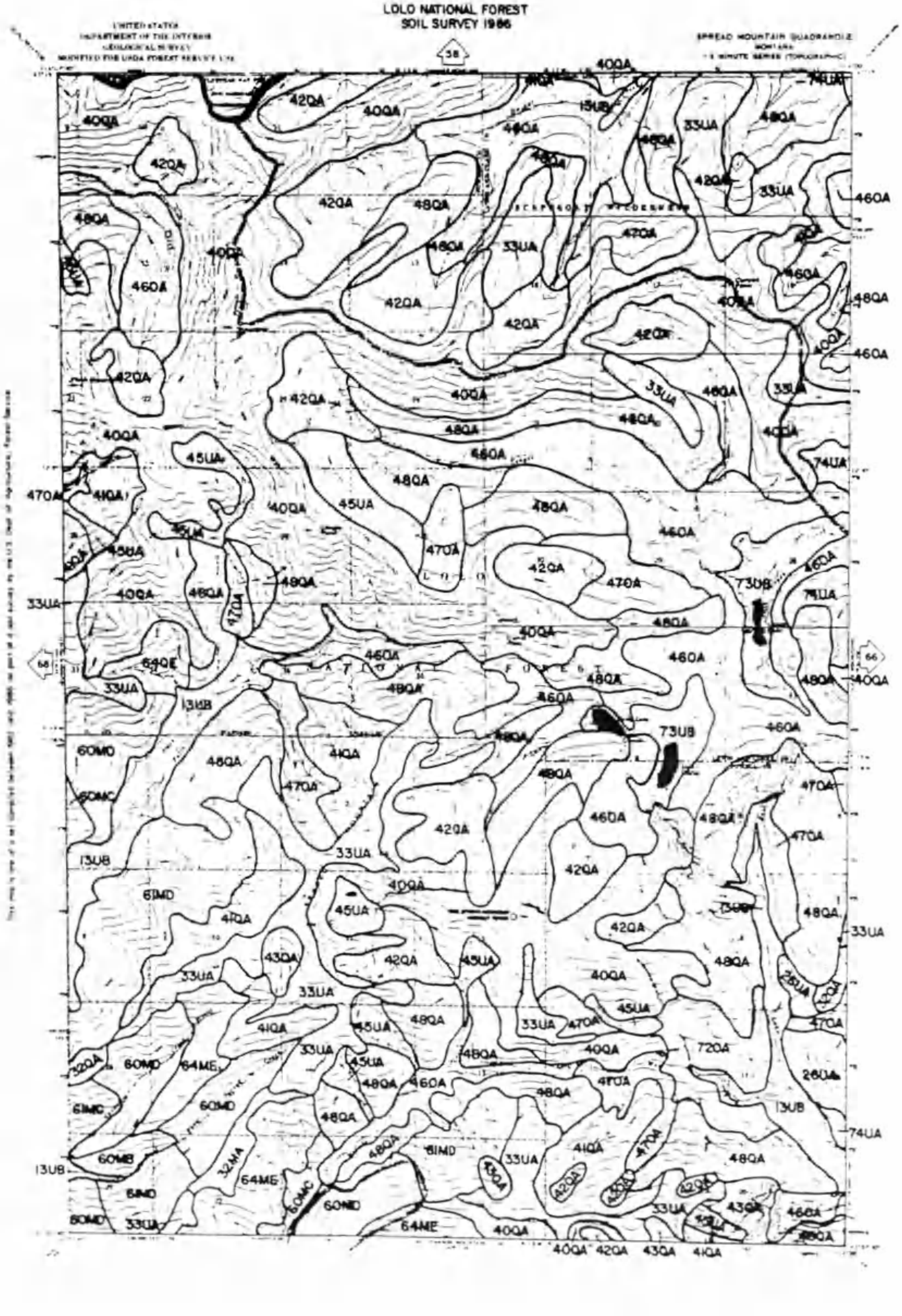
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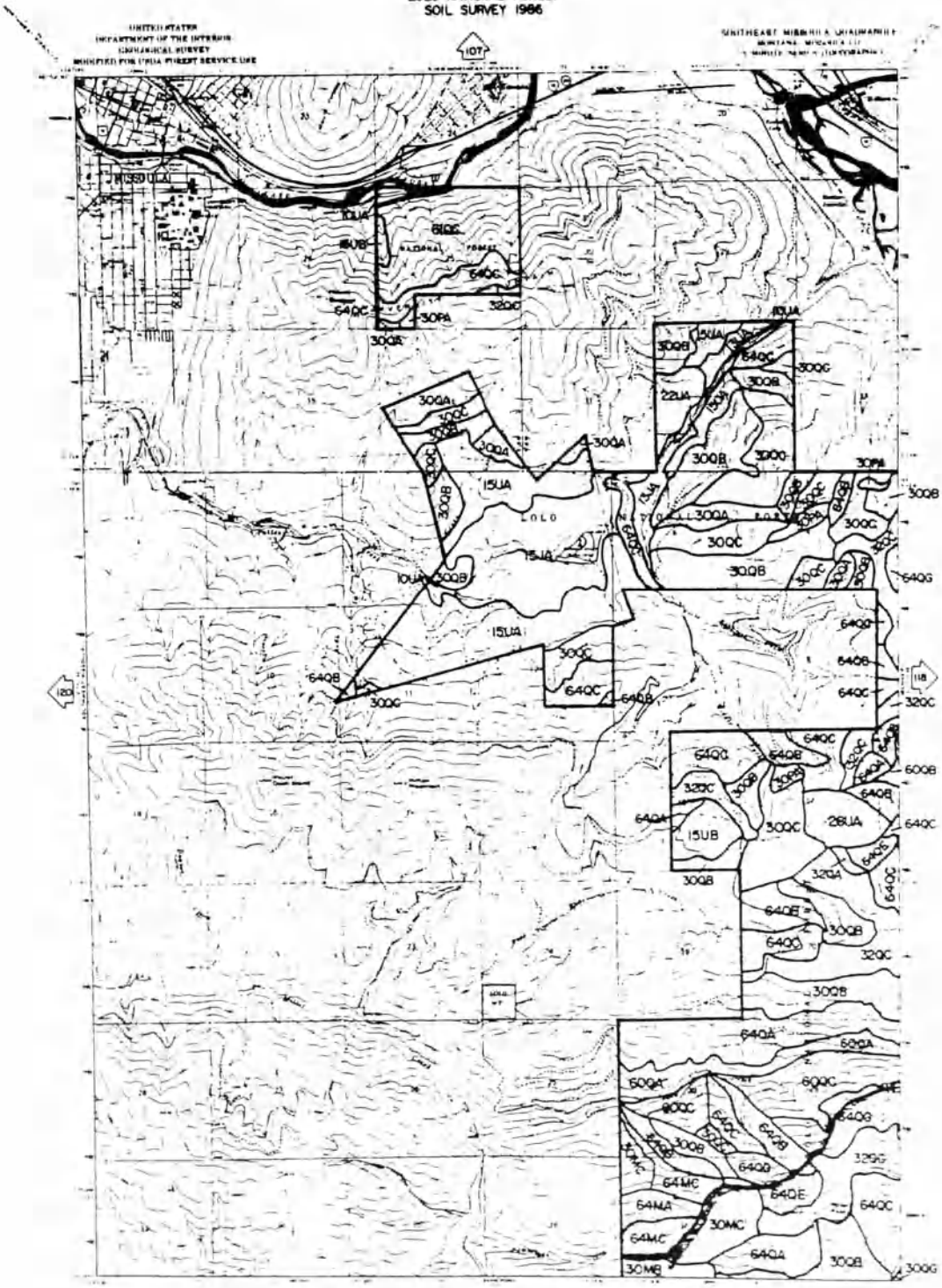
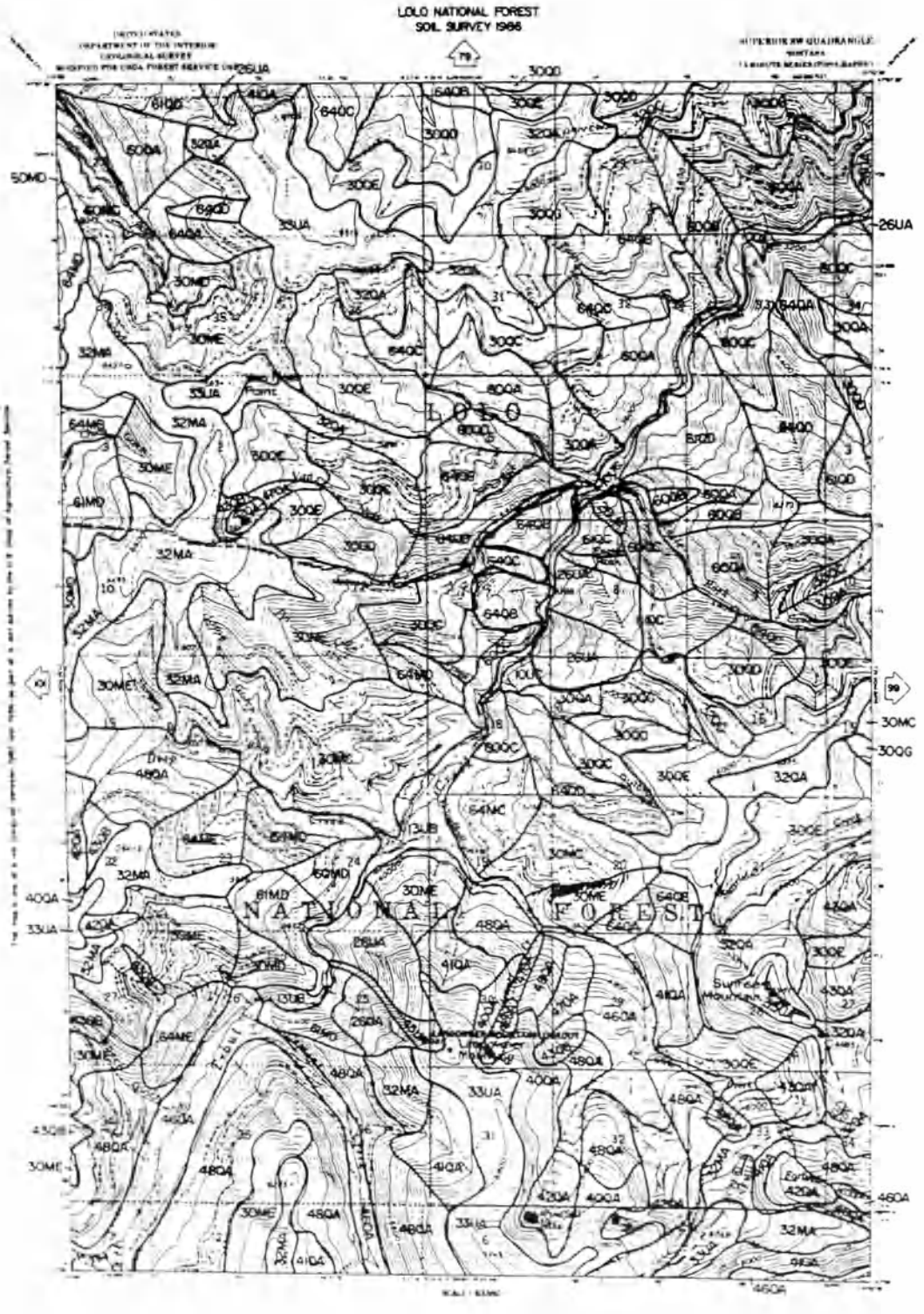
SOIL SURVEY 1986

LOLO NATIONAL FOREST
SOIL SURVEY 1986

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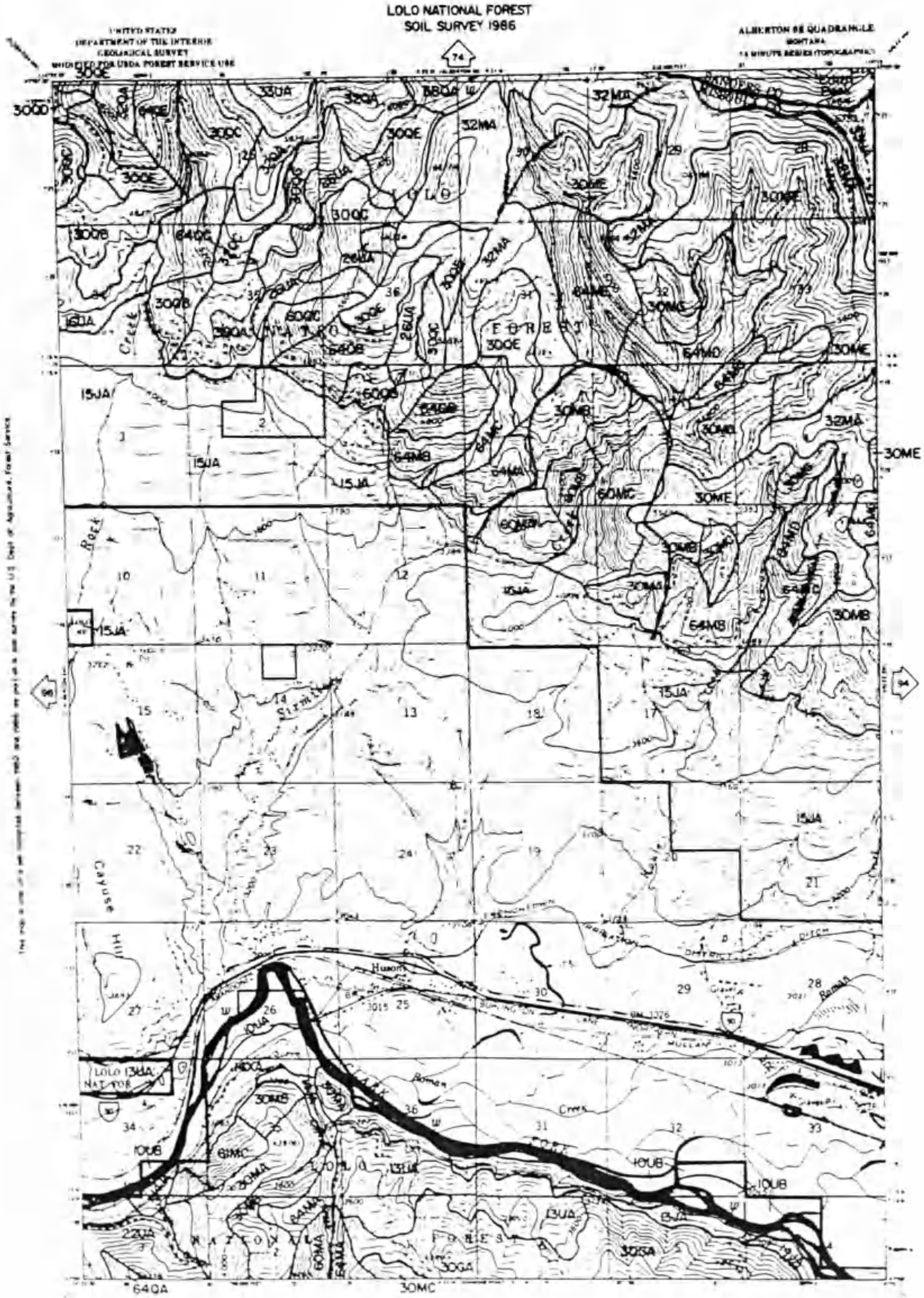
LOLO
NATIONAL FOREST


LOLO NATIONAL FOREST
SOIL SURVEY 1986
UNITED STATES
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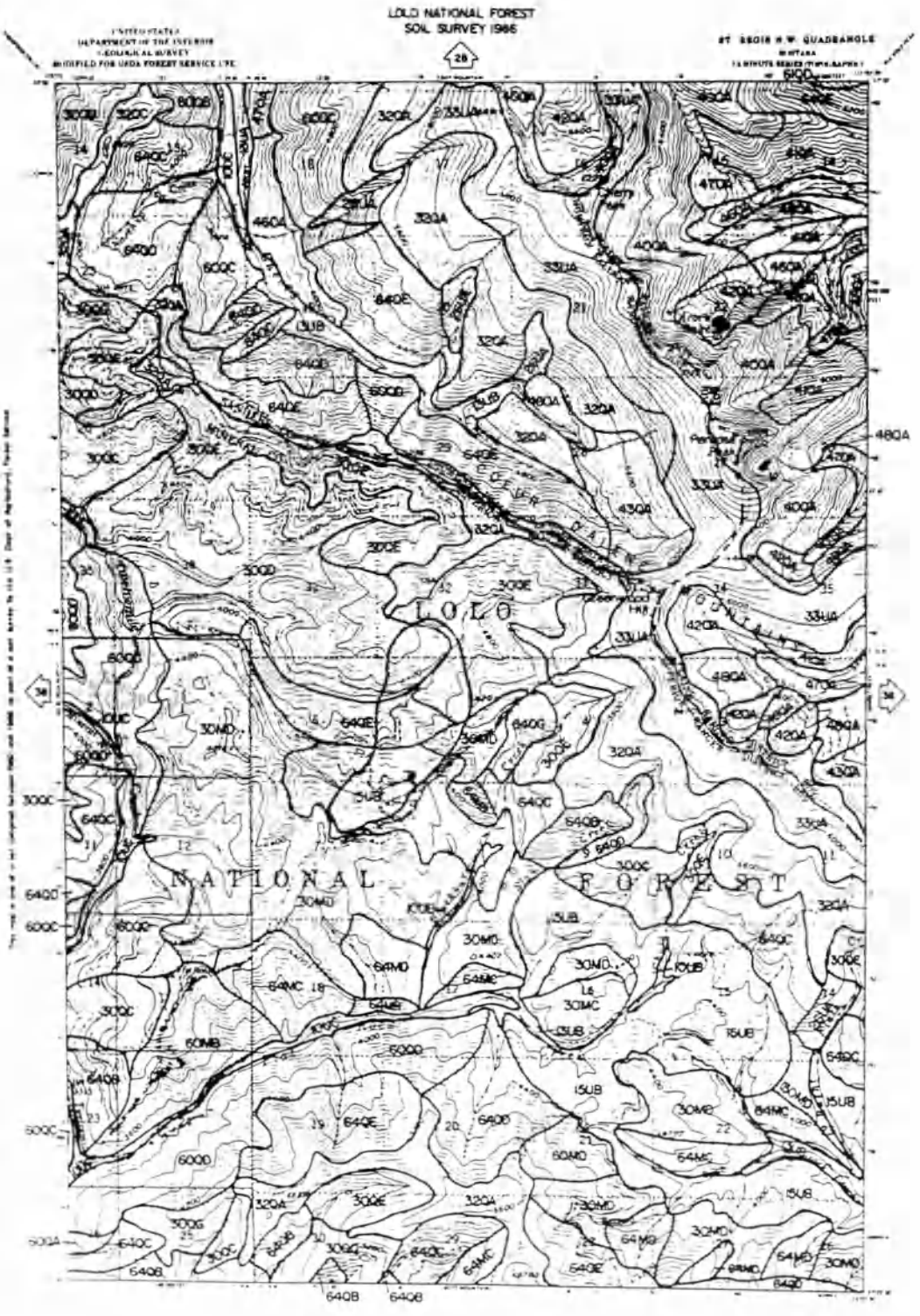
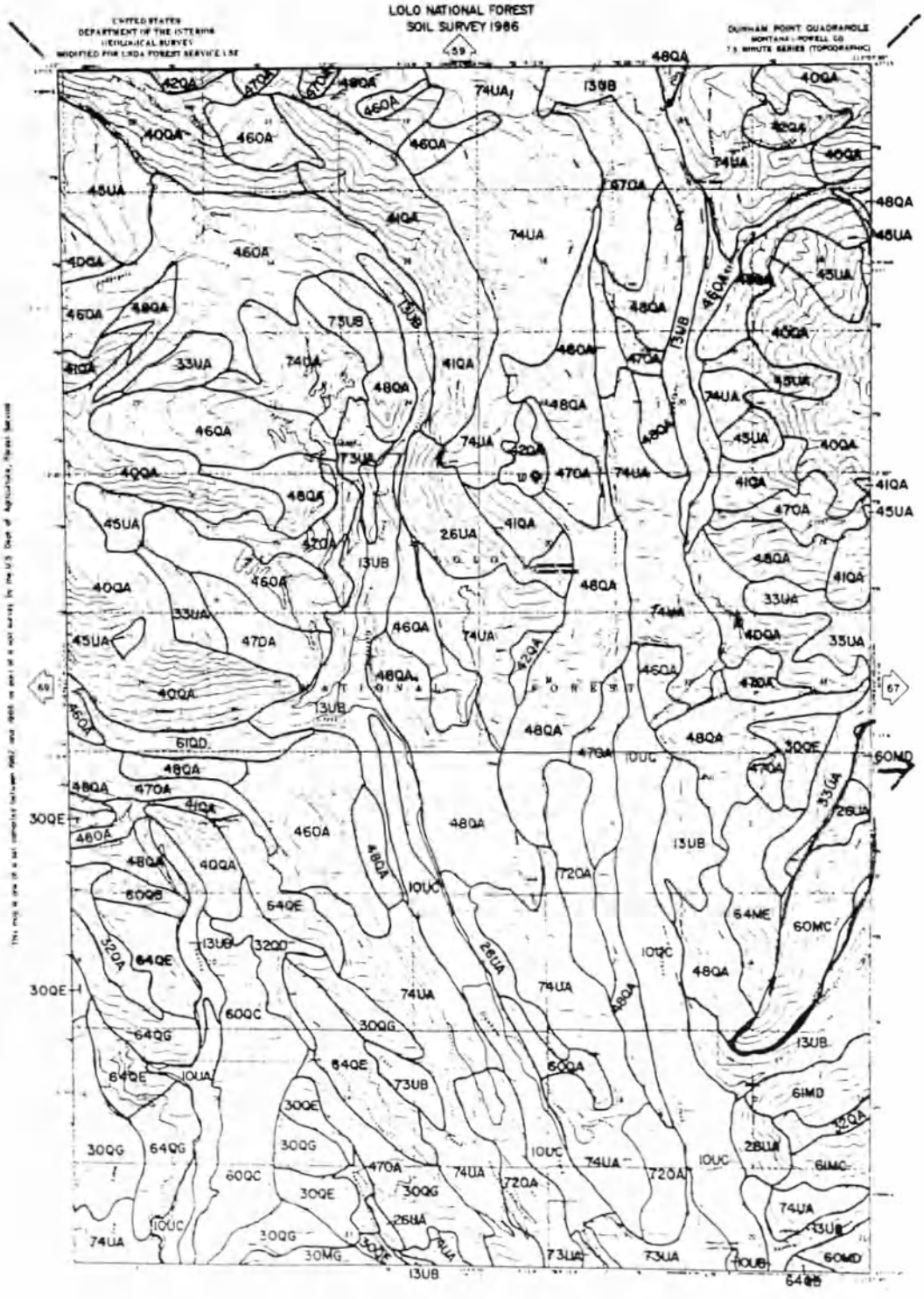
ALBERTON SE QUADRANGLE
MONTANA
30ME
15JA
30MB
64MB
10UB
30MC
64QA


LOLO NATIONAL FOREST
SOIL SURVEY 1986
ST. REGIS N.W. QUADRANGLE
LOLO
NATIONAL
FOREST


LOLO NATIONAL FOREST
SOIL SURVEY 1986
UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
MODIFIED FOR USDA FOREST SERVICE USE
DUNHAM POINT QUADRANGLE
MONTANA - POWELL CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
39
67
69
48QA
40QA
42QA
47QA
46QA
74UA
13UB
45UA
41QA
73UB
33UA
26UA
47QA
61QD
30QE
64QE
60QC
64QG
10UA
30QG
64ME
60MC
10UC
72QA
61MD
28UA
30MG
60MD

APPENDIX II.

Vegetation Characteristics of the Sampling Locations

Although the specific composition of overstory and understory vegetation varied by location, uniformity within habitat type was relatively consistent. The general site and stand characteristics of the habitat types (h.t.s) that were sampled are described in order of frequency. Hereafter habitat types and phases will be abbreviated according to the first two letters each of the genus and species as follows:

Agropyron spicatum = AGSP
Arctostaphylos uva-ursa = ARUV
Calamagrostis rubescens = CARU
Festuca scabrella = FESC
Larix occidentalis = LAOC
Linnea borealis = LIBO
Physocarpus malvaceus = PHMA
Pinus contorta = PICO
Pinus ponderosa = PIPO
Pseudotsuga menziesii = PSME
Symphoricarpos albus = SYAL
Vaccinium caespitosum = VACA
Vaccinium globulare = VAGL
Xerophyllum tenax = XETE

Stands sampled in the PHMA-PHMA h.t. phase were located at 600 to 1710 m. elevation on north to southeast facing slopes. Mature Douglas-fir dominated the overstory in all plots, which also included western larch and lodgepole pine as seral overstory components. All plots in the PHMA phase

supported a dense growth of Physocarpus malvaceus, and in several plots Holodiscus discolor was also present. The understory usually consisted of varying combinations of Spirea betulifolia, Symphoricarpos albus, Arnica cordifolia, Calamagrostis rubescens, Thalictrum occidentale, and Disporum trachycarpum. This phase commonly altered to PHMA-CARU as the exposure became less moist and more southerly. In the CARU phase the Physocarpus understory was less dense and Calamagrostis rubescens, Carex geyerii, and Balsamorhiza sagittata dominated the undergrowth. As in the PHMA phase, mature Douglas-fir dominated the overstory, while ponderosa pine occurred as a major seral overstory component in some plots of the CARU phase.

Plots in both phases representing the PSME-VAGL h.t. were found almost exclusively on north and east aspects at over 1350 m. elevation. Mature Douglas-fir, western larch, and lodgepole pine in varying abundance were present in the overstory. Vaccinium globulare, Spirea betulifolia, Carex geyerii, and Calamagrostis rubescens were representative undergrowth species. Xerophyllum tenax was well represented in the understory vegetation of the XETE phase, but scarce in the VAGL phase, and ponderosa pine was not found in the overstory in plots of the XETE phase. The VAGL phase was associated with slopes over 35% at higher elevations (1500-1900 m.). Plots in the VAGL phase contained western larch and occasional ponderosa pine in the overstory.

The PSME/CARU h.t. commonly occupied southerly aspects, on moderate mid to high elevation slopes and benches. Ponderosa pine commonly dominated the overstory of plots in the ARUV phase, but was absent in plots of the CARU phase. Stands in this habitat type were relatively open grown with a dense mat of Calamagrostis rubescens and Carex geyerii forming the undergrowth.

The PSME/LIBO h.t. was generally restricted to lower elevations (830-1200 m.) and moist locations. In the VAGL phase, lodgepole pine was a dominant seral overstory species, while Vaccinium globulare, Linnea borealis, Calamagrostis rubescens, Arnica latifolia, and occasionally Xerophyllum tenax formed the undergrowth. The SYAL phase of this h.t. was also found in cool, moist locations, however Pinus contorta was absent from the overstory, and Arnica cordifolia, Thallictrum occidentale, and Smilicina stellata, were common in the undergrowth.

Although the PSME/SYAL h.t. occurred throughout many of the sampling locations, very few plots fell into the phases of this type. The drier extreme, SYAL-AGSP, had ponderosa pine dominating the overstory and Agropyron spicatum, and Balsamorhiza saggitata in the undergrowth. Douglas-fir and ponderosa pine were the dominant overstory species in both the CARU and SYAL phases. The distinction between the two being the dominance of Calamagrostis rubescens and Carex geyerii in the undergrowth of the former, and Symphoricarpos

albus in the latter.

The PSME/VACA h.t. was restricted to moist, lower elevation sites (<1150 m.) that appeared to be cold air drainages or frost pockets. Mature Douglas-fir and lodgepole pine dominated the overstory, with Vaccinium caespitosum, Linnea borealis, and Calamagrostis rubescens representing undergrowth species.

The PSME/FESC h.t. was found as a minor inclusion on southfacing, mid-elevation slopes. In addition to the bunchgrass undergrowth, Amelanchier alnifolia was also present on these plots.

Appendix III

Habitat Type Field Form

NAME

DATE

Plot No.					
Location					
T, R, S					
Elevation					
Aspect					
Slope	%		%		%
Topography					
Configuration					

(CODE DESCRIPTION)

TOPOGRAPHY:
1-Ridge
2-Upper slope
3-Mid slope
4-Lower slope
5-Bench or flat
6-Stream bottom

HORIZONTAL CONFIGURATION:
1-Convex (dry)
2-Straight
3-Concave (wet)
4-Undulating

CANOPY COVERAGE CLASS:
0=Absent
T=Rare to 1%
1=1 to 5%
2=5 to 25%
3=25 to 50%
4=50 to 75%
5=75 to 95%
6=95 to 100%

NOTE: Rate trees (>4" dbh) and regen (0-4" dbh) separately (e.g., 4/2)

TREES Scientific Name	Abbrev	Common Name	Canopy Coverage Class		
1. Abies grandis	ABGR	grand fir	/	/	/
2. Abies lasiocarpa	ABLA	subalpine fir	/	/	/
3. Larix lyallii	LALY	alpine larch	/	/	/
4. Larix occidentalis	LAOC	western larch	/	/	/
5. Picea engelmannii	PIEN	Engelmann spruce	/	/	/
6. Picea glauca	PIGL	white spruce	/	/	/
7. Pinus albicaulis	PIAL	whitebark pine	/	/	/
8. Pinus contorta	PICO	lodgepole pine	/	/	/
9. Pinus flexilis	PIFL	limber pine	/	/	/
10. Pinus monticola	PIMO	western white pine	/	/	/
11. Pinus ponderosa	PIPO	ponderosa pine	/	/	/
12. Pseudotsuga menziesii	PSME	Douglas-fir	/	/	/
13. Thuja plicata	THPL	western redcedar	/	/	/
14. Tsuga heterophylla	TSHE	western hemlock	/	/	/
15. Tsuga mertensiana	TSME	mountain hemlock	/	/	/
SHRUBS AND SUBSHRUBS					
1. Alnus sinuata	ALSI	Sitka alder			
2. Arctostaphylos uva-ursi	ARUV	kinnikinnick			
3. Berberis repens	BERE	creeping Oregon grape			
4. Cornus canadensis	COCA	bunchberry dogwood			
5. Holodiscus discolor	HODI	ocean spray			
6. Juniperus communis (+ horizontalis)	JUCO	common (+ creeping) juniper			
7. Ledum glandulosum	LEGL	Labrador tea			
8. Linnaea borealis	LIBO	twinflower			
9. Menziesia ferruginea	MEFE	menziesia			
10. Oplopanax horridum	OPHO	devil's club			
11. Physocarpus malvaceus	PHMA	ninebark			
12. Prunus virginiana	PRVI	chokecherry			
13. Purshia tridentata	PUTR	bitterbrush			
14. Ribes montigenum	RIMO	mountain gooseberry			
15. Shepherdia canadensis	SHCA	buffaloberry			
16. Spiraea betulifolia	SPBE	white spiraea			
17 Symphoricarpos albus	SYAL	common snowberry			
18. Symphoricarpos oreophilus	SYOR	mountain snowberry			
19. Vaccinium caespitosum	VACA	dwarf huckleberry			
20. Vaccinium globulare (+ membranaceum)	VAGL	blue huckleberry			
21. Vaccinium scoparium (+ myrtillus)	VASC	grouse whortleberry			
PERENNIAL GRAMINOIDS					
1. Agropyron spicatum	AGSP	bluebunch wheatgrass			
2. Andropogon spp.	AND	bluestem			
3. Calamagrostis canadensis	CACA	bluejoint			
4. Calamagrostis rubescens	CARU	pinegrass			
5. Carex geyeri	CAGE	elk sedge			
6. Festuca idahoensis	FEID	Idaho fescue			
7. Festuca scabrella	FESC	rough fescue			
8. Luzula hitchcockii (= glabrata)	LUHI	wood-rush			
PERENNIAL FORBS AND FERNS					
1. Actaea rubra	ACRU	baneberry			
2. Antennaria racemosa	ANRA	woods pussytoes			
3. Aralia nudicaulis	ARNU	wild sarsaparilla			
4. Arnica cordifolia	ARCO	heartleaf arnica			
5. Athyrium filix-femina	ATFI	lady fern			
6. Balsamorhiza sagittata	BASA	arrowleaf balsamroot			
7. Clematis pseudoalpina (+ tenuiloba)	CLPS	virgin's bower			
8. Clintonia uniflora	CLUN	queencup beadlily			
9. Equisetum arvense	EQAR	common horsetail			
10. Equisetum spp.	EQU	horsetails & scouring rush			
11. Galium triflorum	GATR	sweetscented bedstraw			
12. Gymnocarpium dryopteris	GYDR	oak fern			
13. Senecio streptanthifolius	SEST	cleft-leaf groundsel			
14. Senecio triangularis	SETR	arrowleaf groundsel			
15. Smilacina stellata	SMST	starry Solomon's seal			
16. Streptopus amplexifolius	STAM	twisted stalk			
17 Thalictrum occidentale	THOC	western meadowrue			
18. Valeriana sitchensis	VASI	sitka valerian			
19. Viola orbiculata	VIOR	round-leaved violet			
20. Xerophyllum tenax	XETE	beargrass			
		SERIES			
		HABITAT TYPE			
		PHASE			

APPENDIX IV

CULTURE AND IDENTIFICATION OF INOCULUM

METHODS AND MATERIALS:

The identification handbook entitled: Studies in Forest Pathology, Vol.VI. (Nobles, 1948), was used as the primary reference for all phases of the culturing and identification of Armillaria inoculum. This manual provides for the identification of the cultures of 126 species of wood rotting fungi using both macroscopic and microscopic identification features.

The following formuli were used for the nutrient agar and tannic acid agar used to culture the inoculum. on.

Nutrient Agar

Difco powdered malt	12.5 gm.
Difco bacto-agar	20.0 gm.
Distilled water	1000.0 cc.

The malt was added to the agar dissolved in water, then this mixture was filtered through several layers of cheese cloth, and sterilized for 20 minutes at 15 lbs. pressure. The agar was then poured into sterile petri dishes.

Tannic Acid Agar

Difco powdered malt	7.5 gm.
Difco bacto-agar	10.0 gm.
Distilled water	500.0 cc.
Tannic acid	2.5 gm.

The malt and agar were mixed with 350 cc. of water. The remaining 150 cc. were kept in a separate flask. The contents of both flasks were sterilized for 20 min. at 15 lbs. pressure. While the sterilized water was still hot, tannic acid was dissolved into it. This solution was added to the slightly cooled malt agar and thoroughly mixed with it before being poured into sterile petri dishes.

To initiate the culture, a section about 5 mm. sq. of sample inoculum was placed in the center of each petri dish. Three plates were made for each sample collected, two on the nutrient agar and one on the tannic acid agar. The transfers were made in an open air environment, needles were dipped in isopropyl alcohol and flamed between specimens to avoid contamination. No other vigorous aseptic techniques were applied. The plates were incubated in the dark at room temperature and brought into the light only for observations. All observations were recorded and keyed for identifying features using the Noble's handbook. Positive identification of Armillaria was made on the basis of both macro- and microscopic characteristics.

A very slow rate of growth on nutrient agar (< 3 cm. at 6 weeks) was observed in all Armillaria cultures. In all cultures, hairlike aerial mycelium that grew in a regular, ringlike pattern outward were observed at 4-6 weeks. The oldest and innermost growth turned a darker, reddish brown color at 10 to 14 weeks, with a pinkish ring remaining next to the white outer margin throughout the length of observations. The center crustose area developed a velvety, plush appearance by 10 weeks, a characteristic also unique to Armillaria cultures. Growth was slight on the tannic acid agar, on which very strong diffusion zones commonly formed one week following inoculation.

When examined microscopically at three to four weeks, the

hyphae were hyaline with infrequent branching and simple septation. At four to six weeks the hyphae took on a light brownish color. In twelve of the isolates I observed cuticular cells on the hyphae, that appeared as a bulbous mass on the hyphal strand. No other microscopic characteristics of notable distinction were observed.

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