THESIS

RELATIONSHIP BETWEEN PONDEROSA PINE AND UNDERSTORY HERBAGE PRODUCTION

Submitted by

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In partial fulfillment of the requirements

for the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

June, 1974

COLORADO STATE UNIVERSITY

June, 1974

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY HARLEY E. METZ ENTITLED RELATIONSHIP BETWEEN PONDEROSA PINE AND UNDERSTORY HERBAGE PRODUCTION BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

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ABSTRACT OF THESIS

RELATIONSHIP BETWEEN PONDEROSA PINE AND
UNDERSTORY HERBAGE PRODUCTION

This study was conducted at the Manitou Experimental Forest in cooperation with the U.S. Forest Service Rocky Mountain Forest and Range Experiment Station and the Range Science Department of Colorado State University. The Experimental Forest is located in the montane zone of the Colorado Front Range about 28 miles northwest of Colorado Springs at 8,000 feet in elevation.

Various understory and environmental factors were correlated with the understory herbage production on 14 permanent sample plots. The overstory parameters of trees/acre, basal area, crown canopy cover and crown canopy density were all significantly correlated ($P<0.01$) with understory yields with correlation coefficients ranging from -.719 to -.940.

The layers of forest floor accumulation were also correlated with understory herbage yields. The amount of litter accumulation was significantly correlated ($P<0.01$) with understory yields with r values ranging from -.791 to -.838. The amount of duff and duff + litter were significantly correlated ($P<0.05$) with understory yields with correlation coefficients ranging from -.522 to -.704, respectively.

The factors of soil nitrate-nitrogen was not found to be significantly correlated with understory yields.

The relationship of overstory factors and forest floor accumulation with understory yields were best represented by

simple linear equations. Each equation accounted for about three-fourths of the variance in understory production. These equations also illustrated that as overstory and forest floor accumulation increases, understory herbage yields decrease.

The growth rates and growth curves of the major herbaceous species were developed. These growth curves indicated the pattern of precipitation received in July and August influences the growth of blue grama, fringed sagebrush, Arizona fescue and mountain muhly which were growing in natural forest openings. For Arizona fescue and mountain muhly under a pine canopy the precipitation influence was not as strong. In addition, peak herbage production of Arizona fescue under a pine canopy was 716 lbs/acre and in a natural forest opening 1103 lbs/acre. For mountain muhly under a pine canopy peak herbage production was 305 lbs/acre and in a natural forest opening 714 lbs/acre.

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June, 1974

ACKNOWLEDGEMENTS

I would like to express my gratitude to Dr. Pat O. Currie for his advice, encouragement and help throughout my master's program. Thanks are also due to Dr. C. Wayne Cook and Dr. Robert D. Heil for the assistance and suggestion in preparation of my thesis. I am indebted to all the employees of the U.S. Forest Service Rocky Mountain Forest and Range Experiment Station who helped in the collection, analyses and reproduction of the data used in this master's thesis.

I would like to express my special appreciation to my family for their support and aid during my entire college education.

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INTRODUCTION

Approximately 38 million acres of commercial ponderosa pine (*Pinus ponderosa* Lawson) forest plus several million acres of open-grown non-commercial ponderosa pine forest occur in the Rocky Mountains and the West (U.S. Forest Service, 1958). In the state of Colorado 4 million acres of ponderosa pine exist on both public and private lands (Costello and Schwan, undated). The ponderosa pine community contributes to the state's ecology by producing valuable timber, forage for livestock and critical winter range for deer and elk.

Determining the relationship between ponderosa pine overstory and understory plants is basic to a better understanding of the structure and function of the montane ecosystem. Development of management systems and ecological models of the montane zone has been hampered by a lack of information describing the growth and production of understory vegetation as related to overstory and environmental factors.

Studies at the Manitou Experimental Forest have shown that ponderosa pine canopy depresses the production of understory vegetation. In other areas of the West, studies have proven that trees adversely affect the growth of herbaceous plants around them. The objective of this study will be to further investigate this relationship and determine the production and growth rates of the major understory species and isolate some factors influencing their growth.

Information gained from this study will be used by the Rocky Mountain Forest and Range Experiment Station in developing a computer model applicable to the montane zone of the central Rocky Mountains. This model will be used for predicting understory production from overstory factors as well as illustrate some of the interactions of the montane ecosystem. This model should also aid forest and range managers in formulating management systems for the ponderosa pine zone of Colorado.

REVIEW OF LITERATURE

Trees reduce the yield and growth of herbaceous plants beneath them. Clearings in a forest produce more herbaceous biomass than do the adjacent areas with a dense tree overstory because of competition for light, water, and nutrients, and possible antagonistic chemical effects. Herbage production has been related to crown cover, tree basal area of tree litter (Arnold, 1950; Cassady, 1951; Gaines _et al._, 1954; Halls, 1955; Pase and Hurd, 1957; Pase, 1958; Ehrehreich and Crosby, 1960; Moir, 1966; Jameson, 1967; Pearson, 1967; Clary _et al._, 1968; Anderson, 1964; Clary, 1969; Anderson _et al._, 1969; Lacey, 1971; Dodd _et al._, 1972).

Early observers at the Manitou Experimental Forest noted the differences in understory plant densities and yield as related to density of the ponderosa pine overstory. Johnson (1953) found that density of the vegetation on open grassland parks was nearly twice that found in the open timber type. He also noted that vegetative cover was least under dense timber. Grass was the most abundant herbage on grassland parks and open timber, but forbs and litter were more abundant in the dense timber (Johnson, 1953; Smith, 1967).

A recent study conducted by Lacey (1971) at the Manitou Experimental Forest showed correlations between various parameters of the ponderosa pine canopy and the quantities of forage produced. He found significant negative correlations (at 95% level) between understory herbage dry weights and the following timber parameters: crown diameter, crown density, stand height, number of trees before logging, number of live trees, basal area before logging, basal area of live trees, average stand DBH of live trees, average stand height before logging, average stand height of live trees, average stand height of lowest live limb, total cubic feet before logging, and total cubic feet of live trees. Of these many significant variables, the correlation between basal area of live trees and understory yield was the best with a correlation coefficient of -.71.

Moir (1966), in a study of the Pinus ponderosa/Agropyron spicatum association near Spokane, Washington, found that the overstory adversely influenced the herbaceous understory. He noted that herb suppression appears early in the development of pine clusters, especially in the dense sapling stages. This decline in understory herbage is first demonstrated by a reduced inflorescence production of grass species and then later a lessened canopy coverage by the understory plants. Moir (1966) also noted that if the trees continue to develop unchecked by fire or artificial thinning, total or near total absences of herbage may be encountered. He concluded the suppression was due to increased light interception by the pine canopy and the poor soil nitrogen under the trees. Under the densest pine canopies the levels of light drop as low as 20% of full daylight. The subsequent decline in herbage productivity under such conditions can lead to the lessened competitive ability of dominant understory plants growing on all soil types.

In addition, Moir (1966) believed that a nitrogen shortage for growth of understory plants might come about as a result of the increasing contribution of pine litter derived material to the soils organic matter. He explains this shortage with the fact that fresh-cast ponderosa pine needles have only about 0.56% N on a dry weight basis. Compounding this low N content is the decomposition rates of pine litter are generally slow because of the high content of resins, lignins, and other organic compounds generally resistant to chemical breakdown. The author also noted that as long as the C/N raio is high, nitrogen is immobilized by soil microorganisms, so that in litter layers and in the upper part of the mineral soil profile nitrogen deficiencies occur. Moir (1966) further states that ultimate mineralization of humus may take place at rates too slow to provide a satisfactory supply to understory plants. There is evidence that competition for available nitrogen was further increased by tree uptake and dense young clusters of pine acted as a strong nitrogen sink.

Using the light level and soil NO_3-N, Moir (1966) accounted for 93% of the variability in inflorescence production and 59% of the variance in understory plant cover. Thus, he concluded that a developing cluster of ponderosa pine detrimentally influences herbaceous ground cover and under conditions of maximum shading and heavy pine litter there was a total or near-total suppression of understory plants.

Working in immature ponderosa pine stands of the Black Hills of South Dakota, Pase and Hurd (1957) found that production of understory vegetation is related to basal area, crown cover, and litter production of the overstory. For example, air dry herbage yield decreased from 1,660 to 22 pounds per acre when basal area of ponderosa pine increased from 0 to 200 square feet per acre. After basal area reached 140 square feet per acre there was little additional decrease in understory yields as basal area increased from 140 to 200 square feet per acre. The authors found this relationship to be a curvilinear function. They derived a curve for estimating total herbage yield (Y) described by the formula log $Y = 3.22260 - 0.0093X$ where X is the basal area of the pine stand. Total herbage yield and percent crown cover or total herbage yield and pine litter showed a relationship similar to that of the basal area. Pine crown cover ranged from 0 to 71 percent and pine litter accumulation from 0 to 19 tons per acre.

Pase and Hurd (1957) also noted some grass and sedge species are more shade-tolerant than others thus relative importance among species changes as basal area changes.

Cooper (1960) in studies of yields of native and introduced grasses in the ponderosa pine region of east central Arizona on the San Carlos Indian Reservation developed a linear equation of the form, $V = 1600 - 21C$ where V = grass production (lbs/acre) and C = percent crown cover of ponderosa pine. The equation accounted for about 81 percent of the observed variance in grass production. For one species, screwleaf muhly (Muhlenbergia virescens), production declined about 21 pounds per acre with each one percent increase in crown cover of ponderosa pine.

Reynolds (1969) in a study on the Kaibab Plateau of northern Arizona, found that production of understory vegetation decreased gradually as basal area of ponderosa pine increased. He compared the herbage production under mature and immature tree age groups within the same basal area classes and found that herbage production was less under immature stands than it was beneath mature trees.

A number of studies have shown that herbage production decreases as the total amount of forest floor increases (Wahlenberg, et al., 1939; Gaines, et al., 1954; Pase, 1958; Jameson, 1966; Clary et al., 1968). Clary et al. (1968) investigated the relationships between herbage production and the individual layers of a ponderosa pine forest floor on the Beaver Creek watershed in northcentral Arizona. They found that herbage yields decreased from over 300 pounds per acre to less than 10 pounds per acre as total forest floor accumulations increased from essentially zero depth to over 2.5 inches. Furthermore, herbage yield decreased as individual layers of ponderosa pine floor increased. The humus layer or total depth of the forest floor accounted for the most variation in herbage production (R^2 = .61 and .58) compared with either the litter layer (R^2 = .42) or duff layer (R^2 = .44).

McConnell and Smith (1971) found that ponderosa pine needle litter had a significant effect on initial survival of fescue seedlings but that subsequent losses of seedlings undoubtedly resulted from the interaction of many factors. They felt the initial losses were important because they suggest that thick accumulations of needle litter (and its by-products) under dense ponderosa pine canopies may exert a strong selective influence on the eventual composition and cover of understory vegetation.

Herbage yields under thinned and unthinned ponderosa pine was studied by Clary and Ffolliott (1966); McConnell and Smith (1965); McConnell and Smith (1970). All the researchers found that average herbage yield was significantly higher where trees were thinned than on untreated areas. In the case of Clary and Ffoliott's

(1966) study on the Beaver Creek watershed in Arizona, herbage yields for a given basal area were significantly greater when basal areas were less than 70 square feet per acre. The slope of the line for herbage-basal area relationship equation for the thinned stands ($Y = 1355.0 - 606.0 \log X$) was significantly steeper than that for unthinned stands ($Y = 808.0 - 331.4 \log X$).

McConnell and Smith (1965) in northcentral Washington, found that three years after thinning, a linear prediction equation could be used to describe the increase in yield of understory as a function of residual growing area per tree ($r = .796$), percent overstory canopy ($r = -.973$), and basal area ($r = -.943$). McConnell and Smith (1965) also noted that when ponderosa pine canopy exceeded 45 percent, forbs produced more than grasses; below 45 percent, grasses were the superior producers. When these same researchers measured plots ten years after thinning, a positive curvilinear relationship existed between increases in understory yields and residual tree spacing. However, a negative linear relationship was shown between increase in yield of understory vegetation and percent overstory cover.

Reid (1965) found that the long term effect of logging ponderosa pine would be to increase forage yield. He also concludes that regardless of the immediate adverse effects of soil disturbance and heavy slash logging will improve herbage yield and deer and elk habitat.

Studies in other forest types have discovered some of the influences the overstory canopy has on the production of understory plants. On bluestem range in the piney woods of Louisiana and east Texas, herbage production was five to ten times greater under very open savannah-like longleaf pine than on well-stocked plantations or second growth stands of longleaf pine and slash pine (Campbell and Cassady, 1949; Cassady, 1961). In the longleaf pine forests of southern Alabama herbage decreased from 1,000 pounds per acre at zero basal area to 475 pounds at 110 square feet per acre basal area and then increased slightly as basal area increased further (Gaines *et al.*, 1954). These authors found that a polynomial equation provided the best mathematical description and could be used to describe herbage yield as a function of basal area. These researchers also noted that as longleaf pine litter increased understory herbage yields decreased.

Dodd *et al.* (1972) found highly significant correlations between total understory herbage yield and crown cover of Douglas fir (*Pseudotsuga menziesii* Mirb.) stands and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) stands. These authors used equations of the form, $Y = a + bx$ and $\ln Y = a + bx$ to express the relationship between understory production and overstory crown cover. They obtained R^2 values for the Douglas fir stands ranging from .384 to .820 when the linear equation was used and from .423 to .686 for the loglinear equation. In the case of the lodgepole pine stands the R^2 values ranged from .351 to .403 when the linear equation was used and from .466 to .657 for the log linear equation. Dodd *et al.* (1972) concluded that the straight line vs log linear relationship was of little consequence when the regressions were split into stands or classes and the results were expressed in terms of animal-unit months of grazing ungulates.

Anderson _et al_. (1969) in a study of herbaceous understory cover in red pine and white pine stands in northern Wisconsin found that understory in this type was more responsive to the amount of throughfall precipitation. Unlike Moir's results, Anderson _et al_. (1969) found that light levels were apparently above minimum thresholds for species comprising the understory in these pine stands. These authors used a linear equation between herbaceous understory cover and percent of overstory canopy to define the relationship between the understory and pine overstory. This relationship was described by a negative function where herbaceous understory cover decreased as overstory cover increased.

In a mixed conifer forest of northeastern Oregon, dominated by Douglas-fir and ponderosa pine, Hedrick _et al_. (1968) described a highly significant negative relationship between tree crown cover and both herbage cover and yield. These authors also found a significant negative relationship between both timber basal area and stems per plot and understory cover and yield. However, coefficients of determination for these relationships were lower than those for overstory cover and herbage cover and yield. Overstory crown cover accounted for 25.3% of the variability in herbage yield while basal area and stems per plot accounted for 10.2% and 9.4% of the variation, respectively.

The factors that influence the production of understory plants also influence the growth rate of these plants. Pearson (1967) found that apparently the soil temperature determines when herbage growth starts in the spring on northern Arizona pine-bunchgrass ranges. He also found that the rate of Arizona fescue growth from

May through July is related to the precipitation falling in a prior month. Because of the physiological changes brought about by phenology, Pearson concluded flowering was more important than precipitation in regulating growth of Arizona fescue. Growth rate and final height of Arizona fescue were greatest in natural openings and decreased as ponderosa pine canopy cover and basal area increased. When Pearson studied mountain muhly it did not respond to the precipitation during spring and early summer but height growth was apparently related to precipitation during July and August. He did not find that mountain muhly growth rates were related to tree overstory.

There are other important factors that may influence the growth of plants. These factors include precipitation, soil properties and plant litter. At the Manitou Experimental Forest a study revealed that crested wheat yields could be accurately predicted using growing season precipitation (Currie and Peterson, 1966). Similar reports of plant growth in relation to precipitation have been made for other parts of the western United States.

Soil properties may also influence herbage production under some ponderosa pine canopies. Geist (1965) found taht soil chemical factors plus slope and elevation were correlated with herbage production in the Montane Zone of northern Colorado. In comparison, Clary et al. (1966) found that a sample of herbage production on 54 areas supporting timber in Arizona indicated no differences between soil types and topographic position under existing timber stocking conditions. In other words, the overstory canopy had a greater influence over herbage production than did the soil type and topographic position.

In summary, it can be noted that in describing the relationship between the ponderosa pine overstory and the understory plants, most investigators have used basal area, overstory canopy cover, and litter accumulation to develop models or prediction equations. In addition to these important overstory factors researchers have found that such environmental factors as soil properties, precipitation and temperature are important parts of the overstory-understory relationship. When the growth rate of individual understory plants was studied, the overstory along with other environmental factors such as precipitation and temperature were the primary influences on growth rates of the understory plants.

DESCRIPTION OF STUDY AREA

The study area for this investigation is representative of the ponderosa pine-bunchgrass range found in the montane zone in many areas of Colorado. The study site is located on the Maintou Experimental Forest, 28 miles northwest of Colorado Springs, Colorado.

The forest is located in a mountain valley bounded by two north-south mountain ranges, the Rampart Range to the east and the West Creek Range to the west. The major drainage of the valley is Trout Creek which flows north to the South Platte River.

Topography of the area varies considerably within the forest. The study site is located west of Trout Creek and Highway 67 on gently sloping benchlands and drainage ways. The study site where sample plots were located has an easterly aspect.

Three alluvial terraces are found in the Manitou Park Basin (Marcus, 1973). The study site is located on the lowest of these terraces. This terrace is in the oldest stage of physiographic development which has produced the gentle rolling slopes (Marcus, 1973).

Soils within the study are primarily developed from alluvial deposits of Pikes Peak Granite (Marcus, 1973). Common minerals include quartz, orthoclase and microcline with biotite as an accessory mineral (Retzer, 1949). Surface soils are reddish brown in color and vary from 8 to 12 inches in depth. These soils are also low in organic matter and slightly acid with a pH between 6.0 and 6.5 (Currie and Smith, 1970). They are classified as sandy loam to loam with a moderate granular structure with soft consistency when wet, but firm when dry. Surface soils, if disturbed, erode readily. Subsoils, if present, are gravelly-sandy-clay loam or coarsely gravelly loam ranging from 6 to 12 inches in depth. Below this thin layer of soil is the gravelly parent material which ranges in depth from 20 to 60 inches.

The climate at the Manitou Experimental Forest is characteristic of most front range areas in Colorado. Winters are primarily dry and cold for long periods. Summers are mild and most precipitation is received during this season.

Climatological data is recorded at a weather station located at the Manitou Experimental Forest headquarters (7,740 feet in elevation). The station is within 3 miles of the farthest point in the study area. Precipitation records have been maintained since 1937 and temperature records since 1942 (Smith, 1967).

Annual precipitation averages 15.5 inches, but has varied from 7.6 to 23.6 inches. About 25 percent of the annual precipitation falls as snow from late September to late May. On south slopes and level areas, snow usually melts within a few days after falling, but in some extreme winters snow may cover the area for weeks. About three-fourths of the annual precipitation falls as rain between early April and late August. Peak rainfall occurs in July and August.

The average monthly temperature is 41°F and ranges from 23°F in January to 61°F in July. Temperature extremes of -40°F in the winter to 90°F in summer have been recorded at the headquarters weather station. The effective growing season for native vegetation starts in April and continues into October and averages about 180 days (Smith, 1967).

Four vegetation types can be found within the study area. They are: (1) Dense timber - a closed canopy of ponderosa pine and large accumulations of pine litter and sparse understory vegetation; (2) Open timber - an open canopy of ponderosa pine with an understory of herbaceous vegetation and pine litter; (3) Grassland parks - natural openings in the forest that are dominated by native bunch-grasses, uncultivated, and have a minimum diameter of more than 1 chain; (4) Abandoned fields - areas once cultivated, then abandoned, and now slowly returning to native cover (Smith, 1967).

On the study area the timber overstory is exclusively ponderosa pine (*Pinus ponderosa* Lawson). The understory vegetation differs considerably between vegetation types. The dominant perennial grasses are mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.), Arizona fescue (*Festuca arizonica* Vasey), and blue grama (*Bouteloua gracilis* (H. B. K.) Lag.). Other grasses found on the study area are western wheatgrass (*Agropyron smithii* Rydb.), pine dropseed (*Blepharoneuron tricholepis* (Torr.) Nash.), little bluestem (*Andropogon scoparious* Michx.). Parry oatgrass (*Danthonia parryi* Scribn.), junegrass (*Koeleria cristata* (L.) Pers.), Kentucky bluegrass (*Poa pratensis* L.), needle and thread (*Stipa comata* Trin. and Rupr.) and sleepygrass (*Stipa robusta* (Vasey) Scribn.). Sedges (*Carex* sp.) were found in all vegetation types. Common forbs include western yarrow (*Achillea lanulosa* Nutt.), Fendler sandwort (*Arenaria fendleri* A. Gary), geranium (*Geranium parryi* (Engelm.) Heller), cowpea (*Thermopsis divaricarpa* A. Nels.), prairie cinquefoil (*Potentilla pensylvanica* L.), trailing fleabane (*Erigeron flagellaris* Gray), lambsquarter goosefoot (*Chenopodium album*, L.), lupine (*Lupinus* sp.), locoweed (*Oxytropis* sp.), and vetch (Astragalus sp.). The half-shrub fringed sagebrush (Artemisia frigida Willd.) was also common on the study area. Bearberry (Arctostaphylos uva-ursi (L.) Spreng.) was the dominant shrub. Other shrubs found on the study area included mountain mahogany (Cercocarpus montanus Raf.) and bush cinquefoil (Potentilla fruiticosa L.).

The study site has a history of multiple use planning. A sustained yield timber management plan along with thinning and pruning to control dwarf mistletoe is being developed. The unevenaged stand with scattered slash piles and stumps is the result of selective timber harvests conducted during the winters of 1967-68 and 1968-69. On 784 acres of the timbered area approximately 20% of the trees were removed, yielding a net volume of 2.829 million board feet (Lacey, 1971).

A grazing intensity study was conducted on the study site, from 1940 through 1958. The three grazing intensities on the six fenced experimental ranges were: light, 10-20% utilization of the production of perennial grasses and sedges; moderate, 30-40%; and heavy, more than 50% use of the plants. During the study plant cover increased on lightly grazed ranges, did not change on moderately grazed ranges and was reduced on heavily grazed ranges (Smith, 1967).

After 1958 grazing on the study area varied annually from non-use for some parts to moderate on others. In 1964 a study to compare cattle gains under rotation and season long grazing was started. For this grazing study five of the original experimental ranges were subdivided into 12 pastures. The one remaining pasture was used in a study to determine what combination of grazing season, herbicide and fertilizer was best to promote range recovery. The grazing on the range recovery study was terminated in 1971.

METHODS AND PROCEDURES

Sampling System

Sample Plots

The field work was started in June, 1972, by locating 14 permanent sample plots. These plots were selected to represent the natural gradient of ponderosa pine density plus natural forest openings (Figures 1, 2 and 3). The sample plots were located in 3 pastures that would not be subjected to grazing until after herbage measurements were completed in 1972 or not grazed at all. Three plots were established in natural forest openings in each of the 3 pastures. The remaining 11 sample plots were established under various timber canopy densities. All plots were similar in that they were: (1) at least .25 acre in size; (2) relatively undisturbed by logging and other soil disturbances; (3) fairly unevenaged ponderosa pine and relatively free of recently occurring natural factors (fire, insects, disease, and windthrow); (4) representative of the same soil and topography. Each plot was represented by a homogeneous understory. Homogeneity of understory was stressed to reduce within-sample plot variation and maximize the between sample plot variation.

Selection of sample plots was done on the basis of basal area of ponderosa pine and homogeneity of the understory vegetation. The point sampling method described by Kulow (1965) was used to estimate plot basal area. This method employs a small prism for a fast visual estimate of basal area. The homogeneity of the understory vegetation was determined by visual survey of each plot. Sample

Figure 1. View of sample plot 40 located in a natural forest opening of native vegetation.

Figure 2. View of sample plot 50 located under an open ponderosa pine canopy (Basal area 43 ft^2/acre and crown canopy density 53%).

Figure 3. View of sample plot 21 located under a dense ponderosa pine canopy (Basal area 91 ft^2/acre and crown canopy density 78%).

plots were selected this way to assure a range of overstory densities with comparable understory vegetation.

Sample plots ranged in size from .25 acre to .98 acre, depending on the number and distribution of the trees along with the homogeneity of the understory. Plots of this size were small enough to allow detailed measurements of the understory, yet large enough that a definite relationship between the overstory and understory should exist (Lacey, 1971). Each sample plot boundary was carefully surveyed and a steel post was used to mark the southwest corner, and wooden stakes were used to mark the remaining corners.

Subplots

Two hundred and fifty subplots were systematically selected on each sample plot. The 1-by-2 foot subplots were used to estimate herbage yields with the Heterodyne Vegetation Meter. The sampling intensity of 250 subplots per sample plot was determined by Lacey (1971) in an earlier Manitou study to find optimum sampling intensity. Two hundred subplots were permanently marked by placing four golf tees at the points where the four support legs of the herbage meter would contact the ground (Figure 4). Also a numbered plastic ribbon was attached to a subplot golf tee for identification and location purposes. By marking the plot in this manner the herbage meter could be placed on the same subplot location each time yield estimates were made. The remaining fifty subplots on each sample plot were to be clipped and were only marked by a single golf tee or small flag. In each plot the subplots were located on 14 parallel pace transects, running north and south. Starting from 3 to 7 steps inside the southwest corner, subplots were located at a uniform interval along

Figure 4. View of subplot 126 marked with golf tees at the points where the four support legs of the herbage meter contact the ground.

the line transects. This uniform interval was either 3, 5 or 7 steps depending upon the size of the plot. The subplots were part of a double sampling system where all subplots were read with the herbage meter and every fifth subplot (number 5, 10, 15, etc.) was clipped and weighed.

Growth Plots

In June of 1973, six growth plots were established to study the growth of individual understory species. These growth plots were used to monitor the growth of understory species in the following categories:

1. Blue grama in natural opening
2. Fringed sage in natural opening
3. Arizona fescue in natural opening
4. Arizona fescue under ponderosa pine canopy
5. Mountain muhly in natural opening
6. Mountain muhly under ponderosa pine canopy

The growth plots were located in areas protected from grazing during the study. The plots in natural openings contained relatively pure stands of the individual species to be monitored. The plots under the pine canopy contained a mixed stand of Arizona fescue and mountain muhly. Within each growth plots 25 subplots were used to estimate herbage production with the Heterodyne Vegetation Meter. Twenty subplots in each growth plot were marked by 4 golf tees and plastic ribbon at the 4 corners where the support legs of the herbage meter contacted the ground. Wooden stakes with numbered metal tags were placed 8 inches from the southwest corner of each subplot for location and identification at a later date. In each subplot unwanted plant species were removed so that each subplot contained only the one species to be monitored. Also plants that were outside the subplot that would extend into the range of the herbage meter sensing probes were trimmed away. During each weekly sampling date, 5 subplots were selected for a meter estimate and clipping to use for determining weight by the double sampling procedure.

Data Collection

Data collected during the study included: (1) herbage measurements from each sample plot and growth plots; (2) timber overstory measurements from each sample plot and growth plot; (3) litter measurements from each sample plot; (4) collection of soil samples for nitrogen determinations. Procedures used for collecting this data are discussed below.

Herbage Production

Herbage production estimates were obtained with the aid of the Neal Electronics Model 18-1000 Herbage Meter, using the technique reported by Lacey (1971). In 1972 three herbage production estimates were made for the months of June, July and August on each sample plot.

The collection of herbage meter data was started by zeroing the herbage meter when it was in place on its transporting box by adjusting the digital readout to zero. The herbage meter was zeroed at the start of each sample plot and rezeroed after every 20 readings or if the operator suspected any drift in the meter reading. After zeroing the meter was placed on a subplot, with the four support legs resting on the four golf tees marking the subplot. The subplot capacitance was estimated by pressing the read button and recording the digital readout on the light emitting diode display (Figure 5).

The double sampling system employed for herbage production estimates used a systematic clipping of every fifth subplot. On each subplot to be clipped, the procedure described by Lacey (1971) for Manitou and used on other studies with the meter was followed (Currie et al., 1973). After the capacitance reading was recorded a 24 inch steel pin was staked at each corner of the herbage meter to mark the space in the subplot (Figure 6). The vegetation extending beyond the effective range of the meter probes was clipped and discarded. The herbage meter was removed from the subplot and a metal quadrat placed around the pins. Vegetation was clipped 1/2 inch above the ground level. Species were clipped and bagged separately as follows: Arizona fescue, blue grama, mountain muhly, sedges, fringed sagebrush, bearberry, other grasses, and forbs. Samples were oven dried between 100°C and 105°C for a period of 24 hours (National Academy of Sciences and National Research Council, 1962, p. 40). To avoid clipping the same subplot location twice in 1972 or again in 1973, subplots were arranged in a non-overlapping pattern. The oven dry weights by species and total herbage was recorded. Also, each time a plot was sampled in 1972 the average maximum leaf height and stage of phenological development was recorded for Arizona fescue, blue grama, mountain muhly and fringed sagebrush.

The herbage meter was used to estimate herbage yields of individual plant species on permanent growth plots. Each subplot

Figure 5. Estimating herbage yields on a subplot with the Model 18-1000 Herbage Meter.

Figure 6. Staking a clipped subplot with steel pins.

in the growth plot study was read with the herbage meter every week beginning July 2, 1973 and ending September 11, 1973. The procedure described previously was used with the exception that all unwanted plant species were removed from the subplots and the vegetation on the subplot border trimmed. This weeding and trimming was employed to reduce outside interference and to assure only the selected species was being measured by the herbage meter.

A double sampling system was again used to estimate the species yield on the growth plots. After the 20 permanent subplots were estimated by the meter an additional 5 subplots were selected to be meter-estimated and clipped. The clipped subplots were weeded and trimmed before the herbage meter was used to obtain a meter estimate of species yield. After the capacitance reading was recorded the subplots were then clipped to a 1/2 stubble height. The green weights and the oven-dry weights of the individual subplot species were recorded.

Overstory

Overstory parameters were measured on each of the 14 sample plots. Trees taller than 4.5 feet were counted and identified by nailing a numbered metal tag to each tree. Diameter tapes were used to measure the diameter breast high (DBH) of each numbered tree to the nearest 1/10 inch. A standard computer program (developed by the Rocky Mountain Forest and Range Experimental Station) was used to calculate the basal area (square feet per acre) on each plot.

The spherical densiometer method described by Strickler (1959) was used to measure density of the crown canopy (Figure 7). This

Figure 7. Using the permanent plot method to determine the crown canopy density with the spherical densiometer.

method is well adapted for permanent plot work and eliminates point duplication bias of other methods. Crown canopy cover was also measured with a "moosehorn" using the method described by Garrison (1949), with the exception that 125 readings were systematically taken and averaged to derive the crown canopy cover (Figure 8). Both crown canopy density and crown canopy cover are expressed as a percentage. The terms canopy density and canopy cover were simply used for easy differentiation of the methods.

Litter

Pine litter was measured on the 11 timbered plots and herbaceous litter was measured on the plots in the natural openings. Pine litter production was determined with the aid of Dr. Michael Fosberg using a procedure developed at Rocky Mountain Forest and Range Experimental Station as part of the National Fire Danger Rating System. In using Fosberg's technique the depth of the litter layer and duff layer was measured along transect lines between trees (Figure 9). The number of measurements varied from 40 to 80 depending on plot size. The depth in inches for each layer was then multiplied by the bulk density (previously determined by Dr. Fosberg) of the respective layer to obtain the weight of litter and duff on each plot. This calculation was done with the aid of a computer program developed by Dr. Fosberg and gave results in pounds per acre of litter, duff and litter plus duff for each plot. The herbaceous litter was determined by collecting litter from 50 systematically placed 1 by 2 foot subplots on each of the 3 plots in natural openings. The litter was oven dried between 100°C and 105°C for a period of 24 hours

Figure 8. Using the "moosehorn" to determine crown canopy cover.

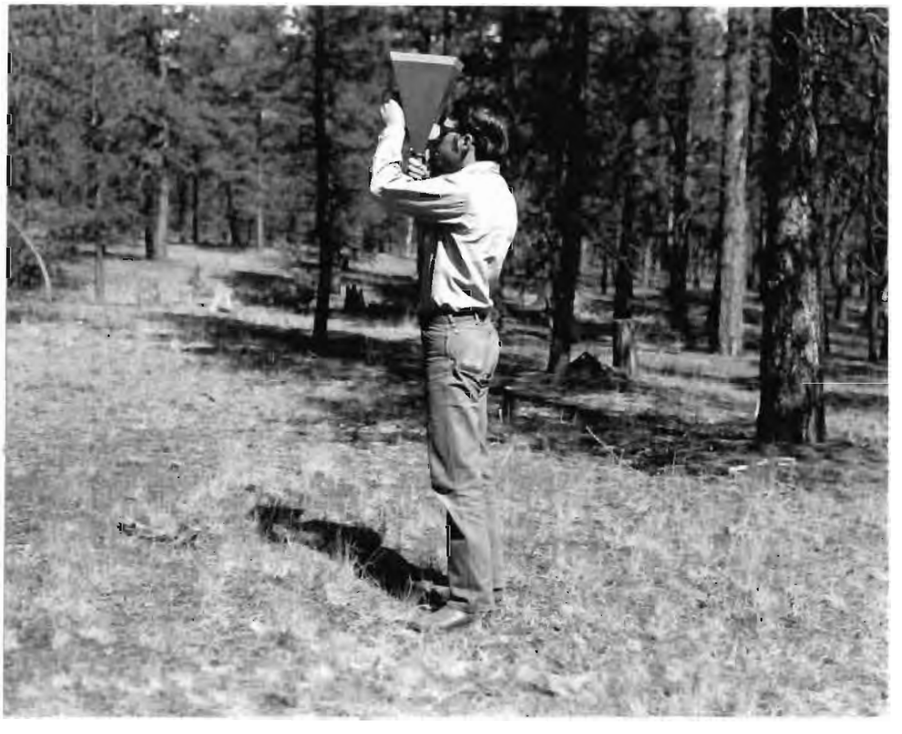


Figure 9. Measuring the depth of litter and duff layers along transects to determine amount of forest floor accumulation.

(National Academy of Science and National Research Council, 1962, p. 50). Litter was also expressed in pounds per acre.

Soil Samples

Soil samples were collected from each plot in June of 1973 for determination of soil nitrate-nitrogen. Six random samples from the top 4 inches of soil on each plot were collected. The samples were air-dried and screened through a 2mm sieve and the percent coarse material calculated. Three screened samples from each plot were analyzed for soil nitrate-nitrogen by the Soil Testing Laboratory at Colorado State University. The three remaining samples were retained in the event extra analyses was needed. The soil nitrate-nitrogen value was corrected for percent coarse material in the sample and expressed in parts per million.

Analysis

Analysis of the data was divided into four parts. The production of understory herbage was handled with a double sampling computer program developed for use with herbage meter data. The second part was concerned with use of correlation analysis to select the significant independent variable correlated with understory production. In the third part, regression analysis was employed to develop herbage yield prediction equations from information derived in part 2. The regression analysis used, included simple linear equation, optimum transformation regression and multiple linear regression. The development of the individual species growth curves made up the fourth part of the analysis. Each part of the analysis was carried out using computer programs developed by the Rocky Mountain Forest and Range Experimental Station or programs available at the Colorado State University Computer Center.

RESULTS AND DISCUSSION

Herbage Production

There was a substantial difference in the amount of understory herbage produced between the 1972 and 1973 growing seasons. The understory herbage produced in 1973 was nearly twice as much as that produced in 1972. This difference in herbage production between 1972 and 1973 may be due to the amount of rain received in the spring and early summer. During the period April through July, 1972 only 6.38 inches of precipitation were received, while for the same period in 1973, 11.28 inches of precipitation were measured.

The understory production for the three sample periods in 1972 showed a variety of responses. On some sample plots there was a slight increase of understory herbage between June and August, while on other sample plots there was a slight decrease. Because most of these changes were relatively small, the overall trend was that production remained nearly the same during all periods. This trend can possibly be explained by the fact that as grass production increased from June to August forb production decreased. This trend may also be due to the below average precipitation (1.82 inches) received in July, which is normally the month of peak rainfall (3.20 inches).

Correlation Analyses

Herbage yields from Table 1 were used as dependent variables in the correlation analyses. The independent variables considered in this analyses included overstory parameters (Table 2), amounts

Table 1. Herbage production of sample plots for the sample periods in 1972 and 1973. (pounds per acre oven dry weight)

	1972			1973
Sample Plot	June	July	August	August
21	70	56	35	125*
23	92	52	69	162*
37	365	347	348	748
40	581	532	465	977*
41	354	381	474	1019
42	263	199	362	778
43	209	204	204	439
44	137	175	206	443
45	657	620	587	1262
46	393	496	449	965
47	347	407	403	866
48	224	161	143	307
49	91	164	125	269
50	224	185	160	336*

*ungrazed in 1973

Table 2. Overstory parameter data points used in correlation analyses.

Sample Plot	Trees/acre	Basal Area (ft^2/acre)	Crown canopy Density (%)	Crown canopy Cover (%)
21	156	90.6	78	44
23	136	84.2	73	44
37	77	55.0	40	21
40	0	0.0	0	0
41	0	0.0	0	0
42	59	38.5	46	21
43	92	60.3	42	24
44	102	65.6	35	26
45	0	0.0	0	0
46	37	26.7	29	13
47	78	52.7	41	23
48	138	65.1	51	35
49	110	86.7	66	39
50	68	42.9	53	28
37a[1/]	75	53.2		
47a[1/]	62	48.1		

[1/] The basal area and trees/acre of plots 37 and 47 changed from 1972 to 1973.

of litter and duff (Table 3) and soil nitrate-nitrogen (Table 4). Correlation coefficients and log transformation for basal area and trees/acre were calculated using the BMD03D correlation program developed by the Health Science Computing Facility at U.C.L.A. The results of analyses between understory herbage production and the various independent variables are presented in Table 5.

All overstory parameters were significantly correlated ($P<0.01$) with understory production for all periods in 1972 and 1973. Crown canopy cover had the highest correlation coefficient (-.940) with understory production measured August of 1972. The transformed variables, log (basal area) and log (trees/acre) proved to have the lowest correlation ($r = -.719$ and $r = -.725$) and for that reason were dropped from the correlation analysis of the 1973 data. There was a slight trend for the untransformed overstory variables to have higher correlations with the understory production measured in August. The correlation coefficients between overstory variables and understory production measured in August 1973 were very similar to those calculated for 1972 August data. These results concur with the findings of Hedrick et al. (1968) in which he found that overstory crown cover basal area, and stems per plot had a high significant negative correlation to understory cover and yield. Also in Hedrick's et al. (1968) study, crown cover proved to have the highest correlation coefficient. Cooper (1960) found a significant correlation coefficient ($r = -.90$) between ponderosa pine crown cover and understory forage production. Dodd et al. (1972) found that the correlation coefficient between Douglas fir crown cover and understory production was $r = -.93$ for some locations studied in British Columbia, Canada.

Table 3. Amounts of litter and duff on each sample plot evaluated for correlation analyses.

Sample Plot	Litter (lbs/acre)	Duff (lbs/acre)	Litter plus Duff (lbs/acre)
21	17,915	36,901	54,816
23	19,717	36,373	56,090
37	19,192	50,649	69,841
40	573	0	573
41	1,562	0	1,562
42	10,415	27,106	37,521
43	15,177	37,074	52,251
44	17,171	29,574	46,745
45	570	0	570
46	11,699	41,383	53,081
47	10,263	43,082	53,345
48	15,702	36,732	52,434
49	19,888	44,000	63,888
50	13,568	29,056	42,624

Table 4. Mean soil nitrate-nitrogen in top four inches of soil evaluated for correlation analyses.

Sample Plot	Soil nitrate-nitrogen (p.p.m.)
21	1.00
23	1.00
37	1.00
40	.66
41	1.00
42	1.00
43	1.00
44	1.33
45	1.00
46	1.00
47	2.00
48	2.00
49	1.00
50	.33

Table 5. Correlation coefficient values relating understory herbage yield to independent variables for unevenaged ponderosa pine.

Independent Variable	Correlation coefficients (r)			
	1972			1973
	June	July	Aug.	Aug.
Basal area	-.888**	-.852**	-.901**	-.907**
Log (Basal area)	-.778**	-.719**	-.727**	---
Trees/acre	-.862**	-.879**	-.918**	-.927**
Log (Trees/acre)	-.780**	-.725**	-.732**	---
Crown canopy cover	-.894**	-.893**	-.940**	---
Crown canopy density	-.869**	-.867**	-.897**	-.890**
Litter	-.838**	-.791**	-.836**	-.835**
Duff	-.625*	-.522*	-.577*	---
Litter and Duff	-.704*	-.615*	-.668*	---
Soil nitrate-nitrogen	-.110	-.052	-.031	---

**Significant at the 1 percent level

* Significant at the 5 percent level

--Not calculated

Negative correlations were also found between the amounts of litter and duff and understory production. For these variables, litter was more highly correlated with understory production than duff or duff and litter together. The values were litter (r = -.838); duff (r = -.625); and litter and duff (r = -.704). The correlation coefficients for litter with understory production were significant at the 1 percent level but r values for duff or litter and duff were only significant at the 5 percent level. These independent variables tended to be the more highly correlated with understory production measured in June than any other period during the year. This negative relationship between forest floor accumulation and herbage production concurs with results found by previous workers (Wahlenberg et al., 1939; Gaines et al., 1954; Pase, 1958; Jameson, 1967; Clary et al., 1968).

Soil nitrate-nitrogen proved to be poorly correlated with understory herbage yields. Correlation coefficients between soil nitrate nitrogen and understory production measured in June, July and August of 1972 were -.110, -.052, and -.031, respectively. None were significant at the 5 percent level. These results do not concur with the relationship that Moir (1966) found. The difference in response is probably due to the large differences between site and soils characteristics investigated in the two studies.

Production of understory vegetation has been shown to relate to several overstory factors and accumulation of litter. As the number of trees per acre, basal area, crown cover, and crown density of the ponderosa pine canopy increases the amount of understory herbage decreases. This same negative relationship exists between forest accumulation of litter and duff and understory production.

Because of competition for light, water, and nutrients, and possible antagonistic chemical effects, this negative relationship is entirely reasonable and has been reported in the literature. A few examples are the ponderosa pine ranges of South Dakota (Pase, 1958); Oregon (McConnell and Smith, 1965); Colorado (Lacey, 1971); Arizona (Reynolds, 1962; Pearson, 1964; Clary et al., 1966; and Jameson, 1967); southern pine ranges (Gaines et al., 1954; Halls, 1955); Douglas fir/lodgepole (Dodd et al., 1972); red and white pine (Anderson et al., 1969); and hardwood areas in Missouri (Ehrenreich and Crosby, 1960). Both Moir (1966) and Anderson (1964) have found that light is a major factor affecting the production of understory vegetation. In the case of competition for moisture and nutrients Geist (1965) noted that a moderate amount of grass roots do occur in the ponderosa pine rooting zone and that the large number of lateral tree roots would indicate that the pines are probably dominating the uptake of nutrients and moisture.

Regression Analyses

The variables that were significantly correlated ($P<0.01$) with understory yields in the correlation analyses were used to develop simple linear prediction equations of the form $Y = A + B(X_i)$. These equations were calculated with the aid of the TWOPLOT and DUBSAM computer programs developed by the Rocky Mountain Forest and Range Experiment Station. The overstory variable crown canopy cover was not used in the regression analyses because it and crown canopy density are measures of the same overstory parameter and the method used to measure crown canopy density was found to be the most efficient in terms of time and accuracy. The prediction equations for understory herbage production for all periods during 1972 and 1973 are listed in Table 6 along with their respective coefficients of determination and standard error of estimate.

All prediction equations accounted for approximately two-thirds or more of the variation in understory yield. Basal area accounted for the most variation (78.9%) of the understory yield measured in June of 1972. The most variation (75.7%) of understory production measured in July of 1972 was accounted for by trees/acre. For estimating understory herbage yields measured in August of 1972 and 1973 trees/acre accounted for 84.3% and 85.9% of the variation of herbage yield measured during these respective dates. The amount of litter accumulation accounted for the least amount of variation in understory production, but for all dates sampled it accounted for at least 62.6% of the variation in understory yields. The important point to note is that the same independent variables accounted for almost the same amount of variation in understory production for August of 1972 and 1973 even though yield estimates in 1973 were nearly twice those of 1972. This indicated that the various independent variables can prove helpful in predicting understory production from year to year by adjusting changes in production with respect to precipitation.

Even though the relationship between the overstory variables and litter accumulation seems to be best represented by a linear regression model a computer program was used to investigate possible curvilinear relationships. This program (REGTRAN) was developed by Carl Edminster of the Rocky Mountain Forest and Range Experiment

Table 6. Equations for predicting understory herbage production (Y = lbs/acre) for all periods sampled in 1972 and 1973.

Period	Year	R^2	Standard Error	Equation
June	1972	.745	25.0	$\hat{Y}$ = 507.3 - 2.9 (trees/acre)
July	1972	.757	24.6	$\hat{Y}$ = 510.0 - 3.0 (trees/acre)
Aug.	1972	.843	19.2	$\hat{Y}$ = 518.9 - 3.1 (trees/acre)
Aug.	1973	.859	38.3	$\hat{Y}$ = 1096.2 - 6.5 (trees/acre)
June	1972	.789	22.7	$\hat{Y}$ = 524.2 - 5.0 (basal area)
July	1972	.726	26.2	$\hat{Y}$ = 515.5 - 4.8 (basal area)
Aug.	1972	.812	21.0	$\hat{Y}$ = 525.1 - 5.0 (basal area)
Aug.	1973	.823	42.9	$\hat{Y}$ = 1109.4 - 10.6 (basal area)
June	1972	.755	24.8	$\hat{Y}$ = 524.1 - 5.9 (crown density)
July	1972	.752	24.7	$\hat{Y}$ = 523.7 - 5.8 (crown density)
Aug.	1972	.792	22.5	$\hat{Y}$ = 529.4 - 6.1 (crown density)
Aug.	1973	.794	46.4	$\hat{Y}$ = 1113.5 - 12.8 (crown density)
June	1972	.702	26.9	$\hat{Y}$ = 549.2 - .0212 (litter)
July	1972	.626	30.6	$\hat{Y}$ = 535.6 - .0203 (litter)
Aug.	1972	.699	26.5	$\hat{Y}$ = 545.6 - .0208 (litter)
Aug.	1973	.697	56.0	$\hat{Y}$ = 1163.2 - .0438 (litter)

Station. The object of this program is to help select the optimum transformation of the independent variables used for regression analyses. The program used a transformation equation of the form:

$$X' = \frac{X^T - 1}{T}$$

In the equation X was the various values of independent overstory and litter variables and X' the new transformed values. The T term was systematically varied (in tenths) from -2.0 to 2.0. The program calculated the new regression equation of the form $Y = A + B(X')$ and correlation coefficient for each change in T. When $T = 1.0$ the relationship between the independent variable and understory herbage yield was assumed to be a linear function.

After subjecting each of the overstory variables; trees/acre, basal area, and crown density and litter accumulation to the various transformations, it was concluded that the relationship between these variables and understory yield was a simple linear relationship (Figures 10, 11, and 12). This linear relationship between overstory variables and understory yield has also been found by Cooper (1960); Moir (1966); Anderson et al. (1969); and Dodd et al. (1954). Many of the curvilinear models fit observed relationships because herbage production generally tends to decrease and then level off under the denser canopies (Gaines et al., 1954; Halls, 1955). This may indicate the canopies investigated by this study were not as dense as those found to show a curvilinear relationship.

In addition to the specialized program described above, a stepwise multiple linear regression program was used to formulate a

Figure 10. Regression of basal area of ponderosa pine against the understory herbage production. Herbage yields were measured in August 1972 and 1973.

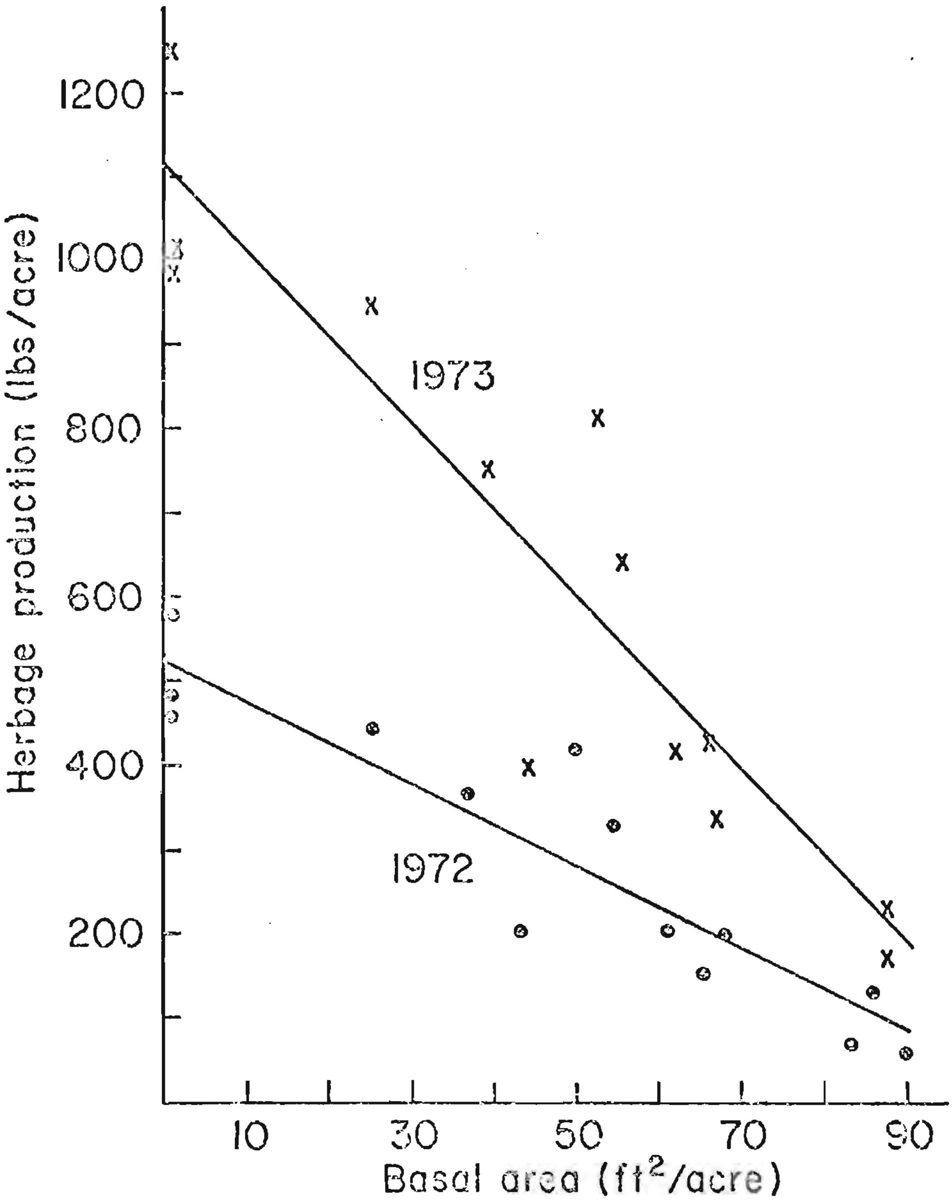

1200
1000
800
600
400
200
Herbage production (lbs/acre)
1973
1972
10
30
50
70
90
Basal area (ft² /acre)

Figure 11. Regression of crown canopy density of ponderosa pine against the understory herbage production. Herbage yields were measured in August 1972 and 1973.

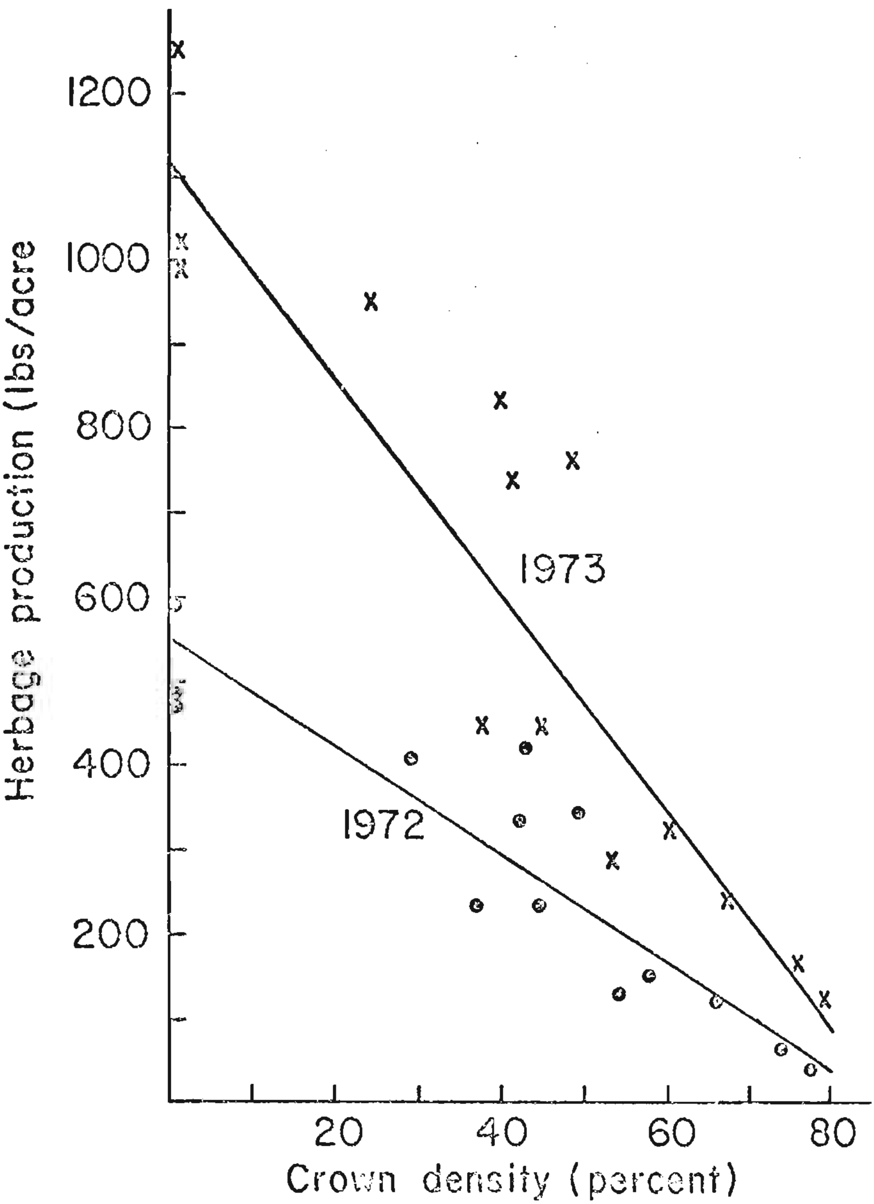
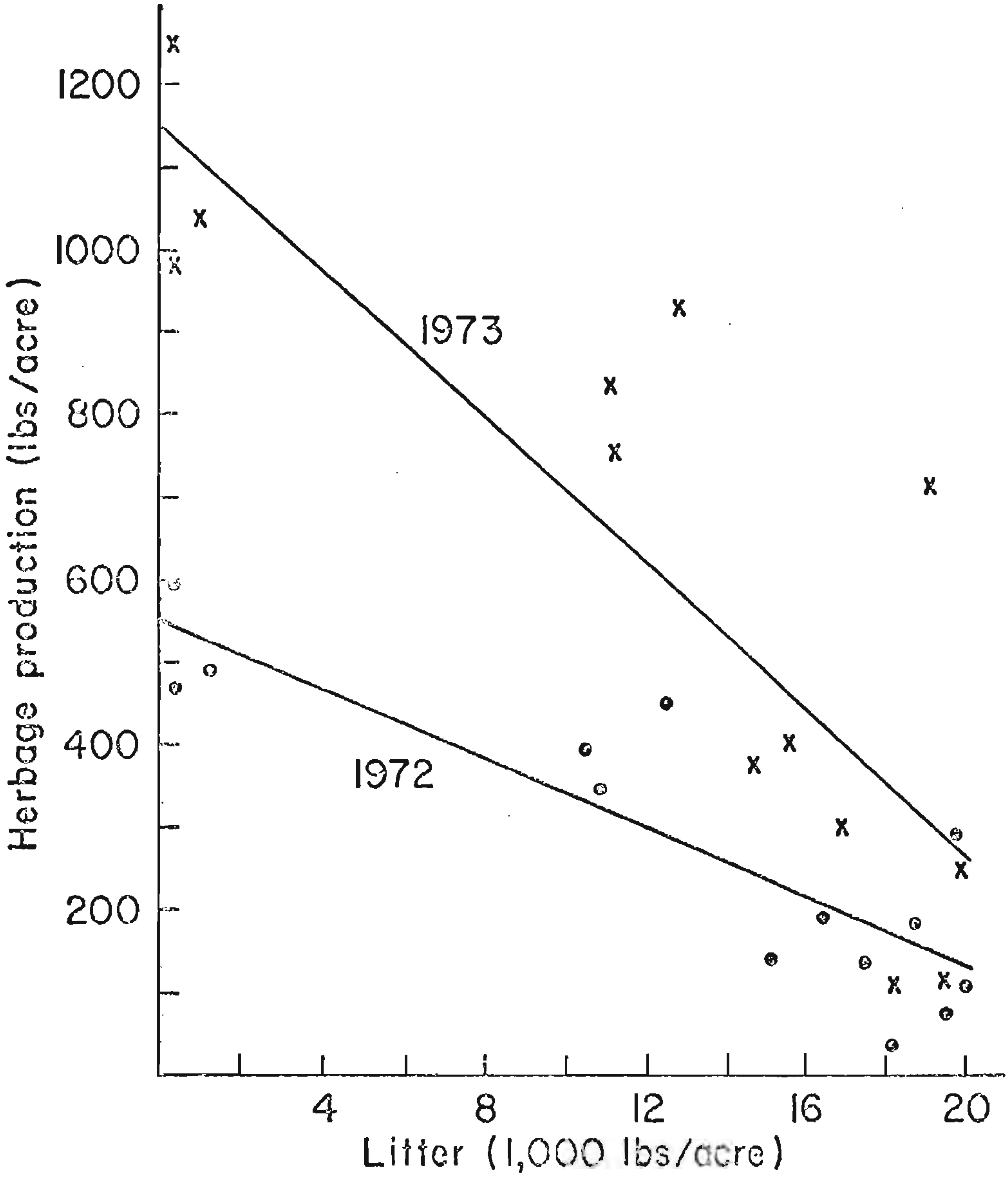

Herbage production (lbs/acre)
1200
1000
800
600
400
200
20
40
60
80
Crown density (percent)
1973
1972

Figure 12. Regression of litter accumulation against the understory herbage production. Herbage yields were measured in August 1972 and 1973.



Herbage production (lbs/acre)
1200
1000
800
600
400
200
1973
1972
4
8
12
16
20
Litter (1,000 lbs/acre)

understory production prediction equation. The program used was STAT38R from the Colorado State University Statistical Laboratory. This stepwise program started with a simple correlation matrix and entered into the regression equation the independent (X) variable most highly correlated with the response in understory herbage production (Y) when considered along with all other independent variables. Then using partial correlation coefficients the program selected the next variable (X) to enter the regression equation and in a stepwise manner continued to select or reject independent variables according to partial correlation values and partial F values. In using this procedure the assumption that all (X) variables are independent of each other is violated because all overstory, litter and duff variables are significantly correlated ($P<0.01$) with each other.

When this stepwise procedure was used to predict understory yields measured in August 1972 the only variable entered into the equation was trees/acre. This variable accounted for 84.3% of the variation in understory yield measured in August 1972. No other variables could be significantly ($P<0.01$) entered into the equation. When the control status of the program was changed to enter more independent variables little additional variation in understory yield was accounted for by the consideration of more independent variables. The entry of crown density and basal area into the equation accounted for only an additional 1.88% and .0003% of the variation in understory production, respectively, compared to trees/acre alone.

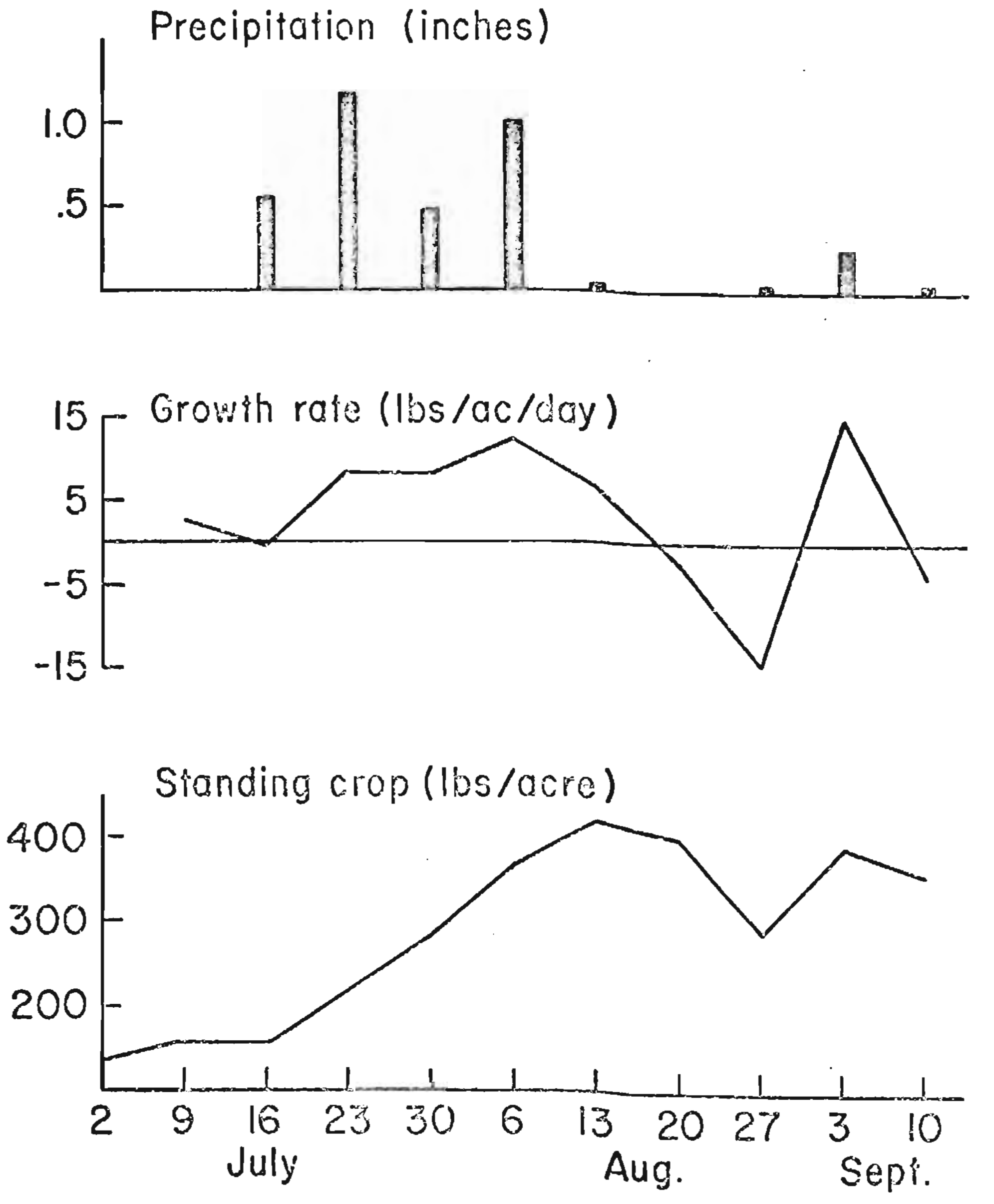
The relationship between the independent variables is best represented in Figures 10, 11 and 12. A figure representing the relationship between trees/acre and understory herbage yield in 1972 and 1973 was omitted because it is very similar to Figure 10. Also, most investigators prefer using basal area because it gives them an idea of both numbers and size of trees where trees/acre does not.

Growth Curves

A double sampling program was used to determine the standing crop for each species on each date sampled. These estimates were then used to develop a growth curve for each species. A growth rate for each species and time was calculated by dividing the amount of herbage produced during a time period by 7 days in each time period. This made it possible for positive and negative growth rates to result.

Blue grama in natural opening--The mean standing crop of blue grama in a natural forest opening at each date sampled in 1973 is given in Figure 13, along with the growth rate and precipitation for the period between each sampling date. Blue grama standing crop increased from a starting value of 141.6 lbs/acre on July 2 to a peak value of 418.7 lbs/acre on August 13 then decreased to 289.5 lbs/acre on August 27 with another peak at 396.1 lbs/acre on September 3. The growth rates show a similar pattern with peaks of 12.9 lbs/acre/day and 15.2 lbs/acre/day for the periods ending August 6 and September 3, respectively and a low growth rate of -15.7 lbs/acre/day for the period ending August 27.

Figure 13. Relationships of blue grama production (mean of all subplots) and growth rates with precipitation in 1973.



Precipitation (inches)
1.0
.5
Growth rate (lbs/ac/day)
15
5
-5
-15
Standing crop (lbs/acre)
400
300
200
2
9
16
23
30
6
13
20
27
3
10
July
Aug.
Sept.

On the date peak standing crop was measured the peak for the maximum leaf height also occurred. On August 13 blue grama reached a peak maximum leaf height of 4.0 inches.

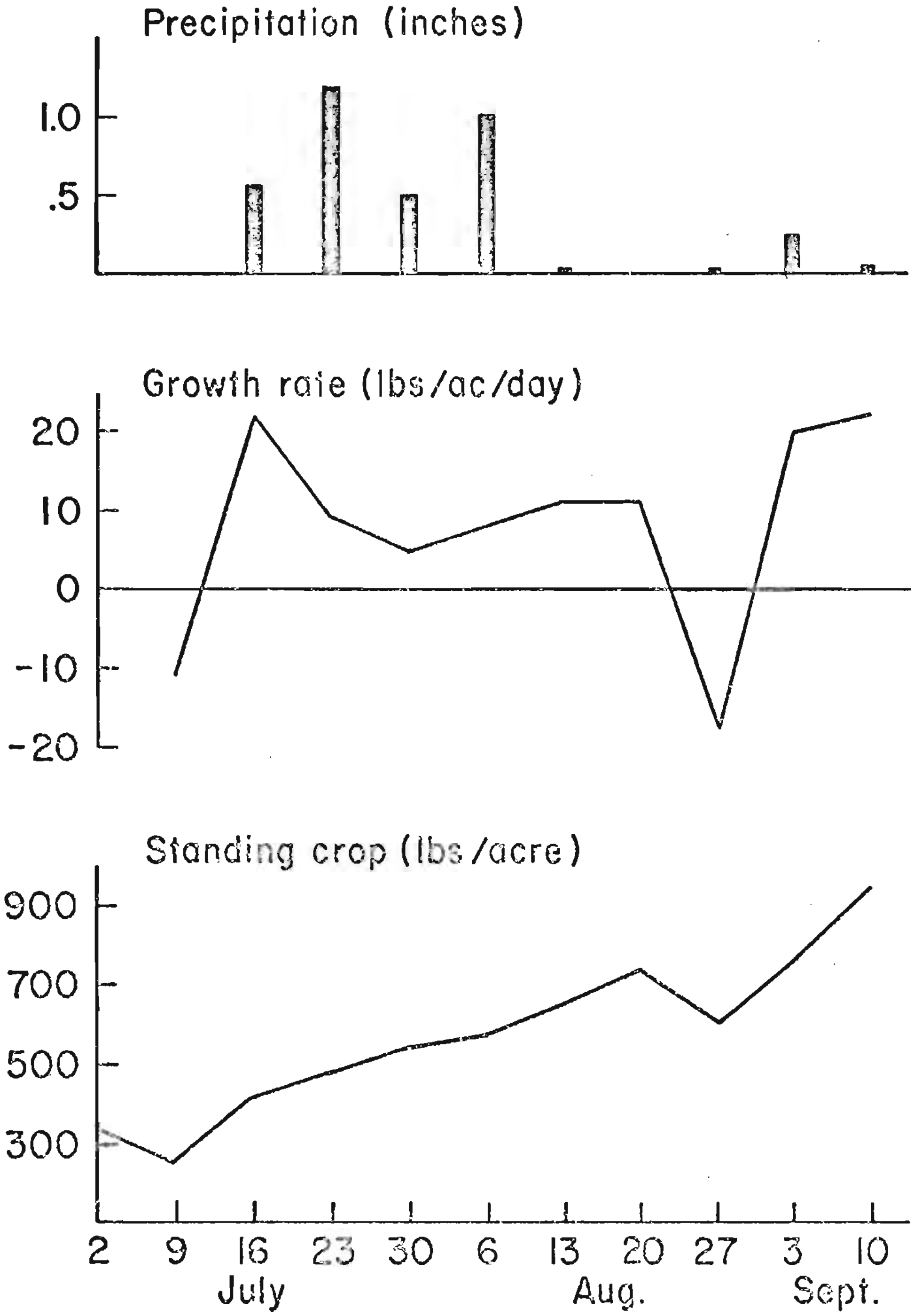
During the periods when the growth rates decreased blue grama seedheads appeared and anthesis occurred.

The pattern of blue grama growth seemed to correspond to the pattern of precipitation received during the period. The periods of increasing standing crop and positive growth rates corresponded to the periods when adequate precipitation was received. During the periods when standing crop and growth rates declined almost no precipitation was measured. The .25 of an inch of rain received during the period between August 27 and September 3 was accompanied by a spurt of blue grama growth.

This relationship between growth pattern and precipitation pattern compares favorably with the results of Smoliak (1956), Bement (1968) and Uresk (1971). These investigators found a close relationship between precipitation and peak standing crop on shortgrass rangelands. Bement (1968) found that surges in blue grama growth was the result of adequate intermittent precipitation in association with suitable summer temperatures.

Fringed sagebrush in a natural opening--The mean standing crop of fringed sagebrush in a natural forest opening at each date sampled in 1973 is given in Figure 14 along with the growth rate and precipitation for the period between each sampling date. Fringed sagebrush standing crop increased from a starting value of 339.5 lbs/acre on July 2 to a peak value of 926.2 lbs/acre on September 10. The periods ending July 9 and August 27 show

Figure 14. Relationships of fringed sagebrush production (mean of all subplots) and growth rates with precipitation in 1973.


Precipitation (inches)
1.0
.5
Growth rate (lbs/ac/day)
20
10
0
-10
-20
Standing crop (lbs/acre)
900
700
500
300
2
9
16
23
30
6
13
20
27
3
10
July
Aug.
Sept.

decreases in standing crop from their respective preceding periods. The growth rates show a similar pattern, with positive growth rates recorded for all periods except the two periods ending on July 9 and August 27. The periods ending July 16 and September 11 showed peak growth rates of 22.1 lbs/acre/day and 24.7 lbs/acre/day respectively. A negative growth rate of -17.2 lbs/acre/day was calculated for the period ending August 27.

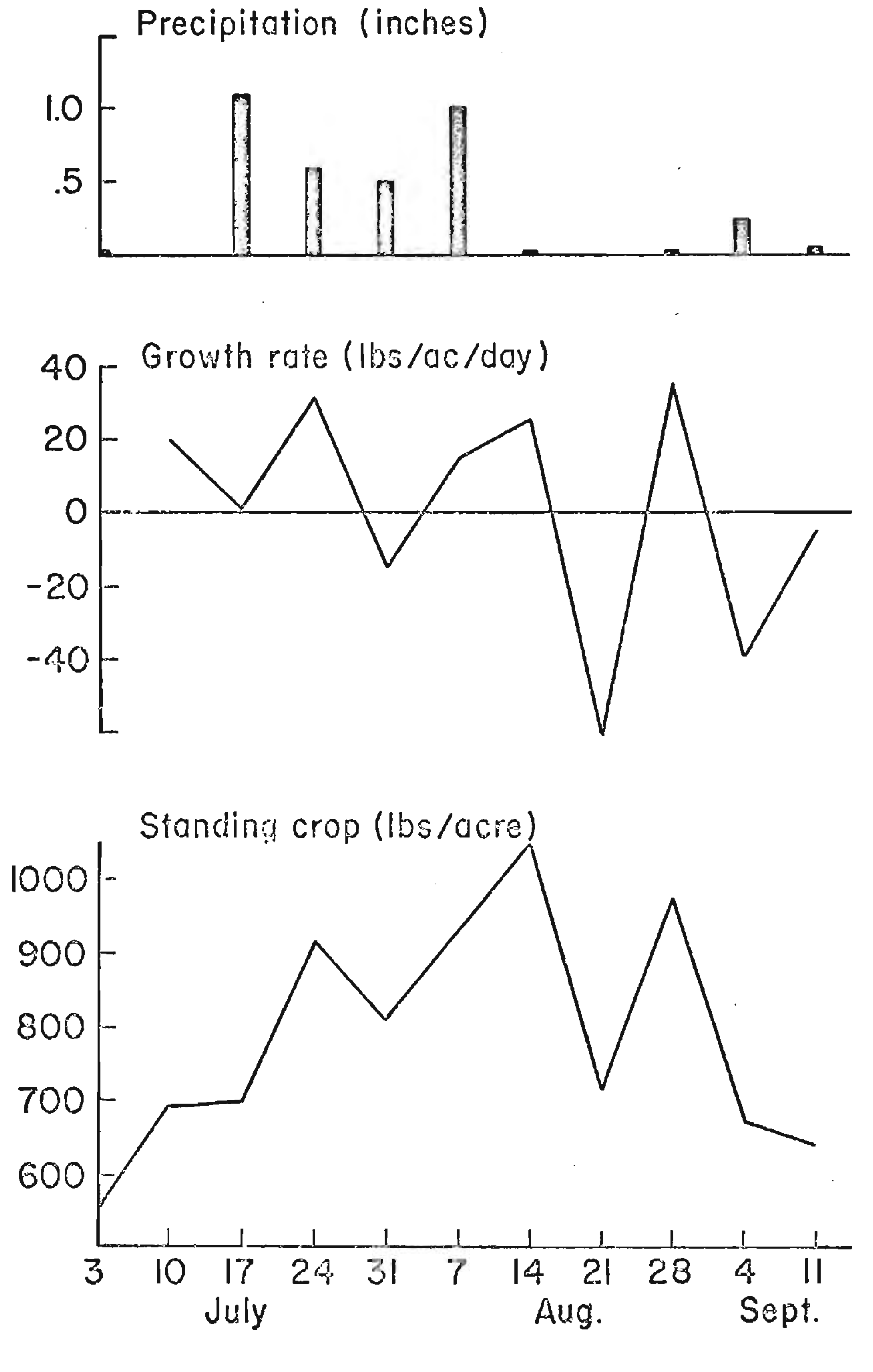
Peak height for leafy stems was 7.0 inches and occurred near the date of August 13.

The pattern of fringed sagebrush growth seemed to correspond to the pattern of precipitation. The period of increasing standing crop and positive growth rates occurred during periods when adequate moisture was recorded. During the periods when standing crop declined and growth rates were negative almost no precipitation occurred. The decline in fringed sagebrush growth for the period ending August 27 was halted and growth increased when .25 of an inch of rain was received.

Smoliak (1956) and Uresk (1971) found that fringed sagebrush growth responded to the pattern of precipitation received on shortgrass ranges. Thus the response shown in this study is entirely reasonable.

Arizona fescue in a natural opening--The mean standing crop of Arizona fescue in a natural forest opening at each date sampled in 1973 is given in Figure 15 along with the growth rate and precipitation for the period between each sampling date. Standing crop for Arizona fescue increased from 552.7 lbs/acre on July 3 to a peak

Figure 15. Relationships of Arizona fescue production in a natural opening (mean of all subplots) and growth rates with precipitation in 1973.


Precipitation (inches)
1.0
.5
Growth rate (lbs/ac/day)
40
20
0
-20
-40
Standing crop (lbs/acre)
1000
900
800
700
600
3
10
17
24
31
7
14
21
28
4
11
July
Aug.
Sept.

of 1103.4 lbs/acre on August 14. Decreases in standing crop of Arizona fescue were recorded on July 31, August 21 and September 4 and 11 also negative growth rates were calculated for the same periods. The largest negative growth rate (-40.8 lbs/acre) was recorded for the period ending August 21.

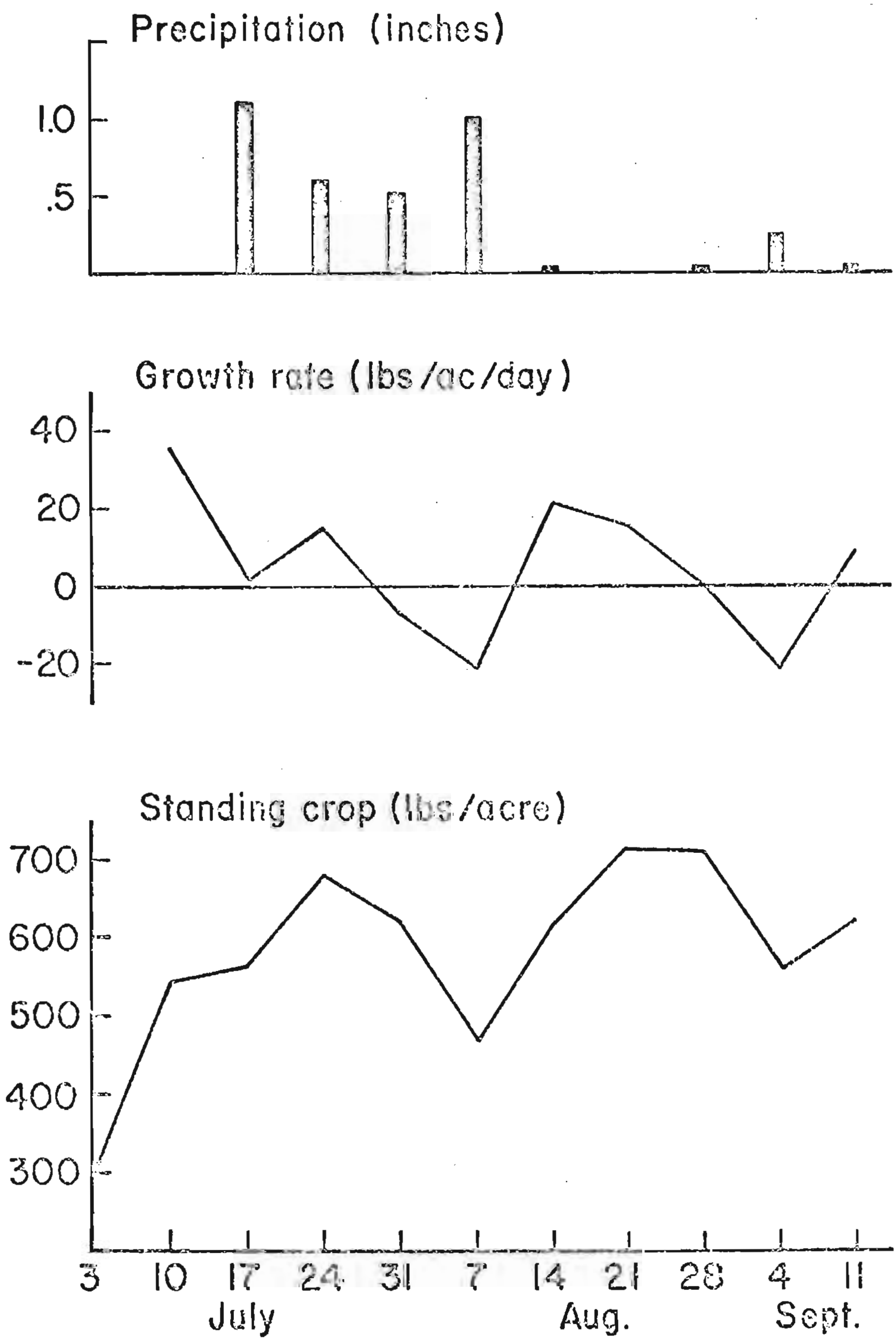
The peak height of leaf growth (16.0 inches) occurred near July 17. After this time (July 24) anthesis occurred for Arizona fescue in the open.

The pattern of Arizona fescue growth in a natural opening seemed to correspond to the pattern of precipitation into mid-August but not after that time. During the last part of August and the first half of September, Arizona fescue showed changes in standing crop not corresponding to any precipitation pattern.

These results show some similarity to those found by Pearson (1967) in northern Arizona. Pearson (1967) found that the growth of Arizona fescue from May through July is apparently related to the precipitation pattern. He noted that during late summer some other factor such as flowering apparently is more important than precipitation since the relationships of precipitation and growth for fescue did not continue past July.

<u>Arizona fescue under a pine canopy</u>--The mean standing crop of Arizona fescue under a ponderosa pine canopy at each date sampled in 1973 is given in Figure 16 along with the growth rate and precipitation for the period between each sampling date. Standing crop for Arizona fescue increased from 292.4 lbs/acre on July 3 to a peak of 678.0 lbs/acre on July 24. Standing crop

Figure 16. Relationships of Arizona fescue production under a pine canopy (mean of all subplots) and growth rates with precipitation in 1973.



Precipitation (inches)
1.0
.5
Growth rate (lbs/ac/day)
40
20
0
-20
Standing crop (lbs/acre)
700
600
500
400
300
3
10
17
24
31
7
14
21
28
4
11
July
Aug.
Sept.

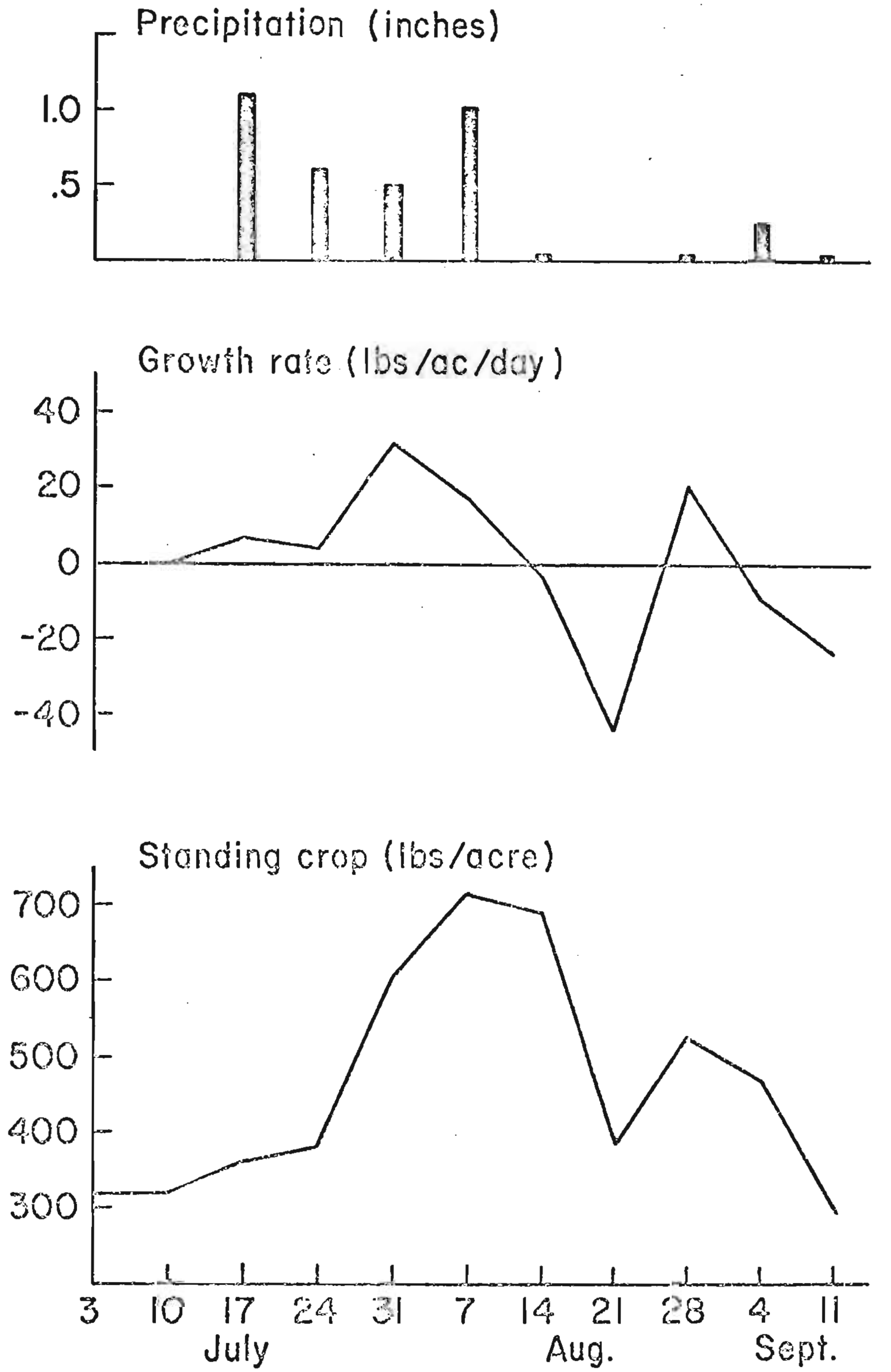
then declined to 470.1 lbs/acre on August 7 only to peak again at 715.9 lbs/acre on August 21. Growth rate showed this same up and down pattern with a maximum growth rate of 36.2 lbs/acre/day for the period ending July 10 and a minimum growth rate of -21.9 lbs/acre/day for the period ending August 7.

Maximum leaf height (15.0 inches) was reached during the period ending July 17. For Arizona fescue under a pine canopy anthesis start July 31.

The pattern of Arizona fescue growth under a pine canopy did not correspond to the pattern of precipitation as species previously mentioned. Arizona fescue under a canopy showed a decrease in standing crop from July 24 to August 7 even though precipitation was received. One explanation of the decline in standing crop is that the decline was artificially caused by trimming the subplots during the sampling periods.

Mountain muhly in a natural opening--The mean standing crop of mountain muhly in a natural forest opening at each date sampled in 1973 is given in Figure 17 along with the growth rate and precipitation for the period between each sampling date. Standing crop of mountain muhly increased from 322.7 lbs/acre on July 3 to a peak of 714.5 lbs/acre on August 7 then declined to 296.3 lbs/acre on September 11. Growth rates were all positive up to August 7 then they were negative with only one period (August 28) showing a positive growth rate (9.0 lbs/acre/day). A maximum growth rate of 31.6 lbs/acre/day was recorded for the period ending July 31 and a minimum rate of -42.9 lbs/acre/day for the period ending August 21.

Figure 17. Relationships of mountain muhly production in a natural opening (mean of all subplots) and growth rates with precipitation in 1973.


Precipitation (inches)
1.0
.5
Growth rate (lbs/ac/day)
40
20
0
-20
-40
Standing crop (lbs/acre)
700
600
500
400
300
3
10
17
24
31
7
14
21
28
4
11
July
Aug.
Sept.

A maximum leaf height of 6.0 inches was recorded for the period ending July 31. For mountain muhly in the open anthesis began around August 7.

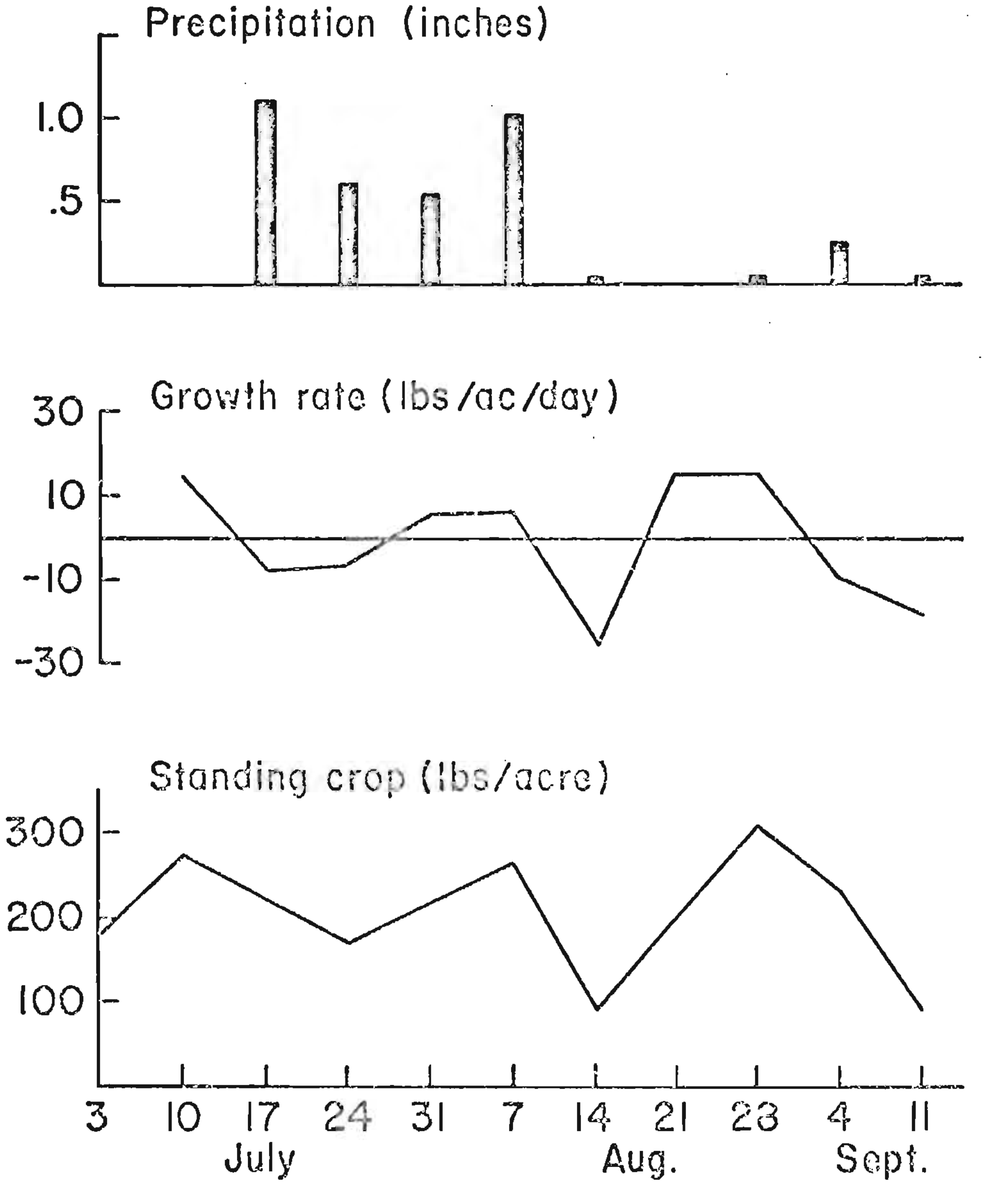
The pattern of mountain muhly growth in a natural opening corresponded to the precipitation pattern. The periods of increasing standing crop and positive growth rates corresponded to the periods when precipitation was received. During the periods when standing crop declined from the peak on August 7 very little precipitation was received.

This relationship between growth pattern and precipitation pattern compares favorably with the results of Pearson (1967). He noted that the height growth of mountain muhly in Arizona was apparently related to precipitation during July and August.

Mountain muhly under a pine canopy--The mean standing crop of mountain muhly under a ponderosa pine canopy at each date sampled in 1973 is given in Figure 18 along with the growth rate and precipitation for the period between each sampling date. The growth curve for mountain muhly showed an erratic pattern. A maximum peak of 305.4 lbs/acre occurred on August 28 with similar peaks recorded on July 10 and August 7. Growth rates followed the same erratic pattern similar to standing crop. Maximum growth rate of 15.4 lbs/acre/day was recorded for the period ending on August 21 and a minimum of -24.6 lbs/acre/day for the period ending on August 14.

The pattern of mountain muhly growth showed very little correlation with precipitation. The growth curve showed little increase in standing crop when precipitation was received. The growth curve did indicate a decline for the period ending August 14 when only a trace of rain was recorded.

Figure 18. Relationships of mountain muhly production under a pine canopy (mean of all subplots) and growth rates with precipitation in 1973.


Precipitation (inches)
1.0
.5
Growth rate (lbs/ac/day)
30
10
-10
-30
Standing crop (lbs/acre)
300
200
100
3
10
17
24
31
7
14
21
28
4
11
July
Aug.
Sept.

The ponderosa pine canopy seemed to influence the growth of Arizona fescue and mountain muhly. The canopy had a crown density of 35% and a basal area of 76 square feet/acre. Peak standing crop for Arizona fescue in the open was 1103.4 lbs/acre compared to only 715.9 lbs/acre for Arizona fescue under the canopy. This is similar to Pearson's (1967) results. He found that growth rates and final height of Arizona fescue were greatest in the open and decreased as the ponderosa pine overstory increased. Also final height of fescue was one inch less when under the canopy and phenological development delayed about one week. Mountain muhly under the same canopy showed a similar response. Peak production under the canopy was 305.4 lbs/acre and 714.5 lbs/acre when mountain muhly was in the open. Also final height was 2 inches less for mountain muhly under the canopy and phenological development was delayed about one week. In north Arizona Pearson (1967) found that growth rates of mountain muhly were not related to pine overstory. Pearson (1967) believed that the retarded growth of Arizona fescue under pine trees indicates that factors necessary for growth of fescue are used by the trees. On the other hand, he concluded that maximum growth of mountain muhly occurred after the growth of pines ceased.

SUMMARY AND CONCLUSIONS

In the Colorado Front Range montane ecosystem the ponderosa pine overstory adversly influences the growth of understory vegetation. It was found that as the basal area, crown canopy density, trees/acre, and litter of ponderosa pine increased the understory herbage production decreased. This negative relationship is best represented by simple linear regression equations using overstory factors as the independent variables and understory herbage yields as the dependent variable. In addition, the growth patterns of the important herbaceous plants in the ponderosa pine-bunchgrass community are influenced by the overstory and the pattern of precipitation.

The study was conducted at the Manitou Experimental Forest located approximately 28 miles northwest of Colorado Springs, Colorado. The area is in a mountain valley of the Rocky Mountain Front Range. This area is composed of ponderosa pine-bunchgrass ranges situated on soils developed from pike peak granite. Elevation is approximately 8,000 feet with annual precipitation of approximately 15.5 inches.

In late spring of 1972, 14 permanent sample plots were established in three experimental pastures. These plots were selected on the basis of basal area of ponderosa and homogeniety of the herbaceous understory. In each of the three pastures a 1/4-acre sample plot was established on a natural forest opening. The remaining eleven plots were then established on timbered range, with basal areas ranging from approximately 25 ft^2/acre to 100 ft^2/acre. These plots ranged in size from 1/4 acre to approximately 1 acre, depending on the number and distribution of the trees and the homogeneity of the understory plants.

In each sample plot production was estimated with the Heterodyne Vegetation Meter-Model 18-1000. In each sample plot forage estimates on 250 systematically chosen subplots (1 x 2 ft) were obtained in June, July and August in 1972 and August in 1973.

Several overstory parameters were measured on each sample plot. Each tree in a plot was numbered and measured for diameter at breast height to determine the trees/acre and basal area of each plot. On each sample plot the crown canopy cover was measured with a "moosehorn" and crown canopy density measured with a spherical densiometer.

Other factors suspected of influencing understory yields were also measured on each sample plot. The amounts of forest floor accumulations were measured and expressed as lbs/acre of litter, duff and litter + duff. Also soil nitrate-nitrogen was determined for samples taken from the top 4-inches of soil in each plot.

In addition to these sample plots, growth plots were established to study the growth pattern of blue grama in a natural opening, fringed sagebrush in a natural opening, Arizona fescue in a natural opening, mountain muhly in a natural forest opening, Arizona fescue under a ponderosa pine canopy and mountain muhly under a ponderosa pine canopy. The standing crop on these plots was estimated with the herbage meter at weekly intervals from July 2, 1973 to September 11, 1973.

Understory herbage production was substantially greater in 1973 than in 1972. The understory herbage production in 1973 range from 125 lbs/acre under dense pine canopy to 1262 lbs/acre on a natural opening. For the same cover type in 1972, understory herbage yields ranged from 35 lbs/acre under a dense pine canopy to 587 lbs/acre in a natural opening.

All overstory parameters measured were significantly correlated ($P<0.01$) with understory yields. Correlation coefficients ranged from -.719 to -.940. Crown canopy cover was the most highly correlated parameter with herbage yields measured on June, July and August, 1972. Trees/acre was the most highly correlated parameter with August, 1973 herbage yields.

Forest floor accumulations were also significantly correlated with understory production during both years. Litter accumulation was significantly correlated with understory yields at the 1 percent level of probability while duff and litter + duff were significantly correlated with the amount of understory vegetation at the 5 percent level. Correlation coefficients between litter and understory herbage were from -.791 to -.838. Correlation coefficients for duff and litter + duff were from -.522 to -.704.

Correlation analyses indicated that soil nitrate-nitrogen was not significantly correlated ($P<0.10$) with understory yield. This may not be a complete picture of the relationship between soil nitrate-nitrogen and understory yield. These results do not concur with the relationship that Moir (1966) found. The difference in response may be due to the large differences between soils investigated in the two studies. Also, soil nitrate-nitrogen was not sampled as intensively as the overstory and litter variables. In addition, soil samples in the present study were collected in mid-June, were very dry, and may not reflect the true soil nitrate-nitrogen content because very little nitrification occurred. Soil temperature and moisture are recognized important factors that influence the vigor of nitrification carried on by soil micro-organisms (Buckman and Brady, 1969). Including measures of soil temperature and moisture would probably show that not only do plants respond to favorable soil temperature and moisture but that an increase of soil nitrate-nitrogen would result and further enhance this response. To better evaluate this influence that soil factors have on understory production, sampling should be done throughout the growing season.

Regression analyses were used to develop understory production prediction equation. The best prediction equation were simple linear ones of the form Y = A + B(X), where Y = understory production and X = overstory parameter. Other types of regression analysis indicated that the simple linear model was the best representation of the relationship between independent variables and understory variables. It was concluded that crown canopy density or basal area were the best independent variables to predict understory production. These two variables were chosen because they account for about 80% of the variability in understory plus they are simple measurements that can be efficiently made. In addition these two variables give a good description of the ponderosa pine canopy.

The growth patterns developed for the important herbaceous plants indicated some important relationships. The individual species in the natural opening seem to respond to the pattern of precipitation received during their growing period. Arizona fescue and mountain muhly under the pine canopy did not respond to the precipitation pattern as did these same species in the open. The production of Arizona fescue and mountain muhly in the open was nearly twice that of their respective species under the pine canopy.

These results point out the adverse effect a ponderosa pine canopy has on the understory plants. In this study as the overstory and the litter accumulation increased the understory production decreased. The negative relationship was accurately represented by linear equations using overstory measurements and litter accumulation as independent variables. Even though understory herbage production was accurately predicted with overstory measurements the growth pattern results show that precipitation, as almost always, is an important factor in the growth pattern of plants.

The results can be helpful in developing management systems. For management recommendations, however, it is of interest that management practices such as logging, thinning or prescribed burning should be expected to increase herbage production. In addition equations from this study may be entered into an ecological model to help better understand and describe the function of the Colorado Front Range montane ecosystem. In turn, the ecological model will help various managers predict the impact or responses that various management alternatives will have on the montane zone without actual testing each alternative. It should be noted that before such models can be truly functional additional studies of this type should be expanded to cover the entire spectrum of canopy densities and environmental factors encountered in the montane ecosystem.

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