BURCKHALTER

Distribution Changes of Primary Woody Plants Across an Ecotone Site, Boulder, Colorado

By Robert E. Burckhalter

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DISTRIBUTION CHANGES OF PRIMARY WOODY PLANTS ACROSS AN ECOTONE SITE, BOULDER, COLORADO

by

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A THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in
the Department of Geography
in the Graduate School of
The University of Alabama

UNIVERSITY, ALABAMA

1985

Submitted by Robert E. Burckhalter

in partial fulfillment of the requirements for the degree of

Master of Science specializing in

Geography.

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Date 12-9-85

ACKNOWLEDGEMENTS

First of all, special thanks are given to Dr. Neal Lineback for his support and encouragement with this research. Also, I thank Mr. H. Donald Hays and Dr. C. Earle Smith, Jr. for contributing to the final form of this thesis. Thanks to Mr. Craig Remington for letting me draw the maps in the Cartography Lab and to Mrs. Linda Lenhard for typing.

The Alabama Academy of Science and Sigma Xi--Scientific Research Society generously contributed grants to help defray the cost of this research. Dr. Archibald Roach gave permission to use the material and information from his thesis.

Many thanks to Dr. Vera Komarkova who helped and encouraged me during the initial stages of this study. Finally, my greatest appreciation goes to Ms. Barbara Young for the darkroom work and without whose emotional support this thesis would not have been completed.

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INTRODUCTION

Over the past million years, climatic changes have caused ecosystem variations along the boundary between the Great Plains and the Front Range of the Rocky Mountains that are gradually being understood by detailed, reconstructive research in biology, ecology, and biogeography. The purpose of this study is to analyze one area of the plains-mountains boundary to determine the continuing spatial ecosystems variations by major woody plant species and to analyze the causes of those variations.

Overview

In the original concept of this research, it was hypothesized that a study could be developed addressing the natural fluctuations of a regional ecotone. Given the location of the ecotone along the eastern edge of the foothills and the peripheral effects of regional human impact, continued research led to an acceptance of a complicated relationship between human and natural forces upon the variations within this forest-grasslands ecotone in central Colorado.

It appears that the lower treeline in the Colorado Front Range has been advancing rapidly. Evidence from one site at the lower ecotone near Boulder was examined, and a hypothesis was drawn for the phenomenon. The outstanding feature of change on Long Mesa within the past 76 years has been the advance of the dominant conifer, ponderosa pine (Pinus ponderosa Laws.), topographically lower in elevation and eastward toward the plains.

Although the ecotone community type is indicated by ponderosa pine, many other arborescent and woody species grow within the study area. The native woody species included in this research are skunkbush (Rhus trilobata Nutt.), hawthorn (Crataegus sp.), and smooth sumac (Rhus glabra L.) (Weber 1976). A few other much less significant species also will be discussed briefly. Fluctuations of the most common species were observed and correlated with the advance of ponderosa pine.

Although there has been little quantitative research in terms of forest tree movement along either an elevational or a horizontal distance gradient (Leak & Graber 1974), one manner in which to examine geographic oscillations of biome distribution has been to study changes in regional community ecotones (Braun-Blanquet 1965, Küchler 1967, Davis 1977). Initial interest for this study of ecotone change developed when this author became familiar with one particular site in Colorado. Primary research revealed that the area known as Long Mesa had been examined in 1908 and again in 1948 by other researchers. This set the stage as a superb location in which to observe recent changes in natural plant communities.

Long Mesa is a site located along the gradient between two major ecological regions east of the Colorado Front Range. The two major biomes are as follows: (1) Foothills of the Front Range, which are dominated by ponderosa pine, exist from about 1,675 meters to about 2,450 meters in elevation and range from 8 to 16 kilometers east-west in width; and (2) High Plains Steppe, which is dominated by native and naturalized grasses and herbs, exists usually between 1,675 meters and 1,225 meters and ranges from the conjunction with the foothills on the west into the high plains of Nebraska and Kansas 160 to 240 kilometers eastward. Vegetational delineation between the two regions is quite extreme and easily observed (Daubenmire 1943, Gleason & Cronquist 1964).

The 1908 studies of Long Mesa were concentrated upon observation of baseline data and included speculation that positioning and composition of geological strata and the various limitations of soil and moisture content were the primary barriers to the spreading of coniferous trees and deciduous shrubs (Dodds 1908, Robbins 1908, Robbins & Dodds 1908). Research for the 1948 thesis indicated that variable concentrations of soil moisture and soil texture acted as the primary distribution controls, but concluded that cattle grazing had diminished turf cover and, therefore, increased the potential for pine seedling establishment (Roach 1948). Comparative distribution maps for 1908 and 1948 showed a rapid advancement of the pine forest both in density and to the northeast within the elapsed 40 years.

In the earlier Long Mesa studies, maps were drawn which showed the major woody species distributions and subsequent distribution changes. In 1984, this author again determined plant distributions on Long Mesa, and as a result, a major methodology of this research consists of the mapped variations across 76 years. Each species represented is exhibited in a series of three maps, wherein species distributions can be observed in 1908, 1948, and 1984.

Much of this thesis is supported by photographs. Some photographs demonstrate present ecological conditions while others represent comparative before and after documentation. A number of locations from pictures taken in 1908 and 1948 were relocated in 1984. The comparisons illustrate very dramatic vegetational changes.

This thesis will attempt to determine the causes for forest advancement onto the mesa and for lesser species fluctuations by examining ten interacting variables, some of which have been proposed by other authors and the remainder by this author:

(1) Extensive and later discontinued cattle grazing.

(2) Protection of the land through fire suppression.

(3) Variable turf cover.

(4) Edaphic controls.

(5) Soil disturbances.

(6) Protection from development.

(7) Greatly increased deer browsing.

(8) Variable lumbering interests.

(9) Climatic controls, primarily precipitation boundary.

(10) More favorable climatic conditions.

The principle hypothesis for this study states that ponderosa pine is advancing onto the mesa while the lesser woody plants fluctuate either in conjunction with pine or independently due to different space and time dimensions. The temporal and geographic sequence will be examined by (1) observing the advancement and expansion of ponderosa pine and examining the causes for change; (2) observing the shrubs and lesser tree species to determine where fluctuations have occurred and examining the relative sequences of change and stability; (3) establishing whether a fluctuation correlation has occurred between all major species, including ponderosa pine, and analyzing the results of their relative change or stability; and (4) analyzing which human and natural environmental factors have affected changes within and across the various species examined.

A special opportunity for research in long-term ecosystem change has been available because of the quantity of previous work in the vicinity and more particularly on Long Mesa. Different species' distribution changes are affected by different environmental factors, and the interaction of natural dynamics with unnatural disturbance factors is highly evident on Long Mesa. Attempts at correlating the changes of ponderosa pine and all of the major woody plant species hopefully will provide a better understanding of plant population variability. It is hoped that this study will contribute to the greater knowledge of vegetation dynamics along the foothills of the Colorado Front Range.

STUDY AREA

Research for this thesis was concentrated on Long Mesa, which is located 1.5 kilometers south of the University of Colorado campus in Boulder (fig. 1). Long Mesa also has been known as Green Mountain Mesa and the National Bureau of Standards Mesa. Long Mesa and adjacent Horse Mesa are collectively and popularly known as Enchanted Mesa (Lanham 1974).

Long Mesa is actually the remains of a partially eroded piedmont extension protruding onto the plains from the eastern limits of the foothills of Colorado's Front Range (fig. 2). While some mesas are outliers from the foothills, many are directly attached topographically and geologically to the adjacent foothills. These flat-topped or sloping ridges are a common feature of the region, particularly from Boulder southward to Golden. Ravines containing either permanent or intermittent streams usually separate the piedmont mesas from one another (Fenneman 1905). The water sources of the creeks range from precipitation run-off, springs, seepages, and other permanent sources between the mesas and in the nearby foothills.

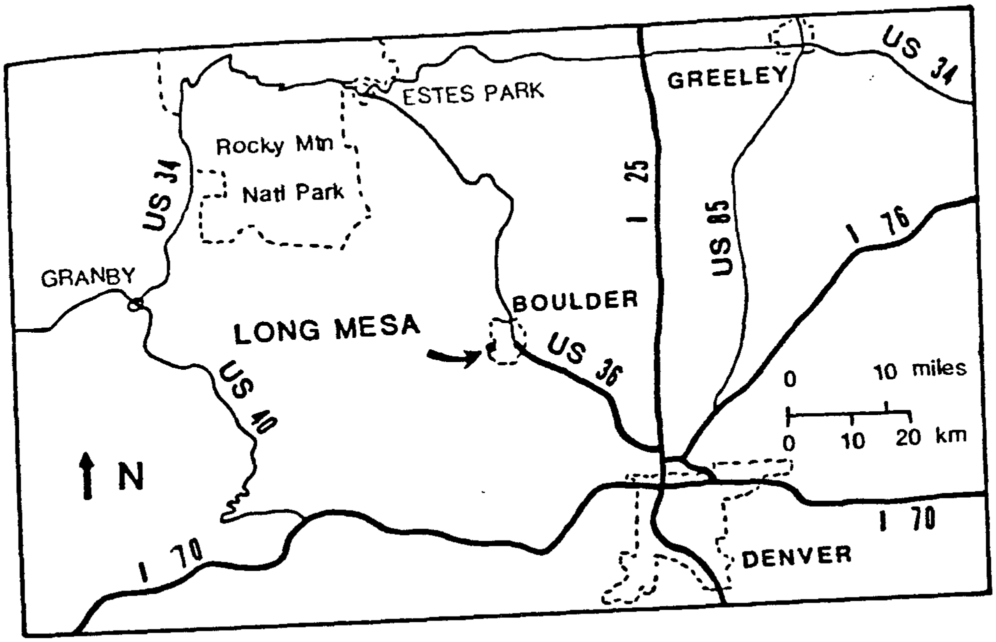


Figure 1. Regional map showing relationship of Denver, Boulder, and Long Mesa.

Figure 2. Looking down on Chatauqua, Horse, Long, and Table mesas from Flagstaff Mountain.

Location and Topography

Long Mesa extends about 1.5 kilometers into the surrounding plain and is about 400 meters in width, with steep escarpments which drop from 60 to 150 meters on three sides (fig. 3). While the western limit of the study area climbs increasingly higher in elevation to the adjacent foothills, the mesa top slopes gently downward as it protrudes northeasterly.

Figure 3. Looking north to Long Mesa from Table Mesa.

To the north, Horse Mesa (fig. 4) is separated by Cemetery Gulch which is an intermittent stream. The head of the creek begins with numerous small intermittent springs, but it is fed primarily by precipitation run-off and snowmelt. Horse Mesa is directly connected to Long Mesa by a sandstone caprock. Table Mesa is 1.2 kilometers due south and is the site of the National

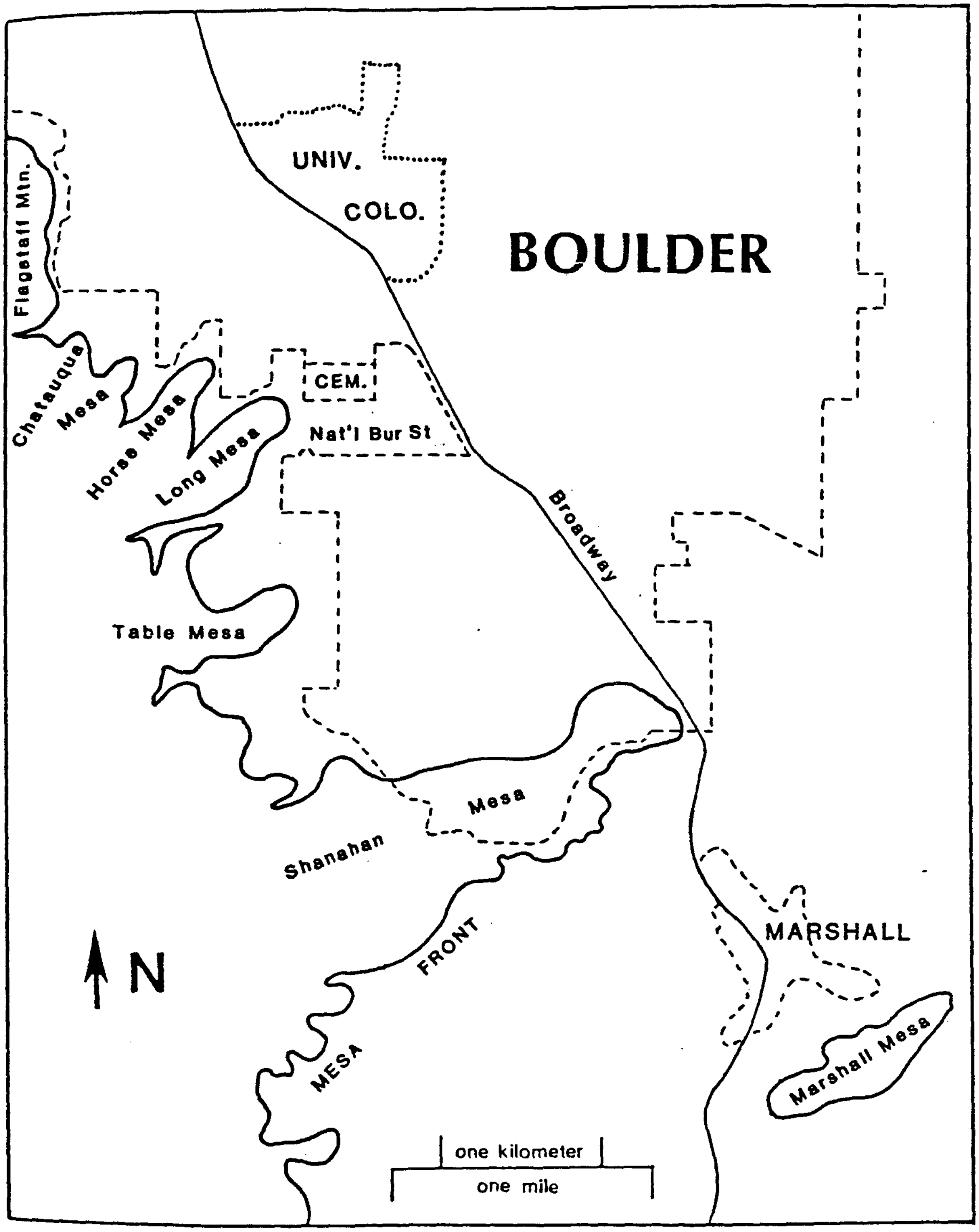


Figure 4. The piedmont mesa region southwest of Boulder.

Center for Atmospheric Research. Table Mesa is approximately 45 meters higher in elevation than Long Mesa and is separated by Pole (or Skunk) Canyon. Pole Creek is situated in a deeper ravine than Cemetery Gulch and has a more permanent water source located further in the foothills. Except for infrequent dry periods, Pole Creek flows throughout most of the year. In more recent years, Pole Creek has been known as Skunk Creek, but for the purposes of this research, it will be known by the older name (Fenneman 1905, Dodds 1908, Roach 1948).

Chatauqua Mesa is generally considered to be the first mesa south of Boulder, followed by Horse, Long, Table, and Shanahan mesas. Marshall Mesa is an outlier mesa 6.5 kilometers southeast of Long Mesa. The plains below Long Mesa are occupied largely by residences, small businesses, and parks. To the northeast, the National Bureau of Standards and a cemetery are located at the base of the mesa.

Geology

The geological construction of the mesa is well documented (Fenneman 1905, Dodds 1908, Roach 1948) and presents a number of insights which interrelate with the ecological and vegetational composition. Long Mesa is a series of uplifted shales and limestones capped with unassorted rock debris eroded primarily from nearby sandstone formations (Dodds 1908).

During the Pliocene, as the new Rocky Mountains pushed upward, the more ancient overriding horizontal sedimentary Cretaceous strata were consequently thrust upward to angles from 45 to 90 degrees. The contact zone between the igneous and metamorphic Boulder batholith and the sedimentary rocks is about one kilometer west of the piedmont region. Within a few kilometers east of the contact line, the sedimentary strata level exponentially to very low angles. Therefore, angles of the sedimentary strata near the contact zone are quite steep and have been highly eroded since before the Quaternary (fig. 5). The result is a picturesque combination of ridges and valleys correlating with sandstones, shales, and limestones.

The two prominent sandstone ridges or hogbacks are the Fountain and Dakota formations. The caprock of Long and Horse mesas consists largely of semi-compacted rock debris from the Fountain and Lyons formations (Dodds 1908). The Dakota Formation is not prominent immediately to the west of Long Mesa. Since the underlying strata are curved upward and consist of highly erodable shales and limestones, the caprock situated above the strata acts to prevent erosion (fig. 6). The cap ranges from 9 meters thick in the western regions to 3 meters in the eastern areas of the mesas. In the ravines, where the weaker strata are not protected by the caprock, active erosion is taking place (Dodds 1908).

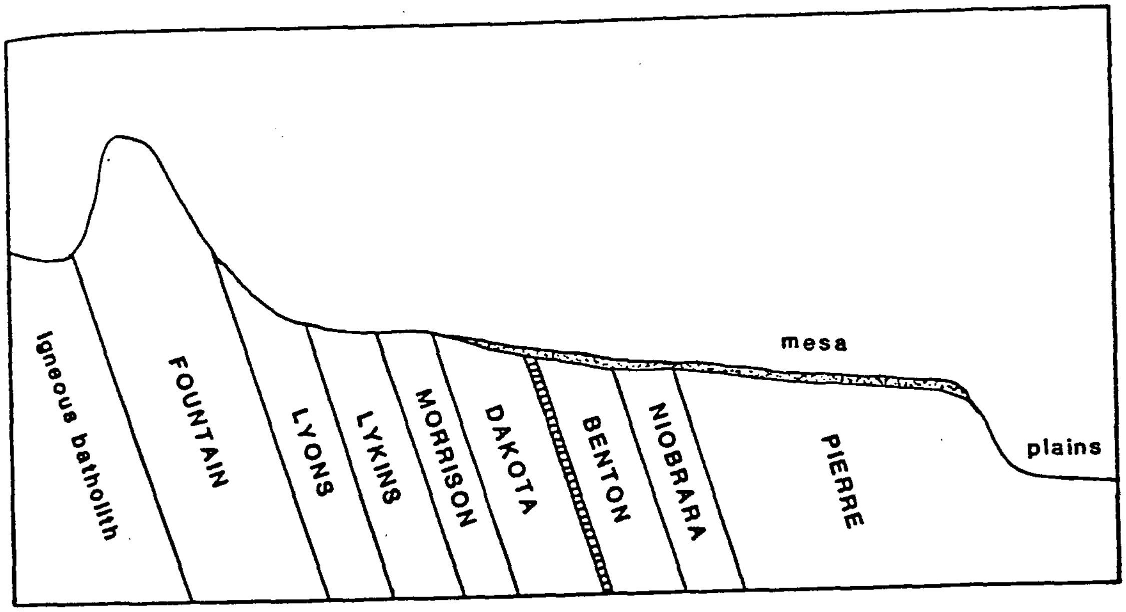


Figure 5. Diagram of the stratigraphy: West-East view. Mesa caprock and major formation names are shown.

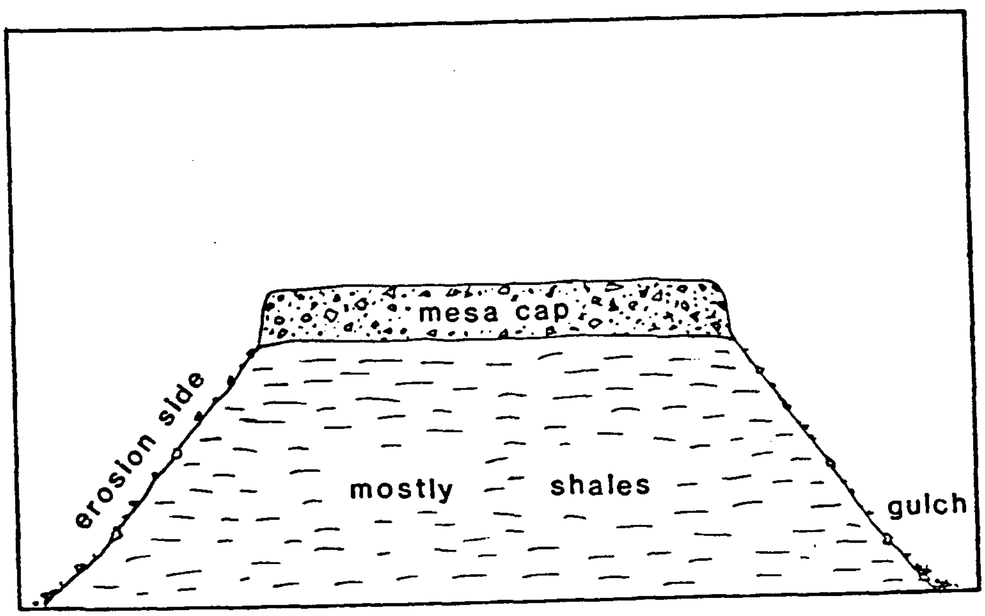


Figure 6. Lateral view of Long Mesa, showing caprock, slopes, and underlying shales.

Many places directly below the caprock are known as amphitheaters. In these regions, the caprock curves around, encompassing up to 180 degrees, and there is a drop-off directly down for a few meters. The result is a small bowl-shaped depression eroded from the shale. The amphitheaters are often the sites of small springs flowing intermittently from below the caprock. They are also frequently locations of higher deciduous vegetation concentrations.

The soils of the plains surrounding the mesa consist mainly of impervious Pierre shales. These are fine textured soils, which are rather unstable and susceptible to expansion and contraction when in contact with higher amounts of moisture. Most of the plains below Long Mesa no longer represent natural ecological regimes.

Climate

The average annual precipitation at Boulder is about 47 centimeters thus classifying the region as semi-arid. The location of Long Mesa and its forest ecotone may be viewed also as a climatic boundary, since mountain climates experiencing greater than 101 centimeters annual precipitation (Barry 1972, 1973) exist only 24 kilometers to the west, and much drier semi-arid conditions are normal 80 to 160 kilometers eastward. Concomitant with the elevational gradient, the annual precipitation gradient levels exponentially from greater than 101 centimeters to 28 centimeters within 110 kilometers. The snowfall average is 171 centimeters annually, with March and April receiving the highest accumulations. However, the spring snowfalls are usually followed by abrupt warming periods which cause greatly increased melt-water run-offs.

Maximum temperature means range from about 8°C in January to about 31°C in July (Boulder Chamber of Commerce 1985). Comparatively mild winters and mild summers encourage vegetation of more arid and cooler regimes to survive in the vicinity of Boulder. The area is known as a refugium for numerous species. The southernmost occurrence of paper birch (Betula papyrifera Marsh.) in western North America is within two miles (Little 1971), and one of the most northern stands of Gambel oak (Quercus gambelii Nutt.), on the eastern slope in Colorado, exists near Long Mesa (Weber 1976). (This author located two Gambel oaks on Horse Mesa in 1984.)

It should be noted that the winter chinooks have caused much property damage in Boulder, and these winds have been attributed to deforestation in the vicinity (Clark et al. 1980) and caused individual treefalls on Long Mesa (Roach 1948, Lanham 1974). Chinook winds create warmer temperatures causing rapid snowmelt and high winds ranging from 160 to 240 kilometers per hour. The area of conjunction between the foothills and the plains appears to be the region of highest wind velocities (Ives 1950, Mutel 1976).

Vegetation

Many of the piedmont mesas are the lower limits of the ponderosa pine forest, which is commonly found in the adjoining foothills (fig. 7). This lower tree limit has been referred to as the grassland-lower montane forest ecotone (Marr 1961) or more recently as the grasslands-forest ecotone. In this area, the forest ends abruptly and the plains grasslands begin to the east (Daubenmire 1943).

Figure 7. Looking northwest to the foothills. Note the limit of the pine forest.

The distribution of ponderosa pine and other coniferous species in isolated locations and outliers of the plains of Colorado, Nebraska, and Kansas are well documented (Livingston 1949, Weber 1965, Wells 196[illegible], Wright 1970). A large coniferous refugium is known to exist from northeastern Las Animas County, 320 kilometers southeast of Boulder. Ponderosa pine is abundant on the Pine Bluffs escarpment 160 kilometers northeast and in bands along north-south ridges 110 kilometers southeast of Boulder (fig. 8). The expansive outlier of the Black Forest, 80 kilometers south of Denver is well documented (Livingston 1949), and various small stands of ponderosa pine are known throughout the eastern plains.

Closer to Long Mesa are pine sites from Marshall Mesa, Valmont Butte, and scattered preserved individuals and small groups east of Boulder. One well-established and reproducing stand in a residential neighborhood, 1.5 kilometers due east of Long Mesa, was photographed in 1984 (fig. 9).

All of the above locations contribute to a greater understanding of pine distributions beyond the well-defined ecotone. The historical significance of the outliers will be examined in the next chapter.

In the ecotone areas of the mesas, dense stands of ponderosa pine grow in the western regions and on the northerly sides of the ridges, often extending across the middle of the mesas in the western portions, but quickly thinning out eastward (Robbins & Dodds 1908, Roach 1948, Lanham 1974). Greater densities of pine tend to grow more toward the exposed edges of the caprock than in the

Figure 8. Ponderosa pine capped north-south ridges, 110 kilometers southeast of Boulder, on the plains.

Figure 9. Isolated pine stand in residential neighborhood on Kohler Drive, Boulder.

centers of the mesas. It has been commonly observed that the northern portions have the highest pine population densities, followed respectively by southern portions and the central areas, while the eastern regions maintain the lowest densities (Roach 1948).

Ponderosa pine is the dominant woody species on Long Mesa, and both the adjacent foothills forest community and the ecotone community are type-indicated by this tree. Pine is so highly prevalent and frequent that competition presented by other woody species is minimal. Other woody species usually exist as either understories and/or occupiers of sites uninhabitable by pine. Ponderosa pine normally grows to heights from 9 to 12 meters in this area.

The second most important woody species is skunkbush. This shrub exhibits two habit and habitat types. In one form, skunkbush grows on the mesa top in small patches as an understory to ponderosa pine. The shrub rarely achieves a height beyond 1/2 meter. The other form occurs on the slopes of the mesa, where skunkbush forms large impenetrable thickets often growing to 1.5 meters high. The largest thicket in the study area measured approximately 140 meters long by 70 meters wide in 1984.

Hawthorn is a thicket-forming shrub or small tree extending in height to 5 meters. It is most common in the gulches, but some groups also grow on the southern slope of the mesa. Another species of sumac, smooth sumac, has isolated distributions in Pole Canyon where it forms groves to 3 meters high. Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) is commonly a tree of higher elevations in the foothills and montane ecological regions. Some Douglas-firs have become established in the lowest reaches of the foothills and extend into the higher portions of the gulches. Douglas-firs are located on Long Mesa along the northern caprock rim at the head of Cemetery Gulch. Douglas-firs can grow to 15 meters, but most individuals on Long Mesa are saplings less than 2 meters high.

Rocky Mountain juniper (Juniperus scopulorum Sarg.) and common juniper (Juniperus communis L.) are infrequent on the mesa. Rocky Mountain juniper exists as small trees to 4 meters high and common juniper as mats less than 1/2 meter high. A single small individual white fir (Abies concolor (G. & G.) Lindl.) was located on the steep side of the mesa immediately below the south caprock rim.

Many other less common tree and shrub species are located on and around the mesa. However, their distributions and locations are at least minimal to this research, and reasons for their exclusion are cited in the methodology chapter.

HISTORY AND PREVIOUS WORK

During the Pleistocene, the Great Plains was a coniferous forest (Borchert 1950, Daubenmire 1968, Mengel 1970, Wells 1970a, Wright 1970) and since the continental glacial ice mass was located much further south and west than its present remnant position (Bryson et al. 1970), coinciding temperature means were much lower. All major climatic regimes were situated compactly further south than during the Holocene and consequently all major biomes were located further south and west (Nichols 1967, Bryson et al. 1970). In North America within the past 11,000 years, a northerly advance of more southerly biomes has accompanied the glacial retreat (Wulff 1943).

Cordilleran flora extended eastward along highlands of the plains during the Pleistocene (Weber 1965), and the eastern Colorado plains supported a remnant forest as recently as the early Holocene (Wells 1970a, Wright 1970). A much reduced remnant forest is isolated on some outliers as cited earlier.

Solidly supported evidence of the arrival of humans in the area places the event at the end of the Pleistocene (Stephenson 1965). Game fires were a predominant means used to control the paths of wildlife, and many fires became uncontrollable and burned unchecked (Stewart 1956). Along with fire disturbance retarding the invasion of forests (Borchert 1950), maximum climatic warming and drying during the latter part of the Hypsithermal (7500-2500 BP) contributed to the demise of the remnant coniferous forest (Wells 1970a). Following the Hypsithermal, there has been a climatic cooling and lowering of the upper treeline in Colorado (Andrews et al. 1975, Petersen & Mehringer 1976). This may have corresponded with a lowering of the lower treeline, and the plains refugia may have begun to expand. However, Indian fires apparently kept the forest from expanding from the foothills into the plains and with the arrival of the nonindigenous settlers beginning in 1858 and 1859, the lower treeline was pushed back further (Clark et al. 1980).

In the Boulder area, many early photographs show extensive denudation of the forest in the foothills. Local timber was used for lumber and fuel, and the foothills were the most accessible area. Ponderosa pine was the backbone of lumbering. Mining experienced a number of economic peaks, but the height of lumbering was between 1890 and 1910 when the lumber industry was as conspicuous as the mining industry (Hess 1959). After about 1910, the demand for wood products began to diminish, and the ponderosa pine forest began to recover.

The mesa region was used primarily for cattle grazing until the 1950s, and grazing is still common in certain locations southeast of Shanahan Mesa. In 1950, the United States Department of Commerce acquired the eastern portion of Long Mesa and has recently placed some radio antenna equipment there. Federal ownership of the land has saved it from massive development. In 1962, the city of Boulder purchased most of Horse Mesa and the western portion of Long Mesa, and the greater area has been preserved as a Boulder Mountain Park. In 1964, a water line connecting reservoirs on either side of Long Mesa was constructed perpendicularly across the eastern portion of the mesa, and in 1983, another water line was constructed north and east within the study area but below the mesa top.

In 1908, both Horse Mesa and Long Mesa were the scene of geological, physiographical, climatological, and vegetational studies (Dodds 1908, Ramaley 1908, Robbins 1908, Robbins & Dodds 1908). The studies emphasized baseline data and cited geological strata and soil moisture content as effecting limitations in distributions of trees and shrubs on the mesa. The studies were not concerned with the dynamics and interaction of expansion or retraction of the forest zone along the ecotone. In fact, the concept of a dynamic ecotone had not yet been grasped.

In 1948, certain vegetational changes on Long Mesa that had occurred in the past 40 years were observed (Roach 1948). Roach recognized the primary ecological barriers discussed in 1908 and considered the overriding feature of change within the elapsed time. The expansion of ponderosa pine had been dramatic. Roach stated that pine invasion of the mesa had occurred first along the northern caprock rim, second along the southern rim, and third into the center of the mesa. Soil moisture and soil texture were considered to be the distribution controls. Greater concentration of soil moisture along the rim of the caprock had determined primary distribution. Speculation was that distribution in the middle of the mesa had been sporadic and dependent upon moisture pockets created and protected by scattered individual boulders and rocks. Due to cattle grazing, secondary seedling establishment was attributed to a diminished competition with the grass cover.

Research in the Black Forest of Colorado observed that the ecotone between forest and grassland was usually very abrupt and that migration of the ponderosa pine ecotone occurred at only a few places (Livingston 1949). Livingston found that usually the vegetational transition was correlated with a similar abrupt transition from coarse gravel to sandy loam soils. Reduced precipitation run-off, more rapid infiltration, and a conglomerate substrate, which acts as a barrier encouraging moisture retention were considered as the causes of pine preference for coarse-textured soils.

Wells (1965, 1970a, 1970b) discussed the preference of pine stands for scarplands and ridges on the plains. It was indicated that the finer eolian silts and sands were derived from the bedrock outcrops preferred by coniferous stands, and, therefore, the plains soils are younger than scarpland soils. However, the finer-textured soils were noted as having maintained successful pine plantings in the Sandhills of Nebraska. Wells concluded that scarplands, ridges, and topographic breaks have acted historically as natural fire breaks and thus retained coniferous stands while the flat lands have been burned.

In southwestern North Dakota, scarpland ponderosa pine stands were found to be invading the adjacent grasslands (Potter & Green 1964). The results showed that the sandy soils of all grassland sites would support ponderosa pine growth. However, soil moisture conditions are restricted by competition from the dense, fibrous root systems of the grasses. There was no evidence of forest retreat and although conditions for expansion were retarded by grass competition, forest advancement was maintaining slow steady progress.

Since the late 1800s, coniferous vegetation in nearby Marshall, Colorado, has shown an outstanding expansion. Mernitz (1971) indicated that before the arrival of settlers, virtually no conifers existed on Marshall Mesa, and before the turn of the century, during the time of the most substantial coal mining activity, conifer growth remained at a minimum. However, since the closing of the major mines during the 1940s and 1950s, conifer growth has increased rapidly both in individual numbers and tree size. It has been speculated that during its height, the effects of coal mining had stunted the natural growth and expansion of forest on Marshall Mesa (Mernitz 1971).

Coal mining only temporarily repressed coniferous growth, and pine advancement patterns on Marshall Mesa have been similar to other regional locations, regardless of the ephemeral and temporary effects of coal mining. Similar to other mesas, there was little or no coniferous vegetation before coal mining prior to 1900, but pine invasion occurred rapidly following the decrease and eventual cessation of mining activity.

On Shanahan Mesa, 3 kilometers south of Long Mesa, a forest expansion of 3 kilometers eastward within 100 years has occurred (Beckman 1977, Beckman & Mitton 1984). The scope of Beckman's work emphasized genetic differentiation between mature established stands and young colonizing stands. The hypothesis was supported that ponderosa pine populations can vary greatly among local microgeographic sites. Canopy, density, community structure, and secondary succession were cited as the causes for genetic differentiation.

A 1980 vegetation map of Rocky Flats, 14 kilometers south of Long Mesa, depicted stands of ponderosa pine isolated on xeric, rocky ridges (Clark et al. 1980). The authors stated that the Rocky Flats area was probably forested in the past (Weber et al. 1974), but that the forest was removed by burning and cutting by Indians and white settlers. Though other areas have recovered through suppression of fire and lumbering cessation, overgrazing and strong chinook winds have maintained deforestation across most of Rocky Flats.

In a Wyoming study, the problem of the ponderosa pine forest-grasslands transition was approached by investigating the environmental conditions of isolated outliers of pine on rocky ridges (States 1968). It was found that two conditions for the survival of ponderosa pine must be met. There must be a relatively permanent subsoil moisture supply, and since ponderosa pine is fundamentally a noncompetitor with grasses, the dense fibrous turf cover must be removed before pine can become established.

METHODOLOGY

The methodology for this study was divided into four parts: field mapping, comparison with previous studies, field measurements, and photographic documentation.

Field Mapping

The major means used to determine vegetation distribution changes in the present study are a series of maps of the most common woody species found on Long Mesa. Species distributions were mapped on a grid system based upon the earlier studies. The grid system was used to locate the position of each tree, shrub, or colony. The earlier systems were based upon English measurements rather than the metric system. Therefore, the 1984 mapping used English measurements, but all measurements have been converted to the metric system. The previous studies used boundaries along 1/256 of Township and Range section lines or 2.5 acre (1.0117 hectare) plots. Portions of the Township and Range sections used on Long Mesa were T1S R70W Section 6, T1S R71W Sections 1 and 12.

The process was repeated in 1983 and 1984 wherein boundaries were set up every 330 feet (100.584 meters) to create 108,900 square foot (10,116.81 square meter) or

2.5 acre plot sections. Then each tree, shrub, or colony was located and mapped within each 2.5 acre grid section. When more detailed specifications were required of individual tree or shrub locations, points were then easily established by setting perpendicular lines at known points along the 330 foot long X,Y axes.

Comparison with Previous Studies

Robbins and Dodds drew maps of conifer distributions on Horse and Long mesas, and Robbins drew maps of the distributions of deciduous trees and shrubs in 1908. Many more species were studied in detail in the earlier research, than were studied 40 years later by Roach. Roach concentrated his effort upon (1) ponderosa pine, (2) skunkbush, (3) hawthorn, and (4) smooth sumac. Therefore, the present research emphasizes a continuum of the species chosen by Roach.

Distributions of less common tree and shrub species were not recorded for this study because many of those sites were riparian systems, and Roach did not include them in his work. Riparian systems are extremely peripheral to the basis of this ecotone research. Those species which were entirely riparian were excluded, as were minor mesa shrubs which had been excluded either in 1908 and/or the 1948 thesis. The species found on Long Mesa and mapped in 1908, but excluded from Roach and the present study, include (1) Douglas-fir (<u>Pseudotsuga mensiezii</u>

(Mirb.) Franco), (2) snowberry (*Symphoricarpos occidentalis* Hook.), (3) choke-cherry (*Prunus virginiana* L.), (4) buckbrush (*Ceanothus fendleri* Gray), (4) Oregon-grape (*Mahonia repens* (Lindl.) G. Don), and (6) yucca (*Yucca glauca* Nutt.) (Weber 1976).

A consistent sequence of distribution verification was sought for each species examined. A series of three maps was drawn for each of the four major woody plants cited above, showing the changes from 1908 to 1948 to 1984. Ponderosa pine mapping was completed in 1983 and corrected in 1984. Minor changes were required in the earlier maps to adjust for former cartographic errors. Overlays were used to standardize the maps, and patterns of tree grouping were adjusted to corrected elevations and relative positions. Base maps were adopted from Roach's 1948 series.

Certain peripheral areas bordering and touching within the study area have become residential in recent years. Because of the presence of unnatural cultivated vegetation, its artificial environment, and suspicious homeowners, those regions were not mapped for vegetation changes in 1984.

Field Measurements

All 1984 maps were verified by large scale aerial photography and field checking. Individual trees and shrubs in less dense areas were located from 1979 aerial photography at a scale of 1:7200 and field checking verified positions and recent seedling establishment. Within certain areas of massive recent ponderosa pine establishment, 17 of the largest trees were selected for tree coring. Those trees, along with other isolated individuals, were checked for comparative age analysis through dendrochronology.

Photographic Documentation

To accompany research in the earlier studies, a number of photographs were taken showing different views of Long Mesa and sites on and near the mesa. Many of the locations from which photographs had been taken 36 and 76 years earlier were relocated in 1984. Those sets of photographs which show the most dramatic vegetation changes have been used in the present study.

The photographs were located in copies of the original texts within the University of Colorado Norlin Library. The original photographs were rephotographed with a 35 mm. camera mounted on a camera stand. A high contrast black and white film was used for both the shooting of the old pictures and the 1984 relocation photographs. All color photographs are prints made from 35 mm. color slide film taken in 1984 only.

RESULTS: PLANT SUCCESSION ON LONG MESA

Within the past 100 years, the range of coniferous stands has been expanding lower in elevation, on to the grasslands, and eastward across the mesas of Colorado's Front Range piedmont region. Evidence from many areas throughout Colorado, Wyoming, Nebraska, and the Dakotas show similar advancement of coniferous vegetation (Potter & Green 1964, States 1968, Wells 1970a, Mernitz 1971, Beckman 1977, Beckman & Mitton 1984). Photographic documentations throughout the northern Great Plains and the central Rocky Mountains compare scenes from 50 to 100 years apart and verify coniferous expansion (Phillips 1963, Gruell 1980a, Gruell 1980b, Rogers 1980). The regional expansion of the forest coincides with the local findings at Boulder which show the advancement of the ponderosa pine-grasslands ecotone northeasterly for approximately 3/4 kilometer.

While ponderosa pine is the main species involved in this research, other woody species are significant and represent secondary effects within the ecotone. Since ponderosa pine is the primary woody species of the study area, it will be examined first, followed by the secondary woody species.

Ponderosa Pine

In 1908, pine was shown to be distributed most heavily along the northern edge of the mesa top in the western region of Long Mesa (fig. 10). A much less dense distribution occurred near the southern edge of the caprock and a fairly consistent density joined the northern and southern stands in the extreme west. A sparse distribution occurred more northerly and easterly made up of easily discernible individual pines. Most pines were located on the mesa top, but a few groups had become established on the north side and very few were located on the south and east sides below the caprock. Pine establishment in the mesa center appears to have vaguely resembled north-south bands. The most general statement of pine distribution in 1908 restricts the trees to the highest elevations and the northern edge of the caprock. A total of 787 individual trees were counted within the study area for 1908.

Within 40 years, the advancement of pine had been dramatic. By 1948, trees had extended densely along the northern rim of the caprock to its eastern limit and less densely near the southern edge of the mesa cap (fig. 11). The western region of the mesa had become very densely populated, and the center of the mesa showed a large increase in pine population. Expansion occurred down the northern slope into Cemetery Gulch, but sparsely on the

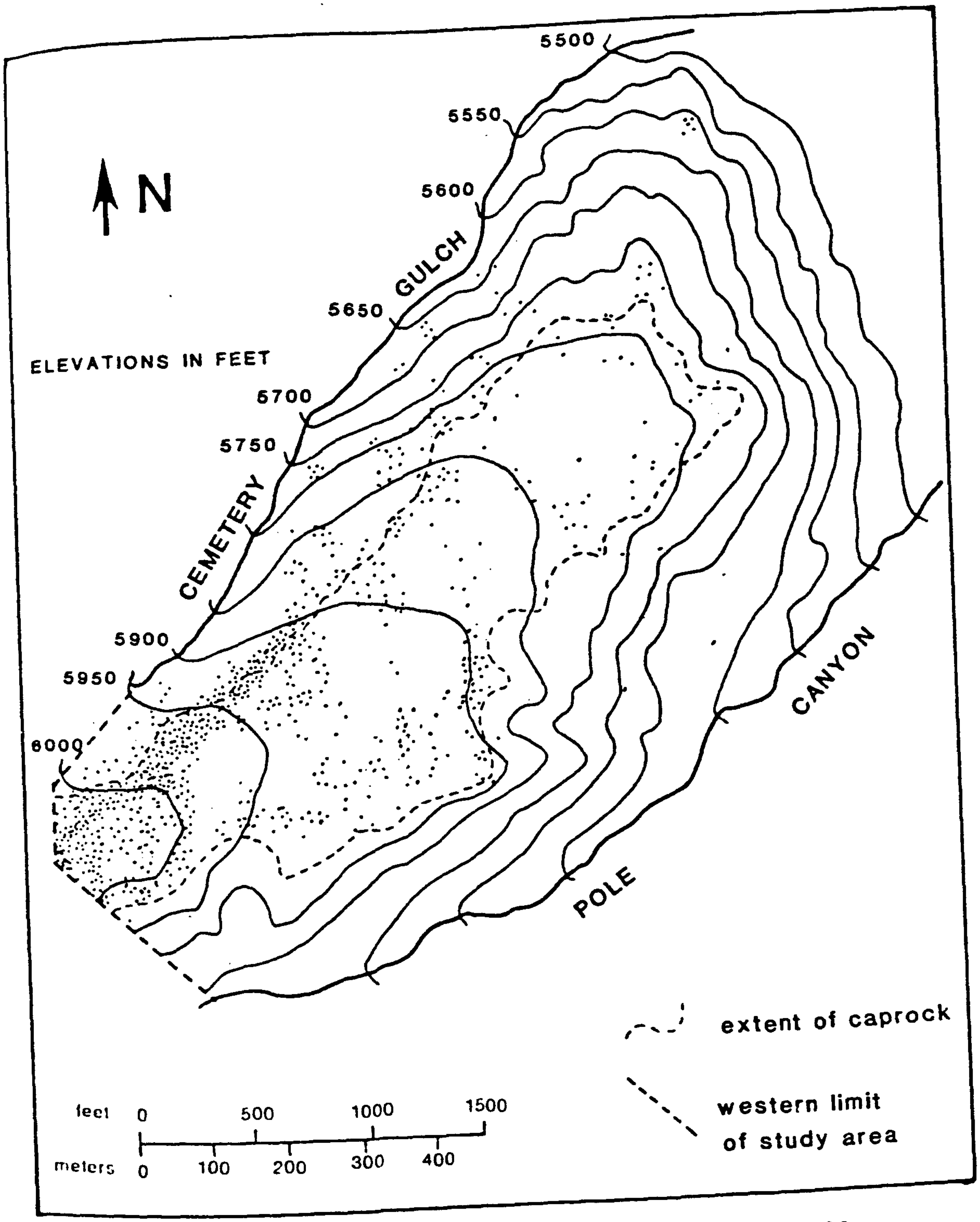


Figure 10. Distribution of ponderosa pine, 1908.

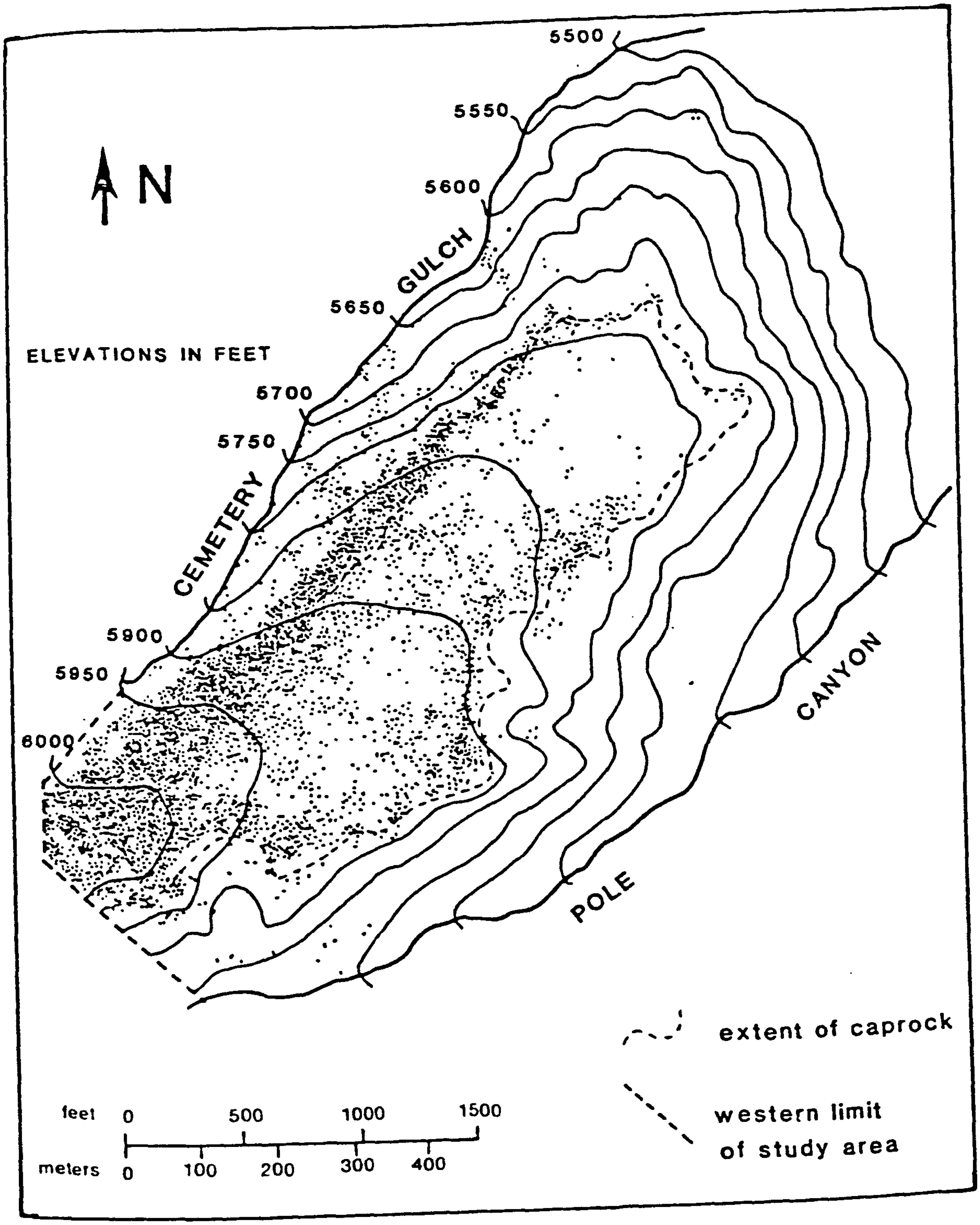


Figure 11. Distribution of ponderosa pine, 1948.

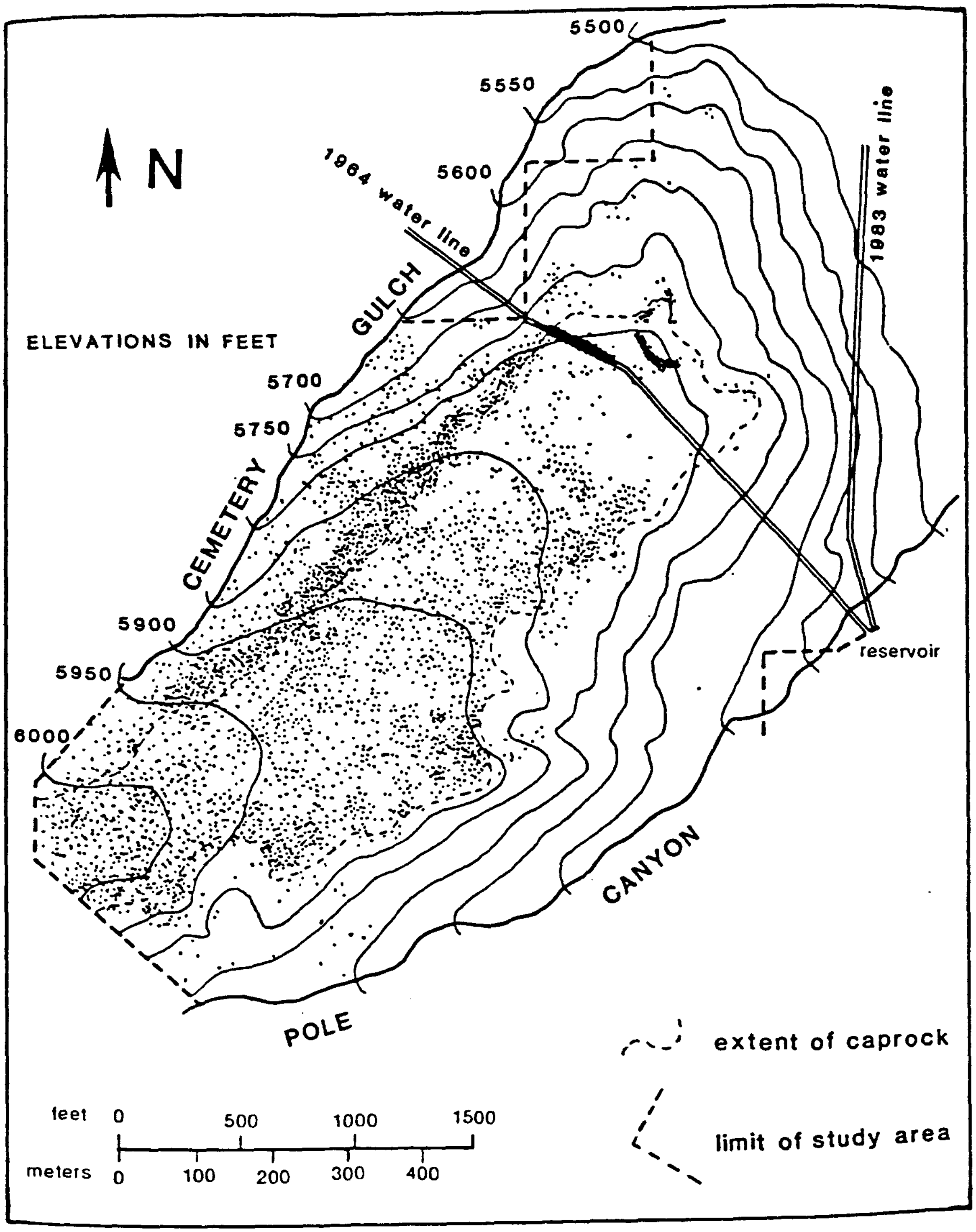


Figure 12. Distribution of ponderosa pine, 1984.

southern slope into Pole Canyon. Only the extreme northeastern quarter of the mesa top remained relatively free of pine. Once again the areas of highest density were along the northern edge of the mesa top and the higher elevations of the western limit of the study area. In addition, the areas which maintained the highest densities also increased in density. A total of 3,307 individual trees were counted for 1948.

Pine distribution in 1984 showed many additional changes and advancements from the earlier results, but the absolute numbers of living trees changed little. A total of 3,242 individual trees were counted within the study area for 1984. There were spatial shifts along with an overall decrease in the rates of new establishments of pine. The distribution along the northern rim continued to grow and expand to the northeast (fig. 12). Thick stands continued to increase near the southern rim, and densities in the mesa center increased to equate with 1908 densities in the extreme western portion of the mesa. Expansion down the sides of Cemetery Gulch continued while invasion into Pole Canyon remained at a minimum.

Comparative photographs from 1908 and 1984 demonstrate the outstanding expansion of pine. Two views of Cemetery Gulch and western Long Mesa from Horse Mesa illustrate invasion of ponderosa pine into the gulch and an increase in density on the mesa top (figs. 13 and 14). Two other comparative views exhibit the same expansion from a greater distance (figs. 15 and 16). The second set of photographs shows the entire north slope of Long Mesa from 1.5 kilometers away. Also, the result of massive residential tree planting is highly evident.

In the western region of Long Mesa, pine density had decreased due to pine bark beetle (*Dendroctonus ponderosae* Hopkins) infestation. Consequently, dead and infected trees were removed by the Boulder Mountain Park Service. A total of 389 stumps were counted in 1984.

A major feature of change in 1984 was two large pine stands near the most northern extreme of the mesa cap (fig. 12). The water line cut in 1964 resulted in a highly concentrated pine distribution along the grade. One hundred and forty-seven seedlings and young trees were counted, and all individuals were shown to be less than 20 years old through selective dendrochronology. Another ground cover disturbance occurred to the caprock to the northeast of the water line. A circular area was cleared, leveled, and resurfaced, wherein surrounding the clearance, a semi-circular ring of 83 seedlings and young trees has invaded the disturbed caprock.

Skunkbush

In 1908, the distribution of skunkbush was found to be most frequent in Cemetery Gulch and Pole Canyon and

Figure 13. Looking south to Cemetery Gulch from Horse Mesa, 1908. Western Long Mesa is left center.

Figure 14. Looking south to Cemetery Gulch from Horse Mesa, 1984. Camera angle is more to the left to include more of Long Mesa.

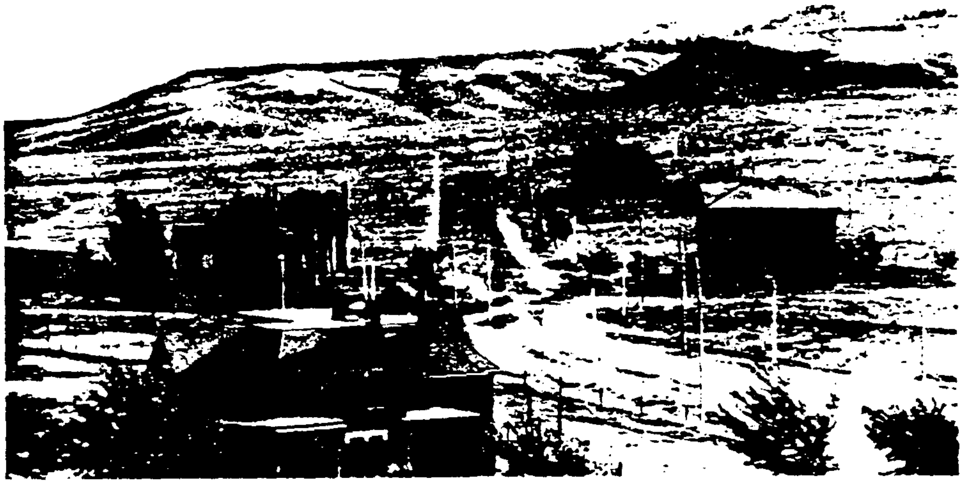


Figure 15. Long Mesa (center) and Horse Mesa (right). Looking south from the roof of Hale Science Building, University of Colorado, 1908.

Figure 16. Long Mesa (center) and Horse Mesa (right), 1984. Camera angle is 15 meters to the right to avoid large tree in left foreground.

in depressions and amphitheaters below the mesa cap (fig. 17). Robbins suggested that, like hawthorn, distribution was concentrated in areas of greater moisture availability. Other isolated individuals were scattered in drier portions of the mesa slopes. Skunkbush was not reported or mapped on the mesa top.

By 1948, the general distribution had diminished. Still no plants were reported from the mesa top, but a few were still reported from the drier areas of the mesa slopes. However, two very large stands still existed below the mesa cap on the south slope, and the shrub was indicated as common along the two creeks (fig. 18).

By 1984, the distribution of skunkbush had changed dramatically. Along the creeks, distribution of the shrub diminished greatly. On the north and south slopes, skunkbush had become the dominant species located in very large and thick mats (fig. 19). One thicket, which consisted of only four small colonies in 1948, measured approximately 140 meters long by 70 meters wide in 1984. The most notable distributions were below the mesa cap where many thickets measured 3 meters in diameter. The shrub was so common that it could be referred to as the type indicator of the slope microhabitat. Another very striking change had occurred on the mesa top. The earlier studies showed no skunkbush on the top, but in 1984, individual shrubs and small clumps were so frequent

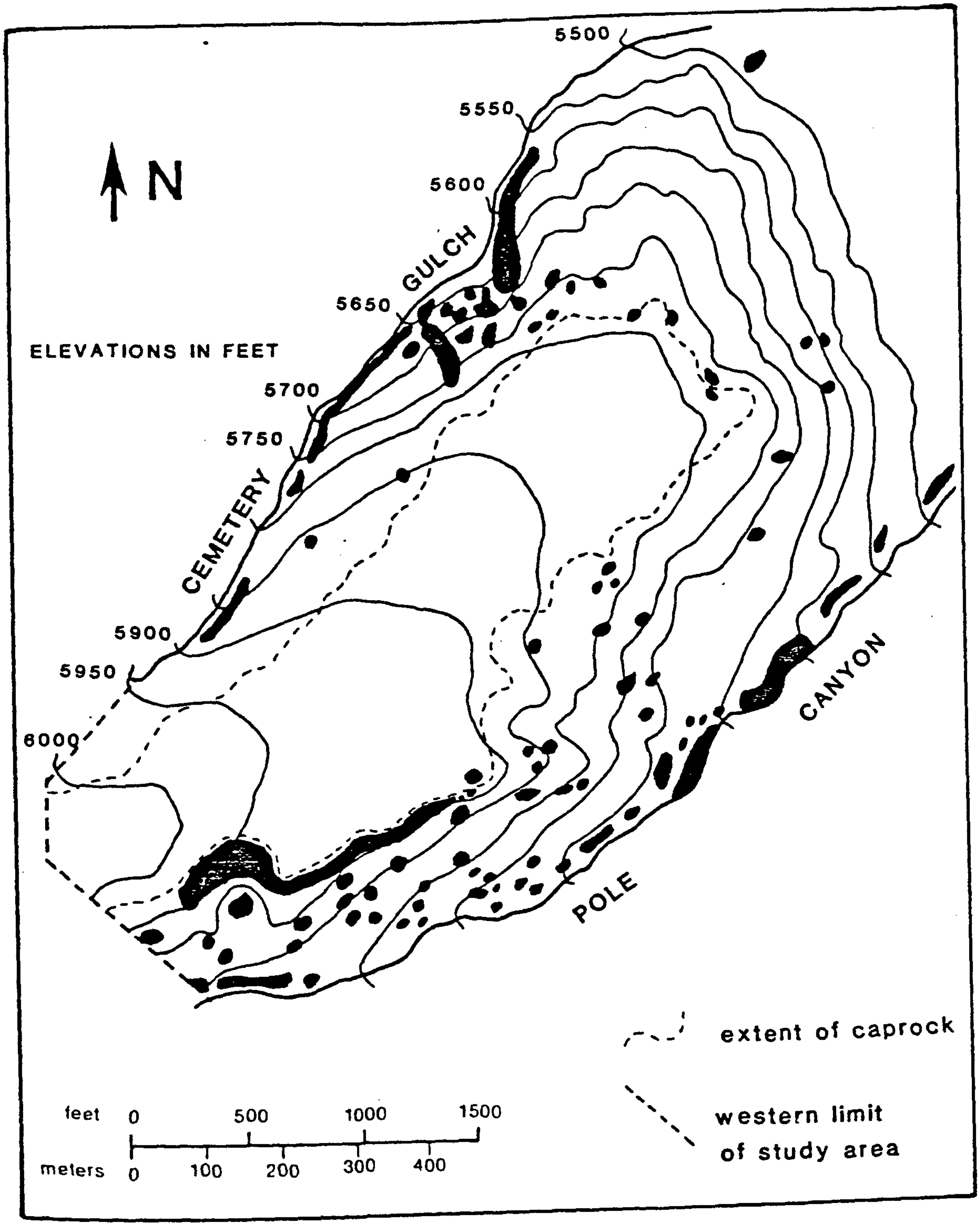


Figure 17. Distribution of skunkbush, 1908.

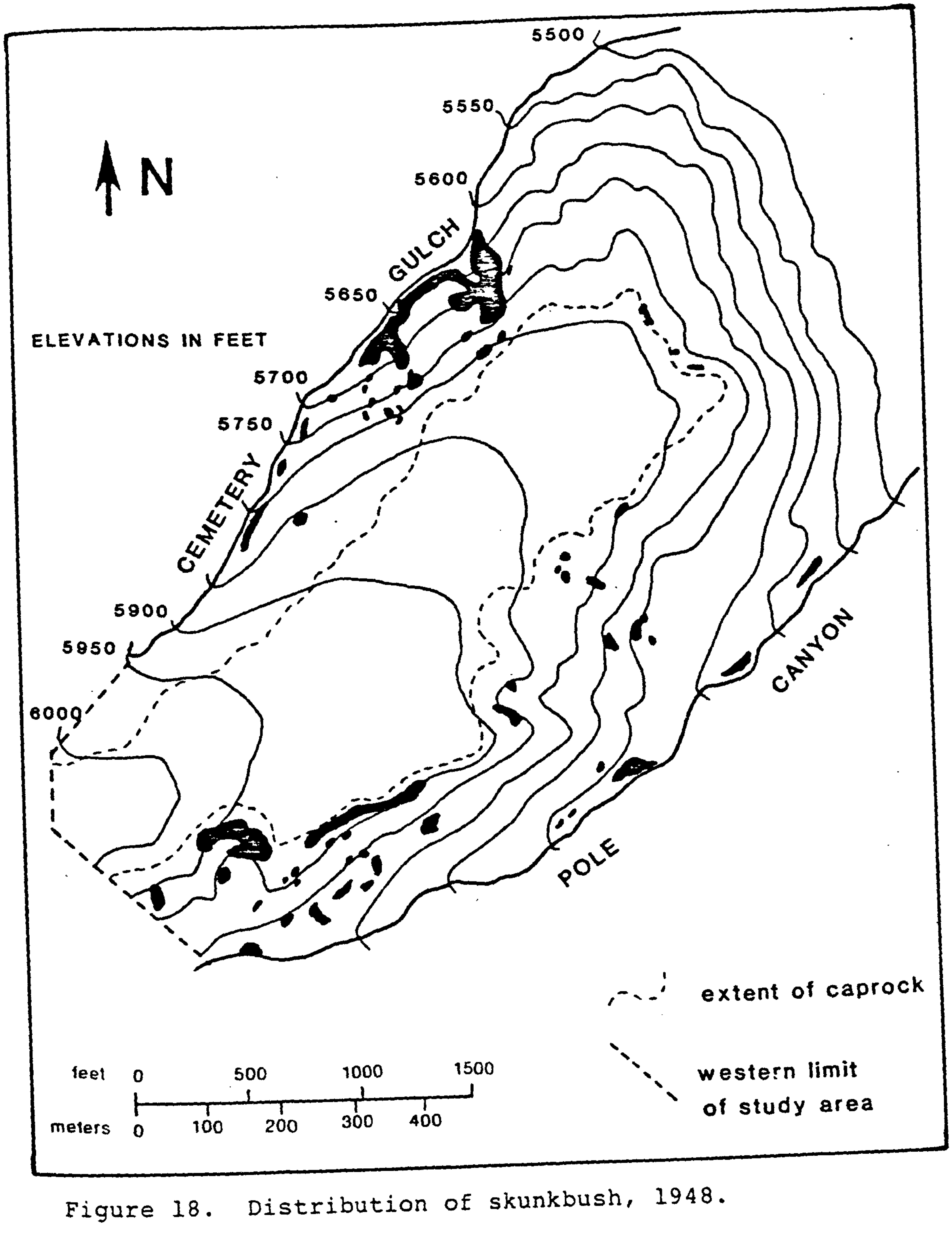


Figure 18. Distribution of skunkbush, 1948.

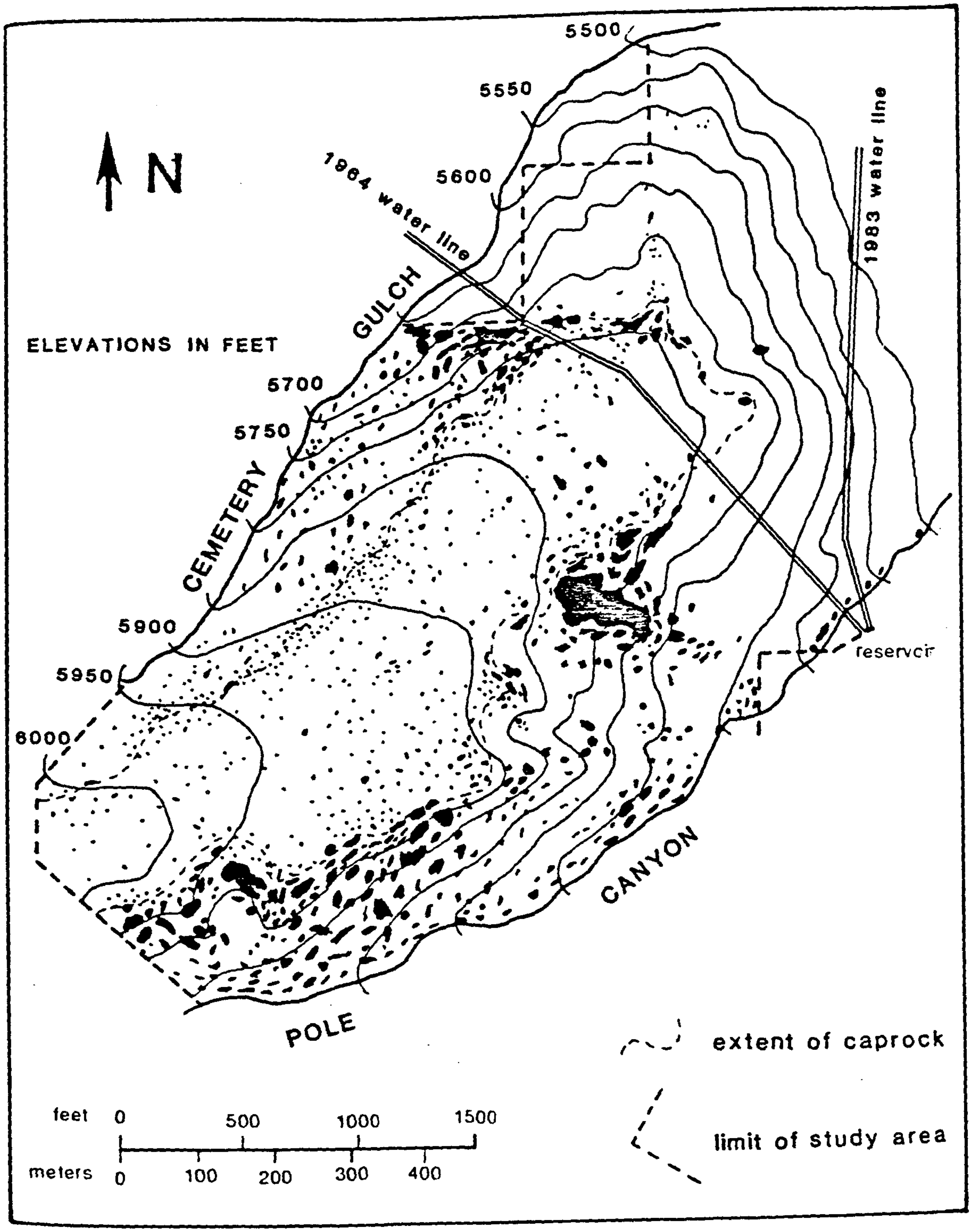


Figure 19. Distribution of skunkbush, 1984.

that they could be considered the secondary woody plant of the mesa top. This shrub was often found as an understory of ponderosa pine, and oddly in clumps on the eastern side of isolated pines, particularly on the eastern end of the mesa (fig. 20).

Figure 20. Ponderosa pines with skunkbush as understories.

Hawthorn

Two species of hawthorn occur in the region, but taxonomy is difficult since infraspecific breeding is very common (Weber 1976). Therefore, the two hawthorns are not treated as separate species. [illegible], the earlier studies treated all hawthorns as [illegible]. In 1908, distribution of hawthorn was [illegible] along

Cemetery Gulch and Pole Canyon (fig. 21). The two gulches were mapped as being dominated by hawthorn above all other woody species. Numerous isolated locations also were noted in depressions and amphitheaters below the mesa cap, particularly south and east. The sites were considered desirable for growth because of water seepage from the bottom of the sandstone cap. It was implied that these would be locations of hawthorn distribution expansion in the future (Robbins 1908). The area covered by hawthorn in 1908 was 55,297 square meters.

By 1948, hawthorn remained common along the gulches, although there was a reduction of its presence from 40 years earlier (fig. 22). Below the mesa's sandstone cap, only five colonies remained as compared with eleven colonies in 1908. The colonies were situated usually immediately below the cap on the south slope, but further down the incline on the north slope. Hawthorn covered a total area of 34,227 square meters in 1948.

Distribution of hawthorn in 1984 was noted as having decreased much more in the second time interval than during the first interval from 1908 to 1948. Though Hawthorn was still common in the gulches, many gaps had appeared (fig. 23). Below the mesa cap on the south side, one very large colony had completely disappeared and two small colonies had become established. Only six

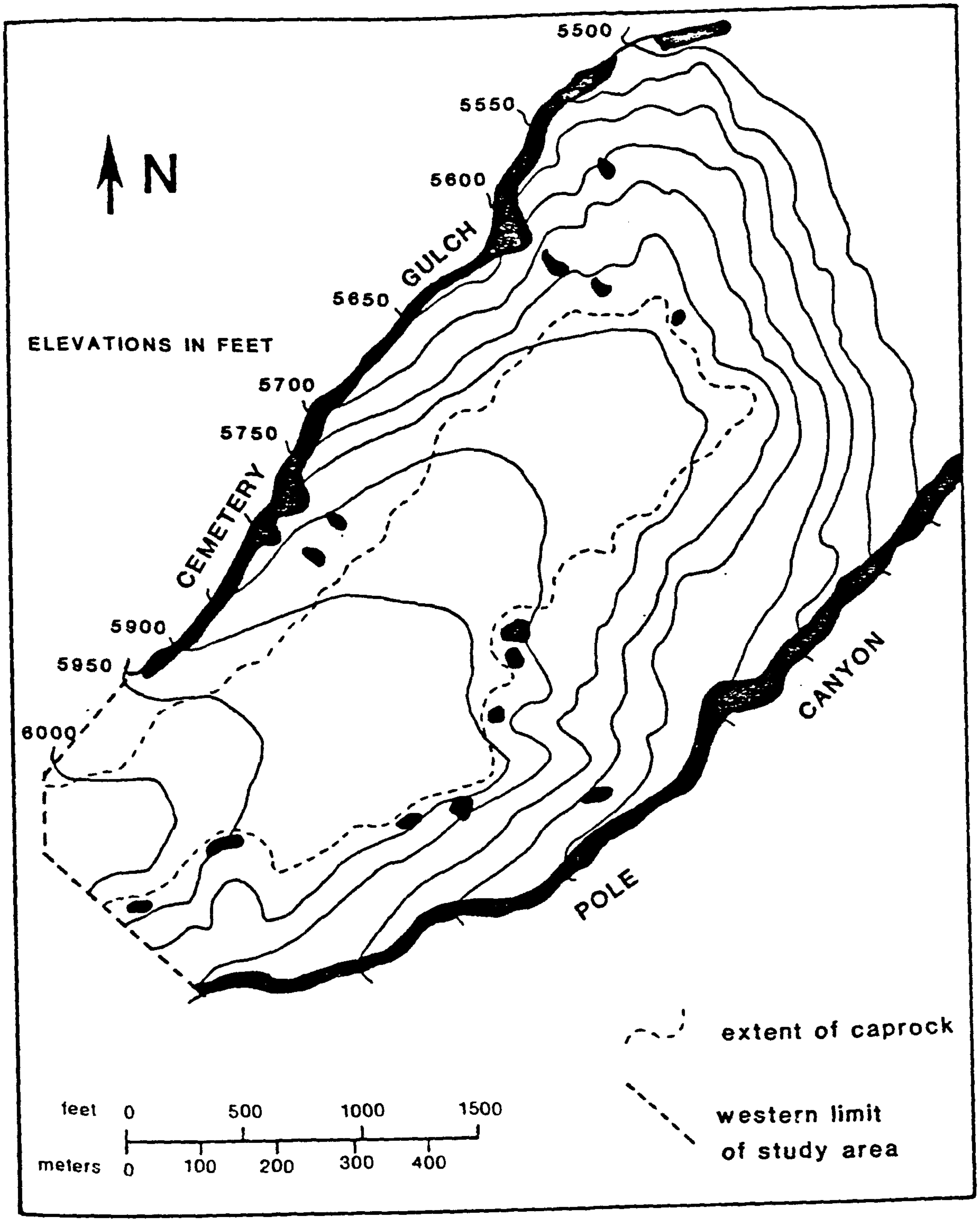


Figure 21. Distribution of hawthorn, 1908.

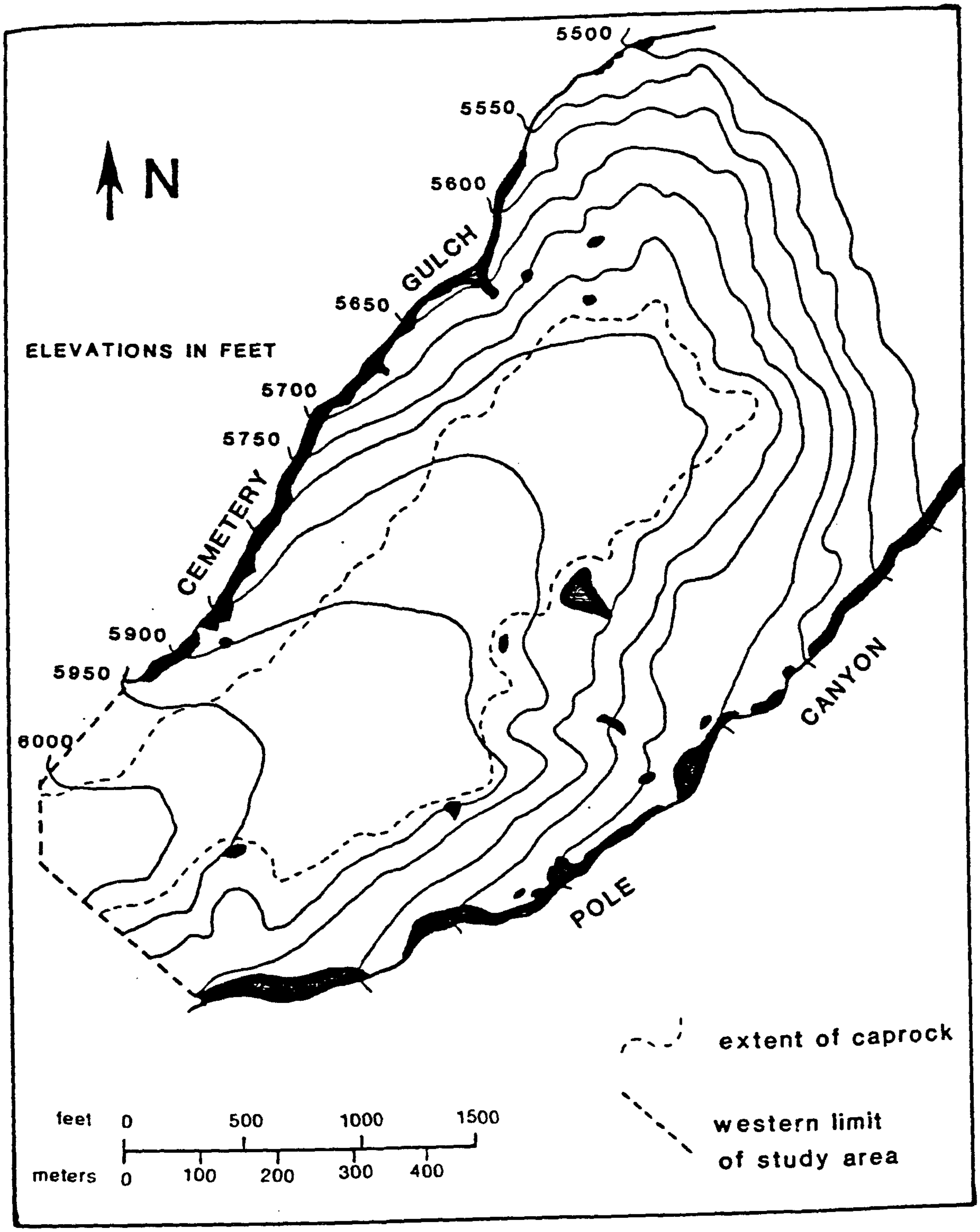


Figure 22. Distribution of hawthorn, 1948.

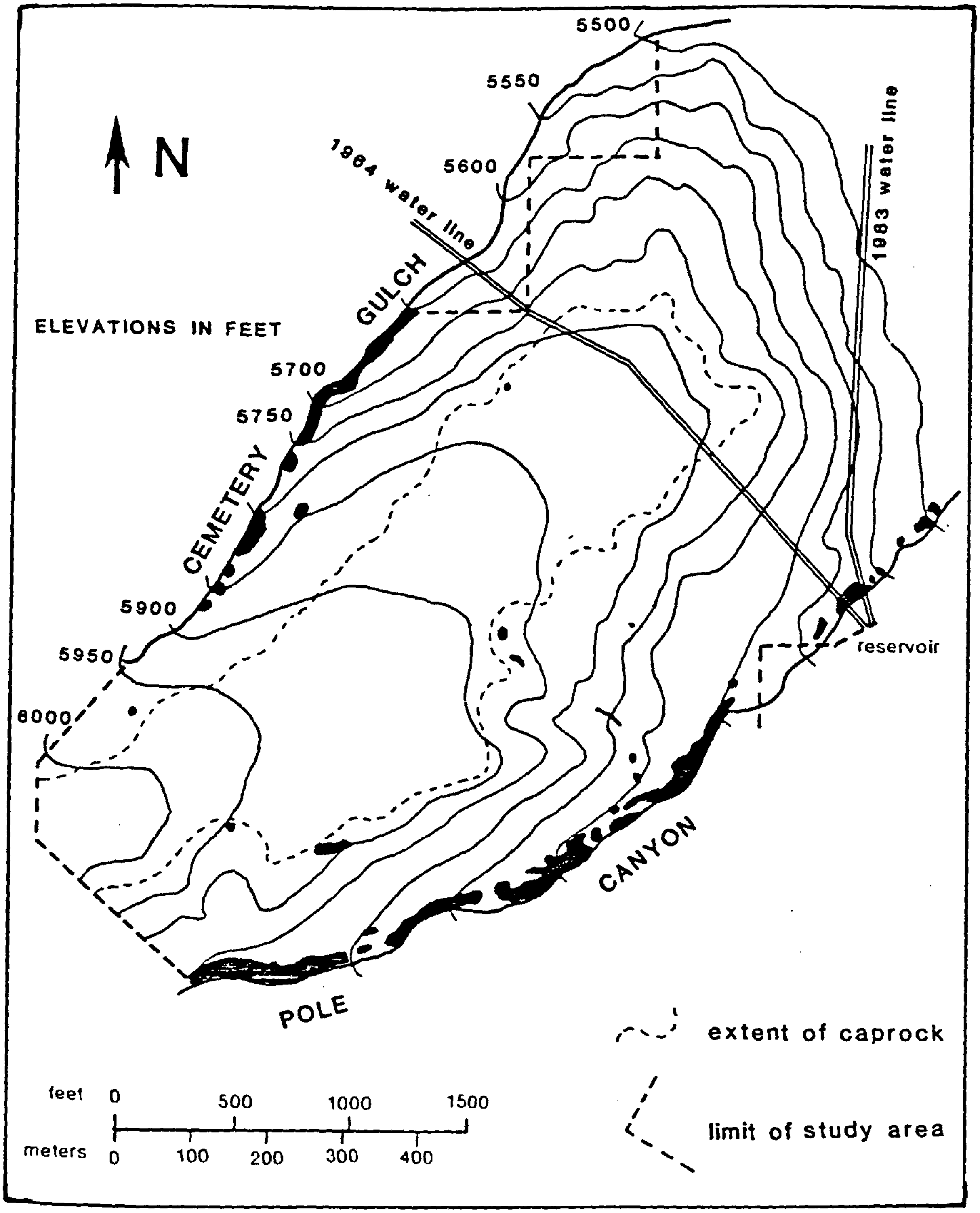


Figure 23. Distribution of hawthorn, 1984.

colonies existed above the gulches and below the cap in 1984, but two single individuals were found on the mesa top near the northern rim. Overall, the distribution of hawthorn within the study area decreased steadily from 1908 to 1984. In 1984, hawthorn covered 23,367 square meters.

Smooth Sumac

This colonizing and arborescent sumac was found to be relatively common from the mesa top to the gulches in 1908 (fig. 24). However, Robbins' western limit of the study area exceeded Roach's, and therefore, a number of prominent stands from 1908 were excluded 40 years later. Yet within the reduced boundaries, eight well-established colonies were noted along Pole Canyon, below the caprock on the north and south slopes and on the mesa top. Smooth sumac covered 12,108 square meters in 1908. All sites were in the western portion of the study area.

In 1948, nine colonies of smooth sumac were shown, but five of those were disjunctions from two formerly larger stands (fig. 25). In essence, an overall reduction had occurred. No longer were there colonies on the north slope or the mesa top. The large colony below the caprock on the south slope declined in size, and colonies along Pole Canyon broke up into smaller units. In Cemetery Gulch, a colony noted in 1908 was mapped as two disjunct stands in 1948. Roach also noted one

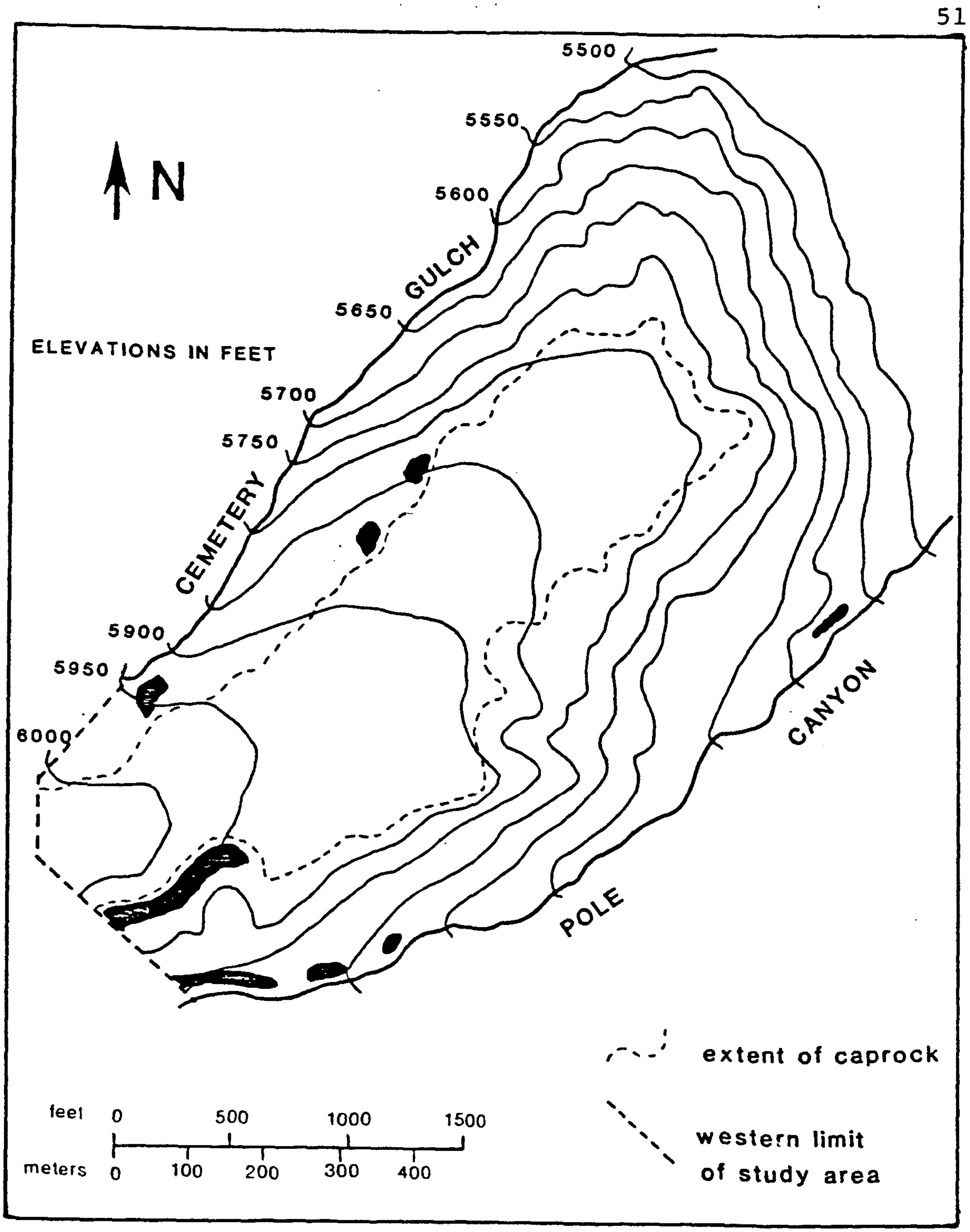


Figure 24. Distribution of smooth sumac, 1908.

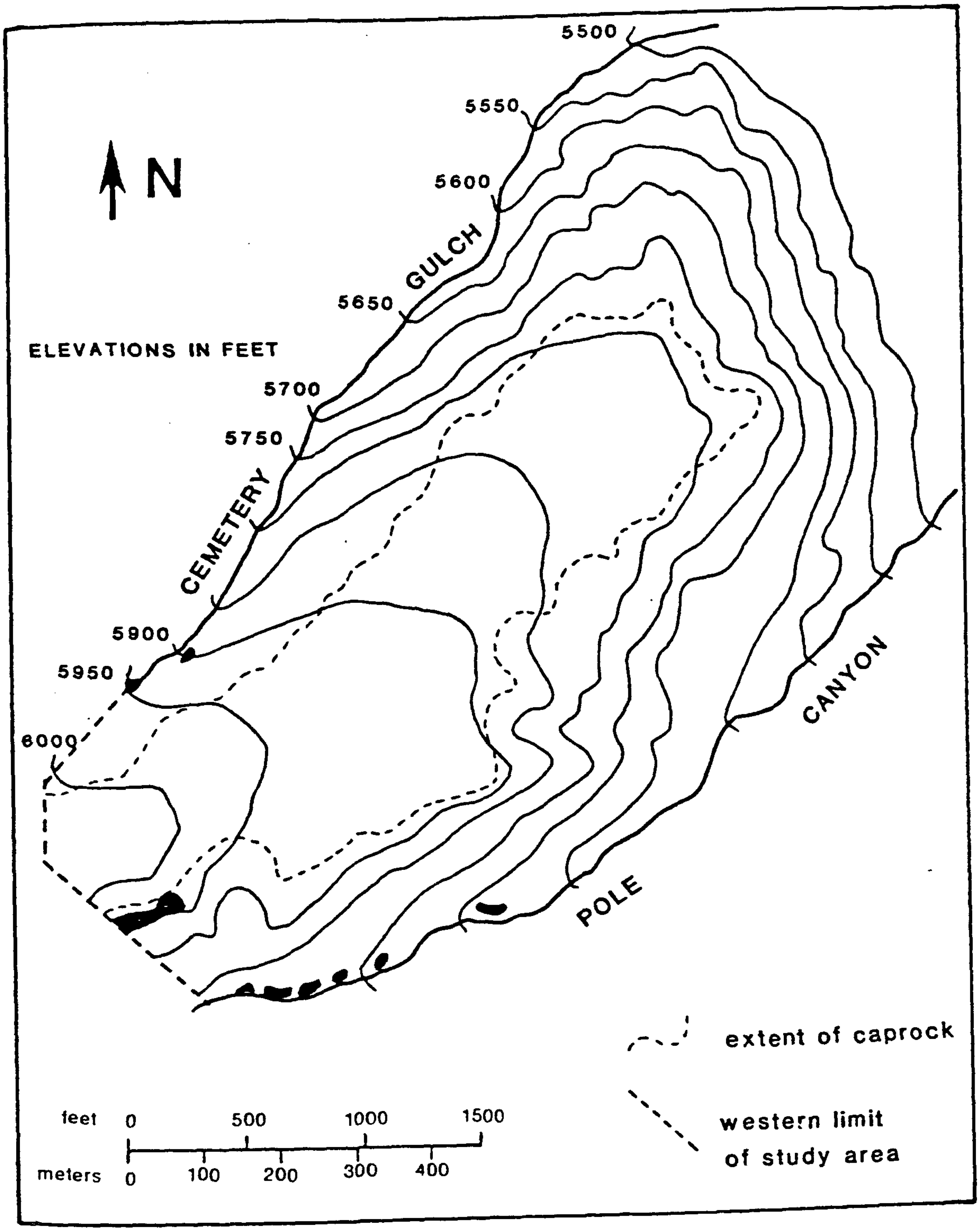


Figure 25. Distribution of smooth sumac, 1948.

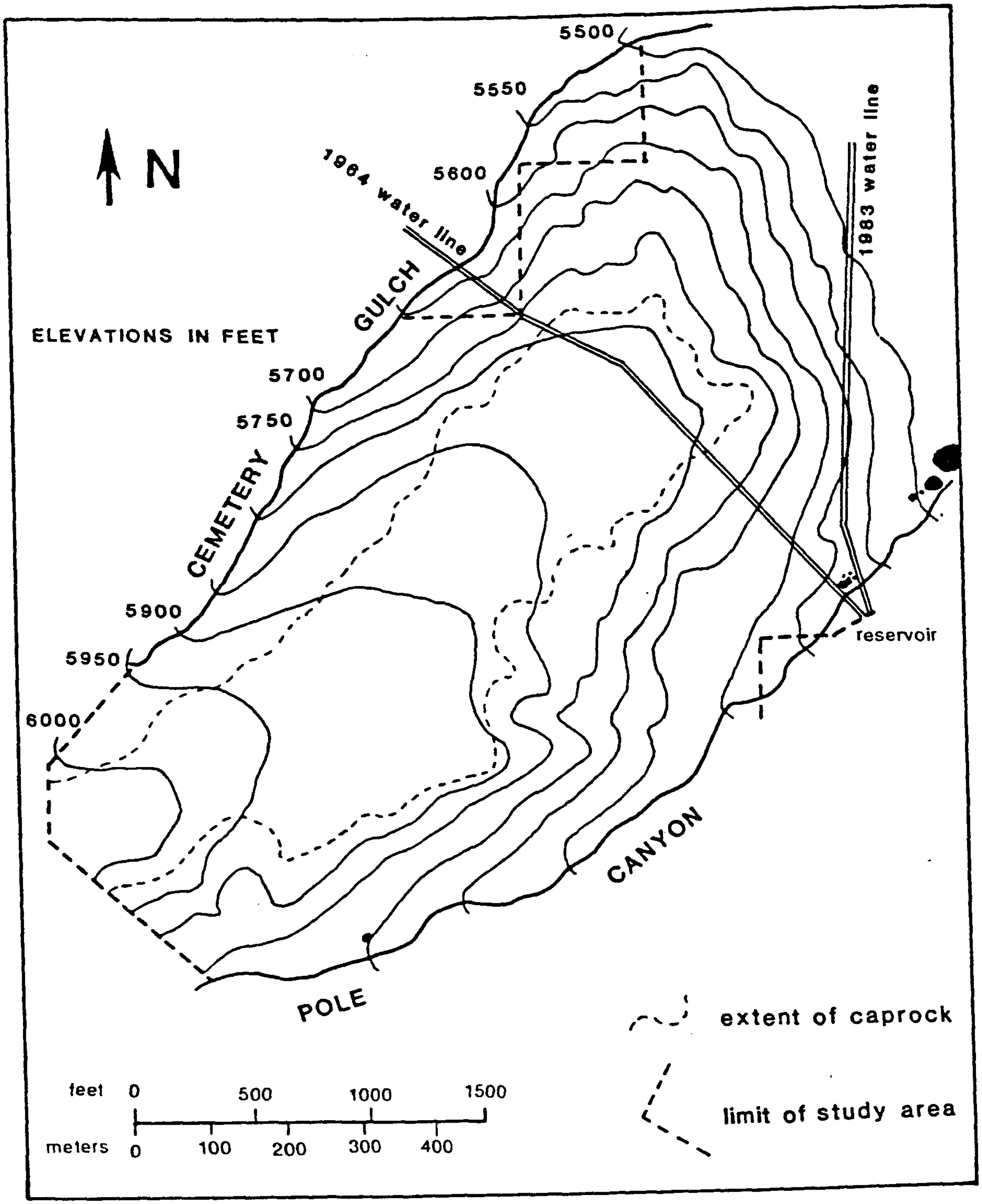


Figure 26. Distribution of smooth sumac, 1984.

additional stand lower in elevation adjacent to Pole Creek. The area covered by smooth sumac in 1948 was 4,290 square meters.

The 1984 distribution of smooth sumac was even more greatly reduced than 36 years earlier (fig. 26). All colonies were located along Pole Creek while signs of previous stands from Cemetery Gulch and the south slope were gone. In upper Pole Canyon, the formerly large and disjunct stands were reduced to a few small trees. However, at the eastern limit of the study area, along lower Pole Creek, two new disjunct colonies had become established and were apparently expanding. The total area covered by smooth sumac in 1984 was 1,827 square meters.

DISCUSSION: ANALYSIS OF THE CAUSES OF FOREST ADVANCEMENT

Many factors are affecting fluctuation in the ecotone of Long Mesa, and these factors are a complication of interactions. Human disturbance has been reacting with natural controls, and thus, neither purely natural environmental forces nor completely human effects can be cited as specialized causes. However, as an overall consequence, the many forms of human disturbance outweigh and encourage changes in the natural factors. The main reason for forest expansion appears to have been the results of a relationship between (1) cattle grazing, (2) fire suppression, (3) the resulting turf cover, and (4) composition of the soil and substrate.

Beyond the relationships of the major reasons for forest expansion, there are many less important and peripheral causes which have had variable effects upon the ecotone. Included among the less effective reasons are disturbances to the turf and soil other than cattle grazing, protection of the site from regional development, greatly increased deer browsing, lumbering interests, and climatic conditions and controls.

Analysis of Interacting Variables

Cattle Grazing

Cattle grazing is probably the greatest contributing factor to pine expansion on the mesa. When the turf cover is thinned or removed through cattle grazing, ponderosa pine can become established (Larson & Schubert 1969, Vale 1982). Some estimates suggest that since the end of the last century, heavy grazing reduced the grass cover by 85 to 90 percent in the region (Benedict 1961). In areas where the turf cover is already thin, as caused by a rocky ground surface, ponderosa pine will establish easily (Livingston 1949). An interaction of a rocky surface and cattle grazing seems to allow for the most rapid development of coniferous stands.

Overgrazing may nearly remove the entire turf cover (figs. 27 and 28), and cattle will sometimes nibble at young pines (Currie et al. 1978), thus destroying attempts at establishment of seedlings. Only after overgrazing is discontinued and vegetation has had some years to regenerate, will pine establishment recur. When temporal parameters are placed on grazing effects, the variability of different intensities can be observed. Regular or intermittent grazing, rather than overgrazing, at present, appears to be the usual procedure, with a steady but not extremely rapid increase of pine. In the past though,

Figure 27. Looking northeast from north rim of Long Mesa, 1948.

Figure 28. Looking northeast from north rim of Long Mesa, same view, 1984.

numerous locations have been known to suffer from the effects of overgrazing.

Suppression of Fire

The suppression of fire has had dual, opposing effects on pine expansion. In one sense, a removal of the turf cover through fire allows for greater seedling establishment (Harrington & Kelsey 1979). Ponderosa pine is a pyrophyte in the sense that old trees are resistant to small fires (Daubenmire 1943). It is a pioneer species following large fires and establishes well because of a thinned turf cover and a high influx of nutrients from the ash (Harrington & Kelsey 1979). Competition returns after one season following a fire, and a number of years must pass before the next fire occurrence to allow for saplings to age enough to be protected from another fire (Vestal 1917). Fire height and intensity are an integral part of the time sequence factor (Bock & Bock 1984). Irregular weak and low fires may be destructive to the turf cover but harmless to saplings, while crown fires may destroy mature trees.

There is a time factor involved, and suppression of frequent fires outweighs the effects of burning. A lack of burning encourages tree and shrub growth because seedlings and understories are not destroyed (Benedict 1961, Vale 1982), and succession will naturally establish hierarchy within the community. There is an advantage to a high influx of nutrients from fire ash, but the value of the nutrients decreases annually in orders of magnitude and, therefore, becomes of no significance after the second year. As a consequence, the advantage of the suppression of frequent fires is usually greater than whatever nutrients are added to the soil by fire ash. The overall effect of the suppression of frequent fires has been to encourage coniferous growth in suitable locations (Vale 1982).

Turf Cover

The density of turf cover resulting from variable degrees of cattle grazing and from suppression of frequent fires has largely determined woody species distribution. Where natural competition between pine and turf cover occurs, the grasses have historically been viewed as dominant (Robbins & Dodds 1908, Livingston 1949, States 1968, Vale 1982). However, one study seems to indicate that pine will successfully compete with grass and expand if the pine community is healthy, and certain climatic conditions will occur at appropriate intervals (Potter & Green 1964). Regardless, where the substrate is very rocky, an even turf cover does not establish well, and pine communities dominate.

The dominance of the dense, fibrous root system of grasses usually outcompetes attempts at woody species establishment. Pine roots extend much deeper into the soil than grass systems, but initial penetration of pine roots is transgressed by most grasses (Larson & Schubert 1969).

It appears that turf cover is the strongest natural biological control of ecosystems in the vicinity. When unaffected by cattle grazing or fire, the only variables controlling the presence, density, or absence of turf cover are soil and substrate type and moisture availability.

Edaphic Factors

Natural edaphic controls are important in understanding the aspects of the natural distribution of plants, especially when disturbance has removed the vegetation cover and exposed the soil. Edaphic controls are tightly linked to the porosity of the soil or substrate type and to moisture availability. Coarse-textured soils are the soil types with which ponderosa pine is usually associated (Livingston 1949). The soils are normally lower in competitive turf cover and allow for a deeper penetration of precipitation (States 1968).

Where the coarse-textured soils comprise a loose conglomerate of a porous recharge area, as on Long Mesa, and the strata under the conglomerate consist of impervious shales, the result is a perched water table just below the sandstone cap. Water seepage occurs in many locations on the slopes immediately below the cap and this water supply has allowed for the maintenance of microhabitats, especially within amphitheaters, suitable to the growth of deciduous trees and shrubs.

An exposed soil surface with a reduced turf cover and, therefore, a higher degree of porosity are the most desirable conditions for pine growth. Where the exposed surface consists of a poorly compacted conglomerate of different-sized particles from sands to small rocks, edaphic conditions appear to be at a maximum for seedling establishment (Livingston 1949, States 1968). The caprock of Long Mesa has a heavy sand and gravel content, and the many rocks and boulders contribute to a decreased turf cover (Roach 1948). The surrounding shales of the mesa slopes and lowlands are relatively impenetrable to moisture and provide a surface for the dense but shallow root systems of grasses and herbs.

Benedict (1961) found that low elevational pine communities near Boulder tend to exist most frequently in acidic soils from pH 5.9 to 6.8. States (1968) showed that pines were consistently found in substrates in which pH concentrations were lower than the surrounding substrates supporting a grass and herbaceous cover. However, acidic hydrogen ion concentrations were a consequence of acidic geologic deposition rather than a result of a microenvironmental change brought on by the natural acidity of pines.

Other Factors

As it is true with cattle grazing, any other type of disturbance to the turf cover or soil encourages pine establishment. Along graded roadsides, pine saplings and young trees are commonly seen growing only immediately adjacent to the road where the original grading disturbed the surface, but where no disturbance has since occurred (Robbins & Dodds 1908). The installation of water lines and the grading of roads through coarse-textured, porous soils usually exposes the bare soil and within a few years pine will become established on the sites of direct disturbance.

When sites are left undisturbed by regional development, an opportunity exists for the contrast and comparison of changes. The lowlands below Long Mesa have been greatly modified in the past 40 years. Some encroachment of residential areas has occurred on all slopes of Long Mesa, but the most pronounced changes on the mesa top have occurred minimally in comparison to the encroachments. A road was built to the top, but its use is highly restricted. Hiking trails are common on the mesa top and slopes, and some nonnative vegetation species have become established, but the reconstitution of a more natural vegetation environment in the present day outweighs the barren overgrazed appearance of nearly 40 years earlier (figs. 29 and 30).

Figure 29. Looking west to the foothills from the center of Long Mesa, 1948.

Figure 30. Looking west to the foothills from the center of Long Mesa, 1984. Note improved condition of the vegetation and deer at right center.

Deer browsing has become a problem in recent years. The deer population has grown quite large and tame. Although there appears to be an abundant food source on the mesas and in the foothills, the population is known by park officials to be unhealthy. Groups of deer can be frequently located in adjacent residential areas consuming the vegetation of the cultivated landscape. Within the Long Mesa study area, deer have been observed browsing skunkbush (fig. 31) and hawthorn. One stand of hawthorn was found reduced to plants only 20 cm. high as a result of this browsing. Hawthorn is cited as not palatable to big game ungulates, but it is an emergency food during periods of stress conditions (McKean 1976). Deer browsing is especially evident in the gulches and on the slopes around Long Mesa.

Figure 31. Young buck browsing in skunkbush.

Lumbering interests have been virtually nonexistent on Long Mesa for at least 70 years. Before that time, ponderosa pine was used extensively for building material and fuel. Much of the foothills region was denuded in the latter half of the 19th century (figs. 32 and 33). Except for an occasional tree cut for firewood, Long Mesa has been spared the devastation of massive timber cutting.

The climatic conditions now are more similar to the cooler Early Holocene than during the warmest and driest part of the Hypsithermal (Daubenmire 1968), when the most damage occurred to the remnant forest. Therefore, present climatic conditions on the plains are more favorable for the return of the forest, but modern human agricultural activities now prevent the possibility of natural forest reestablishment and regeneration in most locations.

Climatic change is naturally too slow to have affected the recent rapid advancement of the pine forest near Boulder. Although long-term climatic variability is an important factor in vegetation change, the rapidity with which ponderosa pine has reestablished is greatly dependent upon the influx of nonindigenous settlers within the past 125 years (Beckman 1977) because of cattle grazing and the other variables cited in this thesis.

Figure 32. Looking southwest to barren Coal Creek Peak from 3.2 kilometers south of Eldorado Springs, 1908.

Figure 33. Coal Creek Peak from 150 meters south of the site above, 1984. Note forested foothills, Rainbow Cut of Denver, Rio Grande and Western Railroad in center.

Analysis of Specific Woody Plants

Ponderosa Pine

Photographs of the area, dating from the turn of the century, show barren mesas and undeveloped plains surrounding the mesas (figs. 15 and 16). Although the plains are now highly developed, Long Mesa has remained uninhabited. The major change to be noted is that now the mesas are heavily forested primarily with ponderosa pine. Comparative photographs 36 years apart show a dramatic increase in pine (figs. 34 and 35). Expansion of pine was even greater in the 40 years preceding 1948.

Seedlings appear to develop best in areas where disturbance has occurred to the surface cover or soil (Robbins & Dodds 1908, Miller 1956). As previously mentioned, disturbance in the form of cattle grazing is highly evident from 1908 to 1948. With a thinned turf cover and an exposed soil surface, pine seedling establishment advanced rapidly onto the mesa. Cattle are known to nibble at pine seedlings under conditions of overgrazing (Currie et al. 1979), and perhaps Long Mesa's less dramatic advancement than that of Shanahan Mesa (Beckman 1977) can be attributed to overgrazing.

From 1908 to 1948, the establishment and growth of pine was much more intense than during the comparable time period from 1948 to 1984. Roach attributed pine

Figure 34. Long Mesa and Cemetery Gulch from Horse Mesa, 1948.

Figure 35. Long Mesa and Cemetery Gulch from Horse Mesa, 1984. Note the 36-year growth of specific trees. Also note the well-developed turf cover.

expansion to soil texture and the availability of moisture associated with the soil type. Cattle grazing was seen as important in removing the turf cover, and, therefore, increasing the probability of pine establishment within the controls of soil texture and moisture. Micro-environments, immediately adjacent to rocks and boulders, were considered to create moisture pockets and therefore encourage seedling establishment.

Upon comparing the past 36 years with the earlier time interval, the argument in favor of a theory more strongly in support of cattle grazing has become apparent. Cattle grazing on Long Mesa ceased soon after Roach's thesis was completed, and a decrease in newly establishing pine became obvious. Many individual trees seen in 1948 can be recognized in 1984 (figs. 34 and 35), and changes in growth can be easily observed. However, the numbers of new seedlings is minimal in comparison with new establishments during the first 40-year interval (figs. 13 and 14). Since cattle grazing ceased, the turf cover has had an opportunity to recover, and the dominance of pine over the grasses has been slowed, if not reversed. Thus, there is now a more natural competition occurring.

Seedling establishment within the past 36 years may be more frequently associated with other forms of disturbance to the turf cover. On the eastern portion of Long Mesa, there are large open areas with no pines, individual pines scattered around, and patches of pine seedlings. Closer examination of the ground around the seedling patches has consistently shown some form of disturbance. It is probable that the isolated trees became established as a result of isolated disturbances such as a treefall or in association with large boulders. The two heavy concentrations of pine near the northern rim are attributed to major caprock disturbances cited on page 38. Seedlings occur less commonly in the heavily wooded areas of the western portion of the mesa, where pine competition and the tree canopy are so great as to prevent young tree establishment.

On the mesa slopes, cattle grazing has had a less dramatic effect on pine expansion. Though it has been shown that pine expansion has occurred down the slopes of Long Mesa, particularly into Cemetery Gulch, seedling establishment has been less frequent than on the mesa top. It has been shown also that seedling establishment will occur in grasslands underlain by less porous soils (Potter & Green 1964) and that pine expansion onto those types of soil and turf environments is less common regardless of cattle-grazing activities. Another possibility to consider is that steep slopes as opposed to flat surfaces may be less desirable to cattle. Though it has not been proven, it may be assumed that cattle would choose first and more regularly the flat mesa top for grazing. Thus, the mesa top would suffer greater turf cover removal than the mesa slopes. Therefore, the less porous soils of the slopes would combine with a more complete turf cover and result in fewer pines becoming established on the slopes.

Pine beetle infestation in the foothill region reached epidemic proportions in the late 1970s and caused extensive denudation of many hillsides. Beetle infestation on Long Mesa caused much damage to the pine population in the western portion of the study area. Within the past 10 years, thinning of infected trees by the park service has decreased the total population of pine by 389 trees. The insect problem is now under control.

Shrubs

Skunkbush has shown very fluctuating distribution changes in 76 years. In 1908, the shrub was primarily located in the gulches and in the amphitheaters below the mesa and secondarily on the slopes. Moisture availability appeared to be the main reason for its distribution. In fact, there was no skunkbush shown from the mesa top.

Within 40 years, the distributions were similar in habitat, but the quantity of the shrub had diminished and stands on the slopes disappeared. The most dramatic changes occurred following cessation of cattle grazing. Along the creeks, competition with other species may have driven the shrub out to drier habitats. Perhaps an increased turf cover was more compatible than competition with the other recovering shrubs in moist habitats.

It is known that deer browse on skunkbush (fig. 31), and it may be assumed that cattle grazed heavily on the shrub. By 1948, cattle had greatly reduced the quantity and distribution of skunkbush through grazing and trampling. It also may be considered that the soil surface was too barren to support the shrub.

Within the following 36 years, skunkbush not only moved out somewhat from its former habitat along the creeks, it successfully competed and expanded in drier regions particularly on the mesa slopes. By 1984, skunkbush was the dominant woody species of the mesa slopes (figs. 36 and 37) and the secondary woody species of the mesa top.

Seventy-six years earlier it was suggested that skunkbush was attracted to moist areas (Robbins 1908) and, in 1948, that concept held true. However, by 1984, the shrub was very prevalent in all habitats. The cessation of cattle grazing appears to be the primary determinant of skunkbush expansion.

Hawthorn distribution and density decreased steadily from 1908 to 1984. Robbins suggested that distribution

Figure 36. Looking east across Cemetery Gulch to the north slope of Long Mesa and the plains, 1948.

Figure 37. Looking east across Cemetery Gulch to the north slope of Long Mesa and residential South Boulder, 1984. Note the increase in skunkbush on the slope.

in 1908 was dependent upon moisture availability, and he speculated that the population may expand, especially in the moist amphitheaters. However, 40 years later, the population had decreased and Roach indicated that an increased competition of hawthorn with pine had encouraged a decrease in hawthorn density.

The effects of horse and cattle grazing on the shrubs was noted as the major disturbance factor and was considered as primary in the disappearance of hawthorn (Roach 1948). After cattle grazing was discontinued, the decrease in hawthorn continued. It is possible that cattle grazing initiated a major decrease in the earlier years, and deer browsing has contributed to the decrease in later years.

It also may be suggested that the effects of grazing were not as dramatic upon the decrease of the shrub as was formerly thought. In fact, a lack of moisture availability may have been the primary factor in the steady decrease of the hawthorn population. In 1984, one stand in a large amphitheater was rapidly dying out because of an apparent discontinuation or decrease of water seepage from under the cap.

Perhaps it is best to suggest that a combination of grazing, browsing, and lack of moisture have all contributed to the steady decrease of the hawthorn population. Regardless, in the gulches, hawthorn remains healthy in large thickets, and its demise there is not soon to be expected.

Smooth sumac has shown the most dramatic decrease of the species studied. Though the population of this shrub comparatively has remained the smallest, its distribution in 1908 was noteworthy. The population was established well in the higher elevations of the mesa just outside of the study area and down into the gulches. Seventy-six years later the remaining population was hardly noticeable.

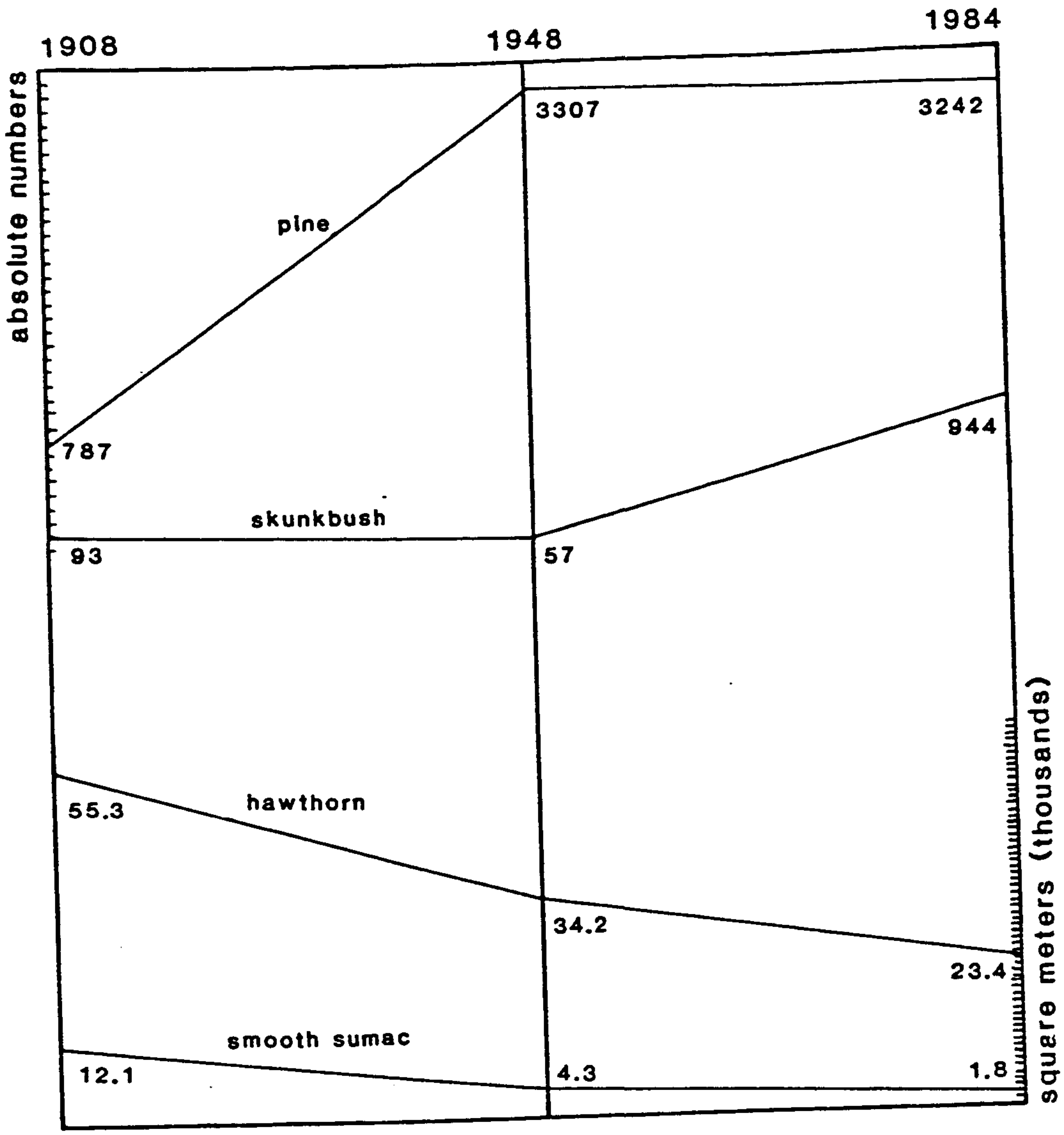
Grazing does not appear to be a direct cause, but it may have acted indirectly when cattle grazing was discontinued and thus an increased turf cover competed successfully. It has been suggested that this sumac appears to be quite common after fires (Vestal 1917) and perhaps the 1908 population was a large remnant from fires occurring before the turn of the century. With the suppression of fires since that time, the present limited population of smooth sumac is probably the last remnant. The one new stand of sumac in the eastern portion of the study area may be associated with a more recent disturbance to the soil surface.

Interrelationships among the Species

The concept of an advancing pine forest was easy to observe and relatively easy to explain. Within the determinant variables, pine continued an eastward advance for 76 years, although the rate decreased from the first time interval to the second time interval. The other woody species of the Long Mesa region present a more complex picture of population dynamics within temporal parameters (fig. 38).

Cattle grazing was the most important variable affecting population fluctuation and the cessation of grazing decreased the rate of pine advancement. There is a direct correlation between skunkbush and pine fluctuation. Although pine decreased in the second time interval and skunkbush increased, both are related to cattle grazing and its cessation. Pine decreased in the second interval because of an increased turf cover, and skunkbush increased because cattle were no longer present to consume the shrub. An increased turf cover does not appear to have discouraged skunkbush from increasing. Hawthorn has maintained a steady decrease, first because of cattle grazing, but, second, because deer browsing replaced destructive cattle grazing. The possibility of less active water seepage appears to be working in conjunction with browsing to decrease the hawthorn population.

The greatest variable affecting the steady decrease of the smooth sumac population is independent of cattle grazing. Although an increased turf cover may be contributing to the decrease of smooth sumac, it is more



Pine--Numbers of individuals
Skunkbush--Numbers of colonies and isolated individuals
Hawthorn--Area of colonies in square meters
Smooth sumac--Area of colonies in square meters

Figure 38. Population fluctuation correlations between pine, skunkbush, hawthorn, and smooth sumac, 1908, 1948, and 1984.

probable that the population is largely a remnant from a fire regime more than 76 years earlier.

Fluctuations between pine and skunkbush are conversely complementary, but not directly related to an interaction between the two. Pine and hawthorn fluctuations are conversely complementary in the first time interval, but parallel for different reasons in the second interval. The populations of hawthorn and smooth sumac are similarly slowly decreasing, but the causes for the similar correlations are highly different.

CONCLUSION

The rapid advance of the ponderosa pine forest on Long Mesa within the last 76 years has been quite obvious, but the changes of the shrub species are less obvious at initial inspection. Ponderosa pine has continued an eastward movement, although the exact numbers appear to show a slight decrease. Skunkbush has shown a decrease, and then a great increase, and both hawthorn and smooth sumac have shown slow decreases.

Certain factors have encouraged forest expansion while other factors have helped retard growth. The variables affecting change and the difference in rates of change apparently center primarily around the effects of cattle grazing. The following are some of the conclusions derived from this study:

1. From 1908 to 1948, cattle grazing appears to have acted as a strong encouragement to pine seedling establishment and a hindrance to skunkbush growth. When turf cover is thinned or removed, competition with grass is greatly reduced and pine establishes easily. Skunkbush is palatable to cattle, and its population was largely destroyed probably through grazing and trampling.

2. From 1948 to 1984, cattle grazing was minimal or nonexistant on Long Mesa. The turf cover had a chance to recover and its renewed competition with pine apparently slowed the rate of pine advancement. Skunkbush experienced a massive increase in population apparently because cattle were no longer present.
3. The slight decrease in total numbers of pines in the study area from 1948 to 1984 is due primarily to the loss of nearly 400 trees infected with insect blight. However, while numbers of trees have decreased to the west, new establishments have continued to the east.
4. Dramatic short-range disturbance to the land surface has allowed for sudden and massive pine seedling establishment in the study area.
5. Soil moisture and substrate type act as natural barriers to pine establishment. Beyond the effects of grazing, pine establishes best in coarse-textured soils and tends to disfavor sandy loams. Ridges and escarpments are preferred while low lands remain barren of pine. Thus, in spite of the cessation of grazing, the rate of pine advancement will probably continue to decrease as a climax community is reached on the mesa top.

6. Suppression of frequent fires apparently has acted as an encouragement to the growth of most major species. The effects of cattle grazing strongly outweighed fire suppression until 1948, but the controlled suppression of fires now appears to act more strongly in encouraging tree and shrub growth.
7. Smooth sumac is pyrophytic and establishes best under conditions of recent fires. It is apparent that the suppression of fires on Long Mesa has continued to discourage the growth of this now insignificant sumac.
8. To a lesser degree, deer browsing appears to have replaced cattle grazing as a force for decreasing shrub populations. With a range limited to the mesa region and an increasing pressure upon the natural ecosystems by the increasing deer population, it is suggested that hawthorn may continue to decrease in numbers. Skunkbush is also an object of deer browsing, but effective damage by deer apparently has not yet occurred. Ponderosa pine is essentially unaffected by deer.
9. Many other variables are included in the determinants of tree and shrub vegetation changes but most variables have been dwarfed by cattle grazing. Since grazing has ceased, some of the other variables such as an increased turf cover and edaphic controls

may become more important in the future to vegetation dynamics on Long Mesa.

10. Theoretically, the present climate is more favorable than during the Hypsithermal for the advancement of the coniferous forest. Although the variable of climatic change should not be overlooked, the rate of pine expansion on Long Mesa has been too quick to give much credibility to that concept.

On a local scale, the primary natural factors which bring about natural vegetation changes are edaphic and microclimatic conditions. The changes which have occurred on Long Mesa basically have been caused by cattle grazing and man-related variables and are, therefore, neither edaphic nor microclimatic conditions. Perhaps in the future, variables controlled by human interference will be lessened and natural vegetation changes will occur as a result of natural causes.

The value of a study which examines distribution changes across an ecotone is important in vegetation ecology and dynamics. It is hoped that this study of Long Mesa has contributed to a better understanding of historical vegetation or ecotone changes along the Rocky Mountain Front.

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