THESIS

COACTIONS OF BITTERBRUSH, PONDEROSA PINE, AND HERBACEOUS VEGETATION

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY BRUCE C. GIUNTA ENTITLED COACTIONS OF BITTERBRUSH, PONDEROSA PINE, AND HERBACEOUS VEGETATION BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

COACTIONS OF BITTERBRUSH,
PONDEROSA PINE, AND HERBACEOUS VEGETATION

During 1966 and 1967, 100 bitterbrush (Purshia tridentata) plants were collected on each of six study areas located approximately 30 miles west of Fort Collins, Colorado. Study areas were selected to provide varying levels of abundance of bitterbrush, ponderosa pine (Pinus ponderosa), and herbaceous vegetation. The object was to relate bitterbrush age structures, growth, and vigor to plant coactions.

Bitterbrush plants were aged by ring count. Living and dead portions of the crown were weighed separately. Various measurements were made at each bitterbrush plant and on the plot where it occurred. These were intended to relate the shrub component to herbaceous cover and indices of ponderosa pine abundance.

Grasses were the most important herbaceous component on all study areas. Ponderosa pine varied from 0 ft^2/acre on study area three to 102 ft^2/acre of basal area on area six.

Sexual regeneration of bitterbrush appears rare on all study areas, but especially where a pine canopy is absent. Asexual reproduction by layering was common.

A chi-square test of homogeneity comparing age structures between study areas yielded significant results. However, no relationship between age structure and pine or herbaceous abundance was evident. Three of the study areas appear to have declining bitterbrush stands.

Investigations of growth rate revealed that bitterbrush may experience a peak growth rate that is at least partially controlled by age. Multiple regression analysis indicated that growth rate is inversely related to ponderosa pine basal area. Bitterbrush plants of a given age are almost always larger in open stands than under a canopy. No relationship with herbaceous cover could be detected.

Attempts to quantify bitterbrush vigor were a failure, because of extreme variation in percent dead crown material between plants. Crown die back could not be related to pine or herbaceous abundance.

Current annual growth production of bitterbrush seems inversely related to herbaceous cover and the percent of dead crown material present.

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Other persons aided in portions of the study and their efforts are gratefully acknowledged. These people include: Mr. Charles Robbins, Mr. Thomas Whitfield, and lastly my wife Janice, without whose moral support the task would have been difficult indeed.

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CHAPTER I

INTRODUCTION

Within the wildlife management profession, and even more specifically in the area of big game management, a serious crisis exists. Preservation of big game winter range, at a time when increasingly greater demands are being made upon it, is possibly the most urgentproblem confronting game range managers. A creeping encroachment on available winter range by a growing human population has reduced both the acreage and forage value of many wintering areas (Klemmedson 1967). It is therefore imperative that every effort be expended to maintain existing ranges in the best possible condition.

Antelope bitterbrush (Purshia tridentata Pursh, D.C.) forms part of one of the more important winter browse complexes in the western United States. Over much of its range, bitterbrush is closely associated with ponderosa pine (Pinus ponderosa Dougl. ex p. Lawson). Typical pine-bitterbrush communities are within the montane zone and are usually valuable winter range. They are also of significant value as a timber source.

Historically, a number of factors have acted to reduce the worth of pine-bitterbrush areas. Among them are fire, certain types of bogging operations, excessive browsing or grazing, insect attack, and small rodent depredations. It is also true that many bitterbrush ranges are experiencing widespread dieoffs, from yet undetermined causes. Obvious decimating factors have been studied in some detail, but the more subtle processes of succession and ecological reasons for bitterbrush deterioration are not well understood.

This study is concerned with coactions of bitterbrush, ponderosa pine, and herbaceous vegetation. A coaction might be defined as the effect of one organism upon another. The most conspicuous coactions are usually those involving the effects of animals on plants. These have been extensively studied and are somewhat better known than the less obvious effects plants exert upon each other. Odum (1953) lists eight categories of coactions based on beneficial or inhibitory effects to the coacting populations. The necessity of the coaction for survival of one or more of the parties is also a consideration. Of the named categories, only about four are significant import to this study. These are listed and defined below:

1 Competition -- Two or more organisms have a need for a commodity that is in insufficient supply for both. Both organisms are generally inhibited as a result of this coaction. In some cases, one of the organisms may even be eliminated.

2 Neutralism -- There is an association of organisms, but no apparent effects result from it.

3 Amensalism -- One organism in inhibited by another, but the inhibiting organism gains no apparent benefit.

4 Commensalism -- An organism obtains a benefit as a result of the coaction, but the other organism is not affected.

Those coactions not defined include; predation, protocooperation, mutualism, and parasitism. Primarily they are animal-animal or animal-plant in nature. The mutualism of nitrogen fixing bacteria and certain legumes, and parasitism of mistletoe are notable exceptions. I believe however, that within the pine bitterbrush community, they are distinctly secondary as plant coactions. Thus the objectives of this study will focus upon the coactions listed previously. These objectives are listed below:

1.) What coactions occur between the major vegetative components of the community?

2.) What are the mechanisms of existing coactions? That is; what component, ponderosa pine or herbaceous vegetation exerts the greatest effect? Also, what effects are peculiar to pine or herbaceous vegetation or a combination of both?

3.) What are the character and magnitude of coactive effects on bitterbrush growth and vigor?

4.) From the standpoint of their effects on bitterbrush, which coaction (s) is likely the most influential?

5.) What are some accurate indices to long term vigor in bitterbrush? This information is needed to provide a yardstick for comparison between varying degrees of coaction.

CHAPTER II

METHODS AND MATERIALS

Selection of Study Areas

During 1966 and 1967 six study sites were selected for investigation. A major objective in site selection was to obtain sites that provided contrasts with respect to the relative abundance or dominance of ponderosa pine, bitterbrush, and herbaceous vegetation.

All six areas should have been physically identical and located within a very short distance of each other. Actual conditions, however, precluded such close control. It is assumed that slight differences of this type will not completely obscure objectives of the study. Hopefully, at least some portion of any variation in bitterbrush growth or vigor between study areas can be ascribed to plant coactions.

Extensive reconnaissance determined areas suitable for study, along with their approximate size and boundaries. Vegetative homogeneity or similarity determined limits on each area. Boundaries were inked on aerial photographs. From these, accurate measurements of acreage were made and a base established for plot location.

Location and Size of Plots

Within each study area, ten plot centers were located, utilizing the long axis of each area on an aerial photograph. Scaling the true aximuth of that line simultaneously determined a direction of travel for pacing and an approximate starting point on the ground. Plots were located by pacing distances obtained from a table of random numbers (Fisher and Yates 1963). Two numbers were required for each plot; one the distance on the predetermined azimuth and secondly, a distance to the left or right of that line. Odd numbers were to the right and even to the left.

The largest plot was a 0.2-acre circular area (52.7 ft radius). Any plot which overlapped another or extended outside the study area boundary was eliminated and new numbers drawn until a satisfactory location was found. Plot centers were marked with a red-topped wooden stake. Instructions for finding the starting point and any desired plot were recorded in the field notebook.

Plot size varied according to purpose. Tree density was measured on the 0.2-acre plot. Estimations of ground cover and a seach for bitterbrush seedlings were made on a 100 ft^2 plot. If seedlings were found, a 1 ft^2 quadrat was placed over each to record detailed ground cover information in the immediate area.

Collection of Physical Site Data

Elevation, Slope, and Aspect

Elevation of study areas was determined from a United States Geological Survey topographic map. Average percent slope was measured from a series of readings with an Abney Level. Determination of aspect or exposure was accomplished by a staff compass oriented in the direction of contours. Exposure was then recorded as the true azimuth at right angles to the contours, pointed downslope.

Soil Sampling

Soil profile pits were dug at approximately the center of each study area. From these, depth of A and B horizons were measured in inches. At the same time soil samples were collected for laboratory analysis of texture and organic matter content.

Mechanical analysis to determine the percent of sand, silt, and clay was accomplished using a hydrometer method. Organic matter content was determined using the "loss on ignition" method (Wilde, Voight, and Iyer 1964).

Collection of Ground Cover Data

Herbaceous Composition and Abundance

On each 100 ft^2 plot, an ocular estimate of percent ground cover was made. The categories recorded were bare gound, rock, litter, and herbaceous vegetation. These estimates are subject to some human error because of the method, but are meaningful in a relative sense. Within the same plot, I attempted to identify all of the grasses, forbs, and half-shrubs encountered. Ocular estimates were made of each species relative abundance and grazing use.

Shrub Cover

The angle gauge was used to measure shrub cover. This instrument is a modification of the glass prism or wedge used in the "Bitterlich Method" by foresters to estimate timber volumes. It establishes a variable plot about any given point that make possible a rapid and accurate measure of percent shrub cover (Cooper 1957).

Forest Overstory

Tree density was measured by counting trees within 0.2-acre plots. All species were counted, although ponderosa pine was easily the dominant tree in all of the study areas.

Basal area determination of each plot center employed a wedge prism, first developed by Grosenbaugh (1952) and later refined by Bruce (1955) and Lemmon (1958). For simplicity, a prism with a basal area factor of 10 was used.

A spherical densiometer was used to measure forest canopy cover. This instrument employs a small concave mirror, upon which there is an engraved grid (Lemmon 1957). Canopy cover in percent is read directly from the grid. Results were not entirely satisfactory because in areas where canopy is less than 30 percent, considerable error is introduced. If for example, a site with an actual canopy cover of 0 percent is measured, the densiometer will read approximately 8 percent. This error progressively decreases until an actual canopy of 100 percent is attained. Thus at 30 percent a correction factor of approximately 5.6 percent must be subtracted.

Measurements on Bitterbrush

Plant Selection

On each study area, 100 bitterbrush plants were selected for study. At each plot center, the ten closest plants were chosen. During 1967 only, one randomly selected individual in each ten was left in place until the current growing season was complete. The 100 plants collected in 1966 were treated alike. Thus only 50 samples were available for current annual growth and oven-dry weight measurements.

Height and Crown Diameter

Height, minimum crown diameter, and maximum crown diameter were measured to the nearest inch. Dead portions of the crown were not included. Living crown area or volume could then be calculated and compared with other variables to provide an index to vigor.

Shrub to Tree Distances

For each bitterbrush plant, the distance to the edge of the crown and bole of the nearest ponderosa pine were measured with a steel tape. A diameter tape was utilized to measure DBH (diameter at breast height) of the same tree. Presumably large trees have a greater competitive effect than small ones.

Measures of Biomass

Two weights were recorded on bitterbrush plants not selected for current annual growth studies. An Ohaus Harvard Trip Balance was used to weigh all of the above-ground parts to the nearest gram. These parts were categorized into living and dead portions of the crown. During 1966, 100 plants from study area one were weighed on a gram-graduated dietetic scale instead of the balance. Therefore, these figures are probably somewhat less accurate than those from study areas two through six.

The fifty plants selected for further study were divided into more detailed categories. Current annual growth was removed and subsequently weighed, measured, oven-dryed, weighed again, and the number of leaders counted. The remaining dead and living woody growth was also oven-dryed and reweighed. An estimate of oven-dry matter content was calculated from these data.

Age Determination

Age of bitterbrush plants was determined by counting annual rings. Each shrub was severed at the root crown with pruning shears or small saw, so that the oldest crossection of stem would be exposed. This portion was then numbered and removed for drying and polishing necessary for accurate age determination.

A polishing apparatus similar to that described by Roughton (1963) was employed in specimen preparation. Rings were counted with the aid of a binocular microscope.

The adequacy of direct ring count for aging bitterbrush is discussed by Roughton (1963). The greatest problem in aging bitter-brush is the frequency of stem rot. Often the oldest rings (i.e., the center portion of the stem) were completely obliterated or missing. In such a case, existing rings were counted and the number remaining estimated. This was done on the basis of width and configuration of existing rings and distance to the projected center of the stem.

Data Analysis

After all data had been recorded on appropriate field forms, it was punched on Hollarith cards for computer analysis (Appendix).

Simple and multiple regressions, analysis of variance, and chi-square analyses were conducted according to standard procedures. Descriptive terms, such as mean and standard error were used to describe study areas.

CHAPTER III

DESCRIPTION OF STUDY AREAS

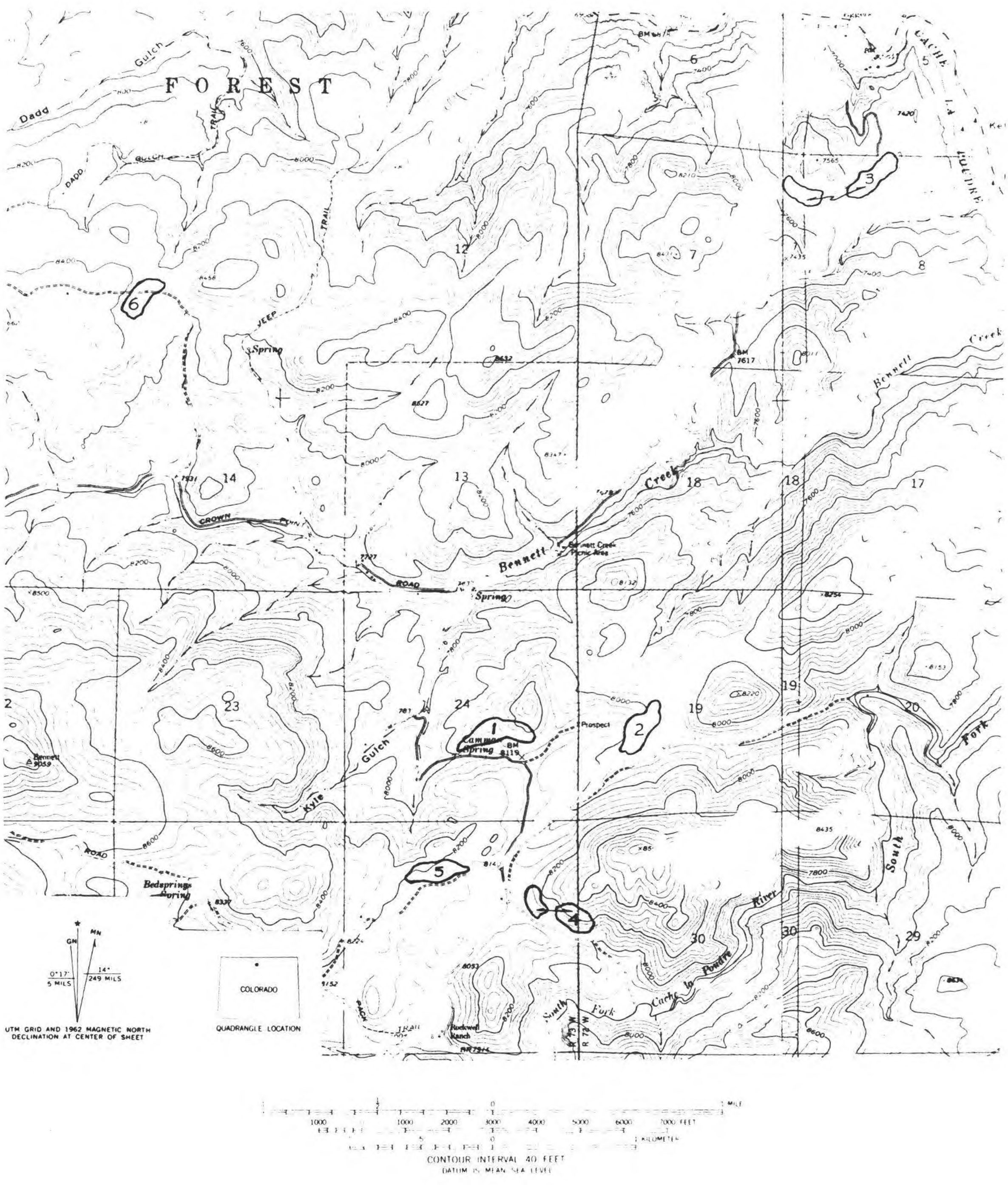
Location and Size

All study areas were located within an approximately 16 sq. mile area straddling two tributary watersheds of the Cache la Poudre River in Larimer County, Colorado. Fort Collins, the nearest town of any size, lies about 30 miles to the east. A legal description of this area includes portions of T8N, R72W and R73W, 6th Principal Meridian.

Study areas one, three, and six are within the Bennett Creek watershed, while the remainder drain into the South Fork of the Cache la Poudre River (Figure 1). With the exception of area six, all study sites are in close proximity to the Pingree Park road. Area six is located approximately one mile north of the Crown Point road.

Size of study areas was determined by photogrammetric methods and can be considered a relatively accurate measure (Table 1). Acreage of a site was assumed a relatively unimportant factor with respect to plant coactions. Therefore, no particular effort was expended to obtain study areas equal in size.

Fig. 1. Map showing number designation and location of study areas.


FOREST
Dadd Gulch
TRAIL
JEEP
Spring
Bennett Creek
Bennett Creek Picnic Area
CROWN
ROAD
Spring
Kyle Gulch
Prospect
Bedsprings Spring
South Fork Cache la Poudre River
South Fork
Rockwell Ranch
CACHE LA POUDRE
Bennett
1
2
3
4
5
6
UTM GRID AND 1962 MAGNETIC NORTH DECLINATION AT CENTER OF SHEET
COLORADO
QUADRANGLE LOCATION
CONTOUR INTERVAL 40 FEET
DATUM IS MEAN SEA LEVEL

Physical Description

Topographic Features

Elevation, slope, and exposure were measured on each study area. It was desired that these be nearly identical between sites. That there was some variation, however, is apparent.

Elevation ranged from 7300 to 8400 feet. Five of the study areas were between 8000 and 8400 feet. Only area three proved somewhat different (Table 1).

Slope was measured in percent and was generally quite gentle. With the exception of area four, all slope percentages were under 20 percent.

Table 1. Physical site factors on six study areas

Study Area	Size (acres)	Elevation (ft)	Slope (%)
1	24	8080	11
2	10	8000	19
3	9	7300	8
4	10	8080	27
5	11	8200	4
6	6	8400	8

Exposure, measured in degrees in true azimuth, ranged from almost due east at study area two, to south-southwest at area four (Fig. 2).

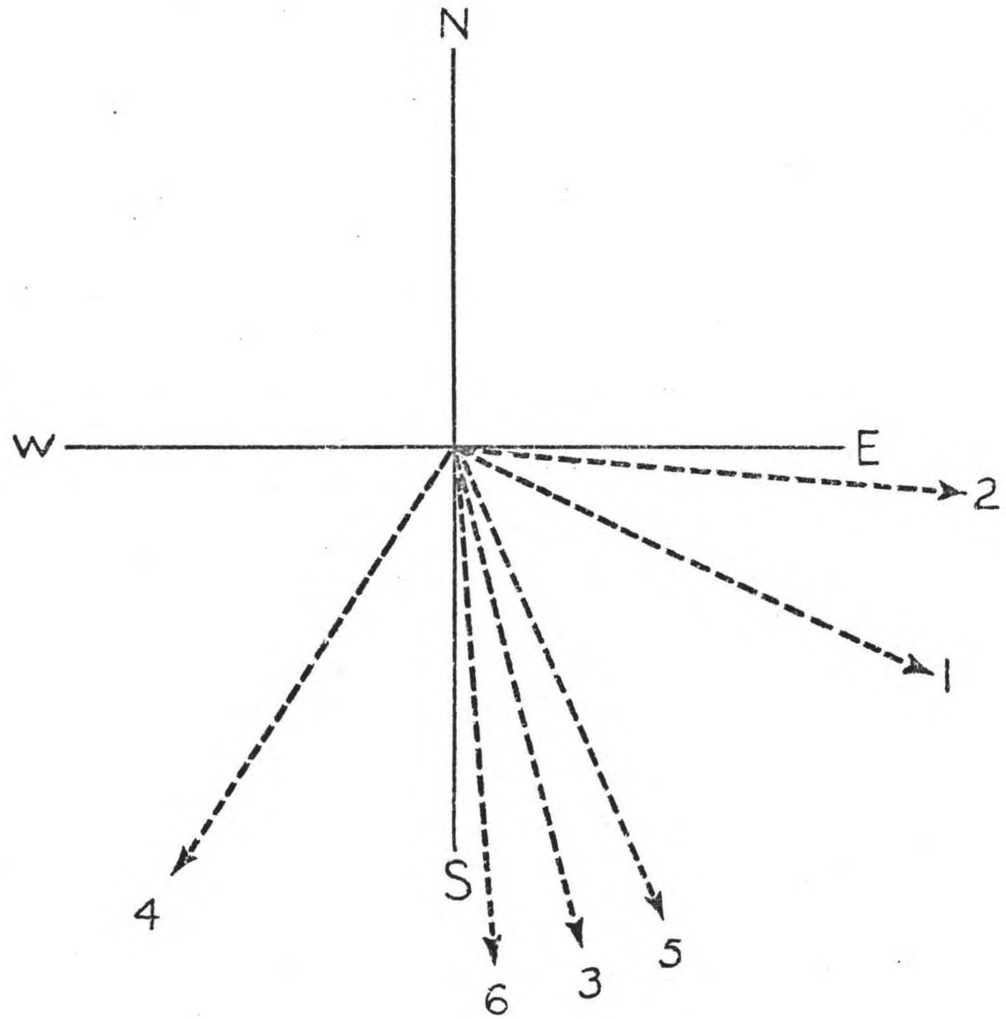


Fig. 2. Approximate exposure of six study areas.

Climate

No climatic data were collected by this investigator, but some information can be gleaned from a recent watershed analysis of this areas, published by the Colorado Cooperative Watershed Management Unit.

Johnson et al. (1963) reported that precipitation occurs during all months of the year. Mean annual precipitation for the entire South Poudre drainage is estimated between 18 and 22 inches. The highest values occur in the upper portion of the watershed. Current study sites are located in the mid-range, so 18 to 22 inches is probably a fair estimate. Much of this total occurs as snow during the period October through April, particularly at higher elevations. In the vicinity of the study areas, June to September rainfall is possibly more important, at least ecologically, if not in total amount. Summer rains in the montane zone are usually the result of intense convectional storms, which may occur almost daily, but are of short duration and localized in nature.

Of more direct application are data obtained from a permanent weather station at Quigley mountain. Located almost in the center of a rough rectangle formed by areas one, two, four, and five, it reveals a mean annual precipitation of about 17 inches for the years 1963 through 1967 (Table 2). Precipitation is primarily a result of summer storms. April to September is the wettest period of the year.

Temperatures in the montane zone of the South Poudre watershed are generally mild, but on occasion they can be extreme. Johnson et al. (1963) reported that a low of -45 F and a high of 83 F have been recorded at Pingree Park, a 9000 ft elevation. The situation in the vicinity of the study areas must be less extreme, at least with respect to low temperatures. However, summer highs are probably significantly warmer.

Mean monthly temperatures compiled from the Quigley station show that January to March is the coldest period of the year. June through August encompasses the heart of the warm season (Table 3).

Table 2. Monthly precipitation for the period 1962 through 1967, Quigley Mountain weather station, Colorado.1/

Month	Year						Mean
	1962	1963	1964	1965	1966	1967	
January	--	1.26	0.37	1.39	0.10	1.32	0.89
February	--	0.64	1.05	0.93	0.32	1.01	0.79
March	--	1.39	1.29	1.84	0.53	1.34	1.28
April	--	0.57	3.36	3.49	1.52	1.78	2.14
May	--	1.10	1.45	2.67	0.62	2.32	1.63
June	1.90 2/	4.17	0.83	2.94	1.80	2.80	2.41
July	2.58	2.00	0.96	2.17	2.97	2.60	2.21
August	0.19	4.65	1.90	0.68	1.06	1.38	1.64
September	0.92	2.64	1.01	2.51	1.31	2.32	1.79
October	0.58	0.39	0.06	0.73	0.85	1.32	0.66
November	0.62	0.19	0.58	0.22	0.37	1.46	0.57
December	0.73	0.66	1.18	0.61	0.39	1.85	0.90
Totals	--	19.66	14.04	20.18	11.84	21.50	17.44

1/ Precipitation in inches.
2/ weather station established June, 1962.

Table 3. Mean monthly temperatures for the period 1962 through 1967, Quigley Mountain weather station, Colorado.1/

Month	Year						Mean
	1962	1963	1964	1965	1966	1967	
January	--	21	23	29	12	28	23
February	--	28	21	23	17	21	22
March	--	27	21	17	29	25	24
April	--	36	34	39	34	28	34
May	--	--	--	43	29	40	37
June	57	53	50	51	52	50	52
July	59	58	63	57	61	57	59
August	60	55	54	54	56	54	56
September	54	50	52	43	51	46	49
October	48	--	41	45	40	39	43
November	39	--	31	33	34	26	33
December	33	--	26	22	26	18	25
Annual Means2/	41	39	38	38	37	36	38

1/ Temperature in degrees Fahrenheit.
2/ In years that have missing data, annual means were calculated by substituting monthly means.

Soils

All study areas occur on the Idaho Springs geologic formation Principal constituents of this formation are metamorphosed sedimentary rock of pre-cambrian origin. Soils are derived from quartz-biotite schists, quartz-biotite-sillimantite schists, quartzite, quartz schists, and quartz gneisses (Lovering and Goddard 1950).

Soil types in the montane zone of the South Poudre watershed are grouped into five major categories; Gray Wooded, Regosol, Lithosol, Chernozem, and Chestnut-Chernozem intergrade. Those occurring on the study areas are predominantly Gray Wooded and Chestnut-Chernozem intergrade (Johnson et al. 1963).

Soil profile pits dug on each study area revealed generally shallow undeveloped A horizons and relatively deep B horizons. Soil material is compact and undifferentiated below the B horizon. Both horizons ranged from 63 to 78 percent sand. All study soils appeared well drained and probably are not capable of holding available water for extended periods (Table 4).

Table 4. Soil characteristics on the six study areas.

Measurement	Study Area					
	1	2	3	4	5	6
A horizon						
Depth (inches)	2.5	4.5	5.0	3.0	3.0	1.5
% Sand	68	63	77	77	72	78
% Silt	25	29	18	18	23	17
% Clay	7	8	5	5	5	5
% Organic matter	3.2	8.5	3.8	8.5	3.6	3.6
B horizon						
Depth (inches)	17	16	14	13	15	15
% Sand	69	69	74	72	72	70
% Silt	24	22	18	22	23	24
% Clay	7	9	8	6	7	6
% Organic matter	2.9	5.0	3.1	3.0	3.0	2.2

Organic matter content apparently decreases with depth, but the rate differs between soils. Areas supporting a substantial herbaceous cover (i.e., areas 2, 3, and 4) tend to have higher organic contents, at least in the upper horizon.

It can readily be seen that all of the soils tested are apparently suited to the growth of ponderosa pine and bitterbrush, both of which require coarse, well-drained soils.

Biotic Description

During preliminary field reconnaissance, the six study areas were subjectively classified as follows:

1 Moderate ponderosa pine, moderate bitterbrush, scattered herbaceous cover.

2 Scattered ponderosa pine, moderate to dense bitterbrush, dense herbaceous cover.

3 Negligible ponderosa pine, moderate to dense bitterbrush, dense herbaceous cover.

4 Moderate ponderosa pine, moderate bitterbrush, dense herbaceous cover.

5 Dense ponderosa pine, scattered bitterbrush, moderate herbaceous cover.

6 Very dense ponderosa pine, scattered bitterbrush, negligible herbaceous cover.

These categories are relative and probably meaningful only in a broad sense, but they provided a scale for site selection. Moreover they proved remarkably accurate when compared to the quantitative data collected later in the study.

Animal Use

All of the study areas are considered prime deer and elk winter range. Browsing could have a profound effect on bitterbrush stands, however, at present, none are more than lightly utilized. Therefore, it seems logical that any ecologic effect upon vegetation from this source is probably minimal. The history of past use is largely unknown, but it is likely that browsing, before the advent of sizeable game harvests, has at some time been relatively intense.

Cattle are on the study areas during the summer, but their numbers and duration of stay are closely controlled by the United States Forest Service. Grazing intensity appears very light on all of the study areas.

In no case were excessive numbers of rodents or insects observed on any of the study areas. During this study, it was assumed that rodent or insect activity was at a normal level or relatively constant throughout the study areas. Thus, the objectives of the study could be realized without a comprehensive study of animal populations.

Vegetative Composition and Abundance

Tree and shrub composition were remarkably uniform throughout the study areas. Ponderosa pine and bitterbrush were unquestionably dominant.

In addition to ponderosa pine, Douglas-fir (_Pseudotsuga menziesii_), lodgepole pine (_Pinus contorta_), quaking aspen (_Populus tremuloides_), and Rocky Mountain juniper (_Juniperus scopulorum_) were occassionally encountered.

Measurements of density, basal area, and canopy cover revealed marked differences in overstory abundance between the study areas (Table 5). Irregularities can generally be attributed to different size and age classes peculiar to any one site. Study area two had only scattered trees, but most of these were large mature individuals. Immature ponderosa pine dominated on all of the other areas, with the exception of number three, which had essentially no trees.

Table 5. Means and standard errors (SE) of some indices of ponderosa pine abundance on six study areas.

Study Area	Trees/Acre	SE	Basal Area (ft^2/acre)	SE	Canopy Cover (%)	SE
6	668	53	102	6	37	3
5	417	58	58	5	45	7
1	357	40	47	9	23	4
4	123	22	46	7	28	3
2	44	12	15	5	15	6
3	10	3	1	1	0	0

Shrubs other than bitterbrush were encountered only rarely. True mountain mahogany (Cercopcarpus montanus), squaw currant (Ribes cereum), skunkbush (Rhus trilobata), common juniper (Juniperus communis), and mallow ninebark (Physocarpus monogynus) were observed infrequently. Maximum variation in shrub composition usually occurred on study areas with a minimum of overstory. Half-shrubs such as fringed sagebrush (Artemisia frigida) and small low growing woody species were considered to have an ecologic role similar to that of herbaceous vegetation. The latter category includes kinnikinnik (Arctostaphylos uva-ursi) and a small rose (Rosa spp.). These species are grouped with herbaceous plants for the purpose of analysis.

Herbaceous composition was dominated by grasses and sedges. Bunchgrasses were ordinarily the most widespread and abundant (Table 6 and 7). Comparisons of frequency and relative abundance furnish a good index to any one species importance in the composition of any given study area.

A sedge (Carex spp.), junegrass (Koeleria cristata), slimstem muhly (Muhlenbergia filiculmis), Wheeler bluegrass (Poa nervosa), and Kentucky bluegrass (Poa pratensis) were the most important grasses over all the study areas. Parry oatgrass (Danthonia parryi) and needle-and-thread (Stipa comata) were also locally abundant, but did not occur on all study areas.

Some 32 species of forbs were identified during the study, in comparison to 16 species of grasses or sedges. There may be more forbs, because often they were identified only to genus. No single species of forb or half-shrub dominated (Table 8 and 9). Fringed sagebrush, kinnikinnik, daisy (Erigeron sp.), and buckwheat

(*Eriogonum sp.*) were the more abundant members of this group. However, even when locally abundant, they were usually secondary to grasses. Kinnikinnik is a possible exception because it tends to form a dense mat that effectively excludes other herbaceous growth.

Table 6. Frequency of grasses and sedges encountered on ten 100 ft^2 plots per study area.

Plant	Study Area 1	2	3	4	5	6
	Percent					
Agropyron spicatum	--	--	40	30	10	--
Agropyron trachycaulum	--	--	10	--	--	--
Bouteloua gracilis	--	--	80	--	--	--
Carex sp.	60	80	90	80	80	60
Danthonia parryi	--	70	--	30	30	--
Festuca idahoensis	--	--	--	10	--	--
Festuca ovina	20	--	--	50	20	10
Hordeum jubatum	--	--	30	20	30	--
Koeleria cristata	10	70	40	90	100	40
Muhlenbergia filiculumis	50	40	20	60	60	--
Muhlenbergia montana	--	40	30	50	--	--
Poa nervosa	80	--	20	50	40	60
Poa pratensis	--	40	30	20	60	10
Sitanion hystrix	--	--	30	--	--	--
Stipa columbiana	--	--	--	--	10	--
Stipa comata	--	70	100	20	10	--

Ground Cover

In most cases, litter and bare ground appear inversely related (Table 10). However, herbaceous cover shows no clear cut relationship to either of these variables. Litter is predominantly composed of pine needles, and is therefore strongly related to overstory abundance. One would expect that canopy cover would be the best index to potential needle fall. However, in this case, basal area seemed more closely related to litter cover. Perhaps the inaccuracy of canopy cover determination was great enough to obscure the expected relationship. Also the relative abundance of underlying herbaceous vegetation would have a possible confounding effect.

Table 7. Mean relative abundance (RA) and grazing classification (GC) of grasses and sedges encountered on six study areas.

PLANT	STUDY AREA											
	1		2		3		4		5		6	
	RA[1/]	GC[2/]	RA	GC	RA	GC	RA	GC	RA	GC	RA	GC
Agropyron spicatum	--	--	--	--	2.50	3.00	2.33	3.00	3.00	3.00	--	--
Agropyron trachycaulum	--	--	--	--	3.00	3.00	--	--	--	--	--	--
Bouteloua gracilis	--	--	--	--	1.50	2.50	--	--	--	--	--	--
Carex sp.	2.67	3.00	1.75	2.75	1.44	2.78	2.25	2.88	2.00	2.75	2.83	2.50
Danthonia parryi	--	--	1.71	2.43	--	--	2.00	3.00	1.67	2.67	--	--
Festuca idahoensis	--	--	--	--	--	--	2.00	3.00	--	--	--	--
Festuca ovina	1.50	2.50	--	--	--	--	2.00	2.20	2.50	2.50	3.00	3.00
Hordeum jubatum	--	--	--	--	3.00	3.00	3.00	3.00	3.00	3.00	--	--
Koeleria cristata	3.00	3.00	1.57	2.71	2.50	3.00	2.78	2.89	2.50	2.80	2.75	3.00
Muhlenbergia filiculmis	1.80	2.40	1.75	3.00	3.00	3.00	1.83	2.67	2.33	2.50	--	--
Muhlenbergia montana	--	--	1.75	3.00	2.33	3.00	1.20	2.80	--	--	--	--
Poa nervosa	1.63	2.38	--	--	2.00	3.00	2.60	2.80	2.75	3.00	2.50	3.00
Poa pratensis	--	--	2.50	3.00	3.00	3.00	2.00	2.50	2.33	2.83	3.00	3.00
Sitanion hystrix	--	--	--	--	2.00	3.00	--	--	--	--	--	--
Stipa columbiana	--	--	--	--	--	--	--	--	3.00	3.00	--	--
Stipa comata	--	--	1.14	3.00	1.50	2.90	2.50	3.00	2.00	2.00	--	--
Means	2.12	2.66	1.74	2.84	2.31	2.31	2.21	2.81	2.46	2.73	2.82	2.90

1/ Relative abundance classes were: 1 = abundant, 2 = common, 3 = rare (these figures cannot properly be compared in an absolute sense between study areas, because of wide variation in herbaceous cover as a whole.

2/ Grazing classes were: 1 = heavily grazed, 2 = moderately grazed, 3 = negligible grazing.

Table 8. Frequency of forbs and shrubs encountered on ten 100 ft^2 plots per study area.

PLANT	Study Area 1	2	3	4	5	6
	Percent					
Forbs						
Achillea lanulosa	20	30	30	70	80	10
Allium sp.	--	--	10	40	20	--
Antennaria sp.	30	70	20	30	80	--
Astragalus sp.	20	60	20	--	50	--
Campanula sp.	--	--	--	--	20	20
Castilleja sp.	--	--	10	--	--	--
Cogswellia triternata	--	--	--	10	--	--
Chrysopsis villosa	--	--	90	20	10	--
Delphinium sp.	10	10	--	--	--	--
Erigeron sp.	20	30	80	10	50	10
Eriogonum sp.	20	30	80	40	10	10
Erysimum sp.	--	--	--	20	--	--
Fern	--	--	--	10	--	--
Fragaria sp.	10	--	--	--	50	--
Geranium sp.	10	--	--	50	20	--
Grindelia squarrosa	--	--	10	10	--	30
Lesquerella montanus	50	20	20	60	--	--
Lupinus sp.	--	--	--	20	90	--
Mertensia sp.	--	30	--	--	--	--
Moss	--	--	30	--	--	--
Opuntia sp.	--	--	10	--	--	--
Oxytropis sp.	--	--	80	10	20	--
Penstemon sp.	--	30	20	70	--	--
Potentilla sp.	40	30	60	50	20	30
Pulsatilla ludoviciana	--	--	--	10	40	20
Ranunculus sp.	10	--	--	--	--	--
Sedum stenopetalum	10	10	--	70	80	10
Senecio sp.	30	--	--	20	20	20
Thermopsis montana	--	--	--	10	50	--
Shrubs and half-shrubs						
Arctostaphylos uva-ursi	30	--	--	30	100	50
Artemisia frigida	70	90	100	90	40	--
Rosa sp.	--	--	--	10	--	--

Table 9. Mean relative abundance and grazing classification of forbs and shrubs encountered on six study areas.

PLANT	STUDY AREA 1		2		3		4		5		6	
	RA[1/]	GC[2/]	RA	GC	RA	GC	RA	GC	RA	GC	RA	GC
Achillea lanulosa	3.00	3.00	3.00	3.00	3.00	3.00	2.71	3.00	3.00	3.00	3.00	3.00
Allium sp.	--	--	--	--	3.00	3.00	3.00	3.00	3.00	3.00	--	--
Antennaria sp.	3.00	3.00	2.29	3.00	3.00	3.00	3.00	3.00	3.00	3.00	--	--
Astragalus sp.	3.00	3.00	3.00	3.00	3.00	3.00	--	--	2.80	3.00	--	--
Campanula sp.	--	--	--	--	--	--	--	--	3.00	3.00	3.00	3.00
Castilleja sp.	--	--	--	--	3.00	3.00	--	--	--	--	--	--
Cogswellia triternata	--	--	--	--	--	--	3.00	3.00	--	--	--	--
Chrysopsis villosa	--	--	--	--	2.78	3.00	3.00	3.00	3.00	3.00	--	--
Delphinium sp.	3.00	3.00	3.00	3.00	--	--	--	--	--	--	--	--
Erigeron sp.	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	2.40	3.00	3.00	3.00
Eriogonum sp.	3.00	3.00	3.00	3.00	2.63	3.00	3.00	3.00	3.00	3.00	3.00	3.00
Erysimum sp.	--	--	--	--	--	--	3.00	3.00	--	--	--	--
Fern	--	--	--	--	--	--	3.00	3.00	--	--	--	--
Fragaria sp.	3.00	3.00	--	--	--	--	--	--	2.60	3.00	--	--
Geranium sp.	3.00	3.00	--	--	--	--	2.80	3.00	3.00	3.00	3.00	3.00
Grindelia squarrosa	--	--	--	--	3.00	3.00	3.00	3.00	--	--	--	--
Lesquerrella montanus	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	--	--	--	--
Lupinus sp.	--	--	--	--	--	--	3.00	3.00	2.22	3.00	--	--
Mertensia sp.	--	--	3.00	3.00	--	--	--	--	--	--	--	--
Moss	--	--	--	--	1.67	3.00	--	--	--	--	--	--
Opuntia sp.	--	--	--	--	2.00	3.00	--	--	--	--	--	--
Oxytropis sp.	--	--	--	--	3.00	3.00	3.00	3.00	3.00	3.00	--	--
Penstemon sp.	--	--	3.00	3.00	3.00	3.00	3.00	3.00	--	--	--	--
Potentilla sp.	3.00	3.00	3.00	3.00	2.83	3.00	3.00	3.00	3.00	3.00	2.67	3.00
Pulsatilla ludoviciana	--	--	--	--	--	--	3.00	3.00	2.75	3.00	3.00	3.00

(continued on next page)

Table 9. (Continued)

PLANT	STUDY AREA 1		2		3		4		5		6	
	RA	GC	RA	GC	RA	GC	RA	GC	RA	GC	RA	GC
Ranunculus sp.	3.00	3.00	--	--	--	--	--	--	--	--	--	--
Sedum stenopetalum	3.00	3.00	3.00	3.00	--	--	3.00	3.00	2.88	3.00	3.00	3.00
Senecio sp.	3.00	3.00	--	--	--	--	3.00	3.00	2.50	3.00	3.00	3.00
Thermopsis montana	--	--	--	--	--	--	1.00	3.00	1.80	3.00	--	--
Shrubs and half-shrubs												
Arctostaphylos uva-ursi	2.33	3.00	--	--	--	--	2.00	3.00	1.70	3.00	2.40	3.00
Artemisa frigida	3.00	3.00	2.56	3.00	1.60	3.00	2.44	3.00	2.75	3.00	--	--
Rosa sp.	--	--	--	--	--	--	3.00	3.00	--	--	--	--
Means	2.96	3.00	2.90	3.00	2.72	3.00	2.82	3.00	2.71	3.00	2.91	3.00

1/ Relative abundance classes were: 1 = abundant, 2 = common, 3 = rare (these figures cannot properly be compared in an absolute sense between study areas, because of wide variation in herbaceous cover as a whole.).

2/ Grazing classes were: 1 = heavily grazed, 2 = moderately grazed, 3 = negligible grazing.

Table 10. Ground cover of six study areas.

Study	Browse Cover (%)	SE	Herbaceous Cover (%)	SE	Litter (%)	SE	Bare Ground (%)	SE	Rock (%)	SE
6	6	3	3	1	93	2	2	1	2	1
5	4	2	27	5	66	6	6	2	1	0
1	19	2	11	2	51	7	33	5	5	4
4	20	2	39	4	39	6	8	2	15	4
2	22	4	41	3	33	5	26	5	2	1
3	16	2	44	3	23	3	32	5	1	1

CHAPTER IV

RESULTS AND DISCUSSION

Bitterbrush Age Structures

Studies of age structor of browse populations are a relatively recent development. Animal population dynamics has for many years been recognized as a vital part of animal ecology. Similarly plant ecologists, foresters, and archeologists have used age studies of trees to good advantage. However, until the late 1950's, browse age structures were largely ignored.

Possibly the most promising application of age structure data may be in defining ecologic status of individual browse stands. Lassen, Ferrel, and Leach (1952) classified bitterbrush on the Doyle winter range in California as young, mature, or decadent. Even this rather crude estimation of age was sufficient to show an apparent successional change. No bitterbrush reproduction was evident and only 2 percent of the sampled plants were classified as young. Over 55 percent were rated decadent. On this basis, the authors concluded that bitterbrush on the Doyle range was very close to the point of extinction. Dasmann and Blaisdell (1959) found a similar age structure on the nearby Lassen-Washoe range. On this wintering area, slightly more than 43 percent of bitterbrush was rated decadent and reproduction was essentially nonexistent. It can hardly be denied that a serious condition exists here also.

Admittedly, the above classification system may actually reflect vigor more than age. Nevertheless, it does illustrate one potentiality of age-structure analysis. Baker (1958) attempted to develop a more precise method of predicting fate of key browse species from age structures. Using big sagebrush (Artemisia tridentata) as test species, annual ring count was used to estimate age. Baker found that annual ring count resulted in excessive error, that led to generally unsatisfactory results for the study as a whole. Roughton (1966) resolved this problem by adapting the technique of "growth ring analysis" to shrubs. He found that if age structure data was plotted against a theoretical "die away" curve, it became possible to classify browse populations as declining, expanding, or stable, purely on the basis of age.

Another possible use of age data might be to relate forage or seed production to selected age classes. To my knowledge, no research has been specifically aimed at these objectives. However, Hubbard, Sanderson, and Dunway (1960) published a paper that touches briefly on the subject. Data they collected, suggests that plants intermediate in size and age are the best forage producers. Presumably, woody plants, such as bitterbrush, experience a period of peak vigor and forage production. To draw an analogy, animals experience a very definite "prime of life" or optimum reproductive period. The same may be true of browse plants.

Management implications of such a phenomenon seem obvious. Not only could key species be intensively managed, but efforts could be directed toward the more productive age groups of that species.

Reproduction

A study of reproduction is preliminary to any age structure analysis. Maintenance of a steady state requires that dying plants be exactly replaced by new seedlings or vegetative sprouts. Deviations from this theoretical norm result in age structures typical of either expanding or declining populations.

Only limited seedling data was collected during this study, because sexual reproduction on the study areas appears relatively rare. On 6000 ft^2 of surface area examined, only nine seedlings were encountered. Three of the study areas had no seedlings. However, the apparent scarcity of seedlings is at least partially compensated for by vegetative reproduction. Layering was common on all areas and may be an important mechanism of stand maintenance. Stanton (1959) reported that in higher, more moist bitterbrush ranges, nearly all plants exhibit layering. Nord (1959a) concurs, and adds that in many areas layering may be the primary means of reproduction. This made age structure analysis difficult, because it is a problem to distinguish individual plants. I considered a plant separate if no living material connected it to another.

A number of factors were measured at locations where seedlings were found. Although, insufficient seedlings were found to warrant any definite conclusions about site favorability, examination of Table 11 permits some speculation.

Seedlings were found only on those areas possessing a noticeable canopy cover. By itself, canopy cover may not be very meaningful, but it suggests a number of possible explanations. First, there may be a direct beneficial effect of shading on soil moisture levels and heat relations of seeds and seedlings. Second, a canopy tends to limit herbaceous cover and hence reduce the severity of moisture competition. Pearson (1930), although speaking about ponderosa pine seedlings, stated that competition from tree roots is less to be feared than that from herbaceous vegetation. The limited evidence available here suggests just this relationship. Competition for soil moisture with herbaceous cover limits reproductive success of bitterbrush more than any other factor. In almost every case, herbaceous cover within the square foot quadrat immediately surrounding the seedling was less than for the 100 ft^2 plot where the search was conducted (Table 11).

Table 11. Characteristics of bitterbrush seedlings and associated microsite factors.

Study Area	Number of Stems	Canopy Cover (%)	Herbaceous Cover on 100 ft^2 plot (%)	Herbaceous Cover on 1 ft^2 plot (%)	Litter Cover (%)	Distance to seed source (inches)
1	1	20	3	5	66	43
1	1	17	2	4	78	43
4	1	30	35	20	55	70
4	3	30	35	25	55	44
4	4	30	35	25	55	30
4	4	43	35	15	55	69
4	1	27	45	5	45	37
6	1	46	10	1	90	10
6	1	43	1	0	98	10

The fact that all seedlings encountered were at least ten inches from the nearest seed bearing bitterbrush plant raises an interesting question. What is the method of seed dissemination? Hormay (1943a) reports that bitterbrush seed is a relatively heavy achene, not easily borne by wind. Seegrist, Neal, and Hubbard, (1966) measured seed-fall patterns and found that the majority of seed falls within the canopy of the parent plant. Obviously, some means of dispersal is needed to move seed to more favorable locations. The consensus of findings in the literature is that rodents are important in this respect. Rodents disperse, bury, and establish caches of seed (Hormay 1943a). Other research indicates that planted seed has a much higher germination rate than that which is broadcast (Hubbard 1956c). There is also evidence that seedlings originating from multiple seed caches have a somewhat higher survival rate through the critical first three years of life than do single plants.

Only three of the seedlings encountered had more than one stem. These were almost certainly rodent-established. Means of dissemination for the others is unclear. Perhaps they were originally only single caches or sole survivors from multiple groups. There is a real need for research in this area.

Age Distribution

Considerable variation in age structure is apparent between the six study areas. Mean ages, based on samples of 100 plants ranged from 28 to 49 years (Table 12). The oldest plant encountered was about 110 years old. A two way nested analysis of variance was used to reject the hypothesis that variation in age was greater between plots than between study areas. A significant F test indicates that there are real differences in mean age between study areas.[1/]

Table 12. Age in years of bitterbrush populations on six study areas.

Study Area	Mean Age	Standard Error
1	36	1.7
2	48	1.3
3	35	1.7
4	44	1.3
5	28	1.2
6	49	1.7

1/ Throughout the remainder of the text, the .05 level of significance will be used. An asterisk (*) will denote statistically significant figures.

Stanton (1959) studied what he considered to be an old bitterbrush stand and found a mean age of 37 years. If this be true, five of the six areas studied could probably be construed as "old". It is advisable to consider terms such as "old" or "young" as relative, depending upon the character of the site involved. Stanton did his work in Oregon, on somewhat more moist sites. Nord (1959a) found that in the California bitterbrush stands he studied mean age ranged from 32 to 44 years. Winter range areas tended to have markedly older bitterbrush populations than neighboring summer range. No such relationship was apparent in this study. In fact, the area of highest elevation, number six, also had the oldest bitterbrush stand. Mean age of the other areas shows no recognizeable altitudinal pattern.

Roughton (1966) studied five bitterbrush populations on nereby Poudre Canyon locations, albeit somewhat lower in elevation than the present study. He did not calculate mean ages for these areas, but they must have been significantly younger, because of a preponderance of individuals in the zero to four year age class.

Histograms of age structure in 20-year age classes show few plants in the 0-19 year age class (Fig. 3). Several possibilities exist, one of which is a sampling bias. Plant selection involved a variable size plot, whereby the ten closest bushes were chosen. Under such a system it becomes extremely difficult to effectively

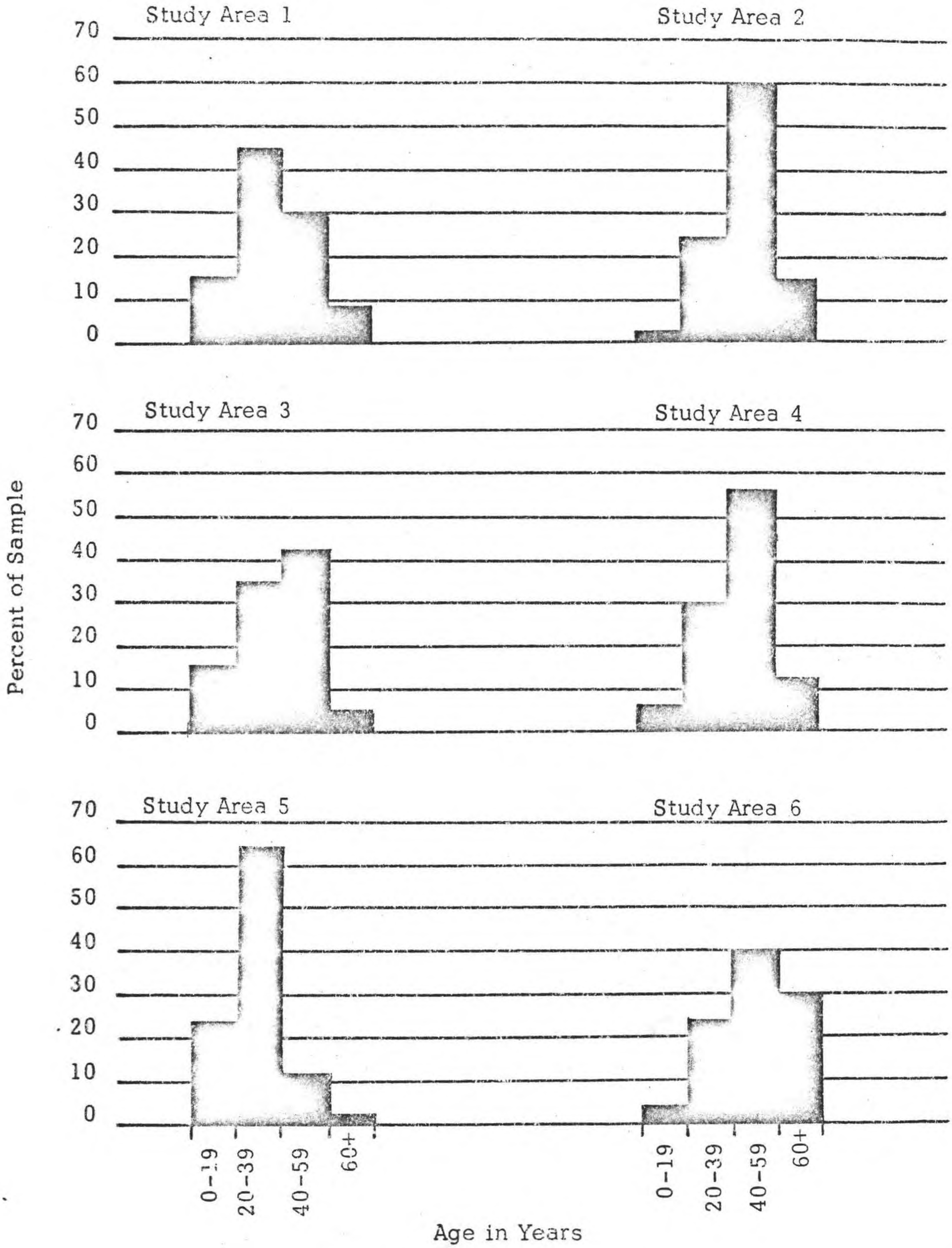


Fig. 3. Bitterbrush age structures on six study areas.

search for seedlings or very young plants. Hence, some of these were undoubtedly missed.

A second possibility is that widespread reproductive success is a relatively rare occurrence. Although large seed crops may occur at frequent intervals, a successful stocking requires that one or more favorable precipitation years coincide with a good seed-fall. Pearson (1949) and Arnold (1950) studied reproduction of ponderosa pine and discovered that only once in a 30-year period did such a combination occur. Nonetheless, this one year's reproduction was sufficient to maintain the stand and successfully invade many grassland parks. They concluded that infrequent reproductive success is a normal condition. The same may be true of bitterbrush populations. Certainly this is a question for future research.

A third possibility is that the age structures presented in Figure 3 represent the ecologic status of the six populations for a fixed point in time. If one applies Roughton's die-away curve, the resulting histograms would approximate a normal distribution, indicating a stable population. If replacement rate greatly exceeds death rate, then the curve should slope sharply away from the youngest age class. Skewness in the opposite direction indicates a decadent situation, where death rate exceeds replacement.

A comparison of age distributions as they appear, reveals two salient points. First, areas one, three, and five have a greater number of plants in the youngest age class than in the oldest. Areas two, four, and six show an exactly opposite pattern. In addition, only two populations, areas one and five, have age peaks in the 20 to 39 year age class. All others peak in the 40 to 59 year category. Taken together, an apparently adequate replacement of dying plants and location of the age peaks suggests that study areas one and five possess the healthiest bitterbrush stands. The principal common denominator linking these stands is that both occur under a mixed-age ponderosa pine stand that forms a moderately dense canopy.

A chi-square test of homogeneity was used to test the null hypothesis that age structure on the six study areas was identical. A significant chi-square was obtained and therefore the null hypothesis was rejected. Interpretation of the analysis indicates that the sampled bitterbrush plants are from different populations and cannot properly be pooled into one large sample for age structure studies.

It is apparent from the above discussion, that if one is to properly evaluate age structure, those factors influencing shape of the histogram must be properly weighed. Certainly it is difficult to make definitive statements concerning the histograms presented here.

Effects of Ponderosa Pine

Analysis of possible effects of ponderosa pine on bitterbrush age was accomplished by a three-factor multiple regression using plot mean of age as the dependent variable. Independent variables were percent shrub cover, percent herbaceous cover, and tree basal area. Presumably these variables represent all coacting vegetation. To provide a suitable range of observations, study areas were grouped for this analysis, resulting in an effective sample size of 60. Age ranged from 19 to 62 years and basal area from 0 to 130 ft^2/acre.

The multiple regression was barely significant and percent herbaceous cover proved nonsignificant (Table 13). The standard error of the estimate was 9.6 years. Basal area is apparently the best predictor of age. This is somewhat misleading, however, because none of the measured variables show a strong relationship with age. The coefficient of determination reveals that these variables can account for only about 14 percent of the variation in bitterbrush age. Obviously some other factor(s) are of primary importance.

Table 13. Multiple regression analysis of bitterbrush age on other vegetational paramenters.[1/]

Factor	Partial Regression Coefficient	Standard Partial Regression Coefficient	Simple Correlation	Partial Correlation
Herbaceous Cover	0.06	0.12	-0.07	0.09
Basal Area	0.11*	0.42	0.15	0.29
Shrub Cover	0.39*	0.39	0.22	0.35

1/ The constant term for the equation was 27.6.

Effects of Herbaceous Vegetation

Analysis of the effect of herbaceous vegetation on bitterbrush age structures proved generally inconclusive. The multiple regression analysis covering this factor has already been discussed. The problem in relating bitterbrush age to herbaceous cover is that at any given instant no relationship may be evident. However, over a long period of time, the herbaceous component undoubtedly has an effect on the ecological history of other vegetation. One can speculate on the kind of influence, but the magnitude is difficult to assess. Herbaceous influence is most likely made manifest through competition. The reproduction data already presented suggests that herbaceous competition is severly limiting to sexual regeneration of bitterbrush. Therefore, it might be reasonable to expect older age structures in areas of dense herbaceous cover. Booth (1947) tends to confirm this hypothesis. He found that grass competition substantially reduced reproductive success of big sagebrush. Determination of age structure indicated that in areas where grass competition was heavy, older sagebrush generally prevailed.

A second effect of herbaceous vegetation is its ability to reduce growth rate and vigor of mature plants. By this mechanism longevity is reduced. Hubbard and Sanderson (1961b) studied the effects of perennial grasses on the vigor and growth of mature bitterbrush. They found that heavy grass competition often results in a condition of poor vigor at a somewhat earlier age than in plants grown on grass-free areas. Although annual leader production on poor-vigor plants was significantly less than on plants in good health, a release from competition resulted in approximately equal increase in leader length. Apparently the response to herbaceous plant removal was independent of vigor, indicating that vigor status is not necessarily irreversible.

A possible management application of such knowledge is that overage, poor-vigor bitterbrush stands might be rejuvenated by a program of weed removal maintained for a period of years. New plants would have a chance to become established and the vigor of existing plants might be improved.

Intraspecific Effects

Comparisons of shrub cover and bitterbrush age were made from pooled data (Table 13). Browse plants other than bitterbrush were practically non-existent on all of the study areas. Thus, shrub cover can be effectively interpreted as bitterbrush cover.

The standard partial regression coefficient of 0.39 was significant, but variability was so great that prediction of age from an angle gauge reading would be little better than a guess.

Roughton (1966) attempted to correlate bitterbrush density with age structure, but obtained generally non-significant results. A plot study comparing mean age, rather than structure, with density may have promise in this respect. However, certain fallacies in this design are evident. A simple determination of density does not take into account seed-producing capabilities of the counted plants. It is probably this factor, coupled with intraspecific competition for soil moisture which determines density and age. A great number of seedlings conceivably could become established on a given area, but obviously all of them cannot grow to maturity. Cover and density must therefore be inversely related.

Growth and Vigor of Bitterbrush

Total Biomass Production

Growth Rates

Two facets of growth rate will be discussed in this section. The first relates to the total amount of biomass produced by a plant. Dividing total weight by age results in an average rate of growth over the entire lifespan.[1/] The second takes into account changes in growth rate with increasing age. Logically, bitterbrush should reach an age where growth rate is at a maximum. If this can be determined, it would be an important criterion of vigor as well as a promising management tool.

No accurate quantitative data concerning bitterbrush growth rates has been published. Some indirect clues are furnished in a

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1/ Unless otherwise stated, all plant weights presented in this thesis are undryed figures.

paper by Hubbard, Sanderson, and Dunway (1960) that compared age with forage production. Their results indicated that plants intermediate in size and age produce the greatest weight of leaders. The reduced vigor of older plants made them relatively inefficient at producing forage. The length or number of leaders is not necessarily synomymous with growth rate, but should be a reliable index.

Regression analysis of total weight/age by age on each of the six study areas indicates a great deal of variability among bitterbrush plants with respect to growth rate, even when growing in supposedly similar environments (Table 14). Actually, I may have made an error in attempting to fit these data to a linear design. The possibility of growth rate peaks should have suggested, that something akin to a normal curve may have been more appropriate. Some of the scatter diagrams bear a faint resemblance to this type of distribution. This was particularly marked on study areas two and three. On both sites bitterbrush is the dominant vegetation. Ponderosa pine cover is minimal, although it is more of a factor on area two. Maximum growth rate on study area two appears to be in the neighborhood of fifty years (Fig. 4). Area three shows a peak at about forty years (Fig. 5). Scatter diagrams of the other study areas show no recognizeable pattern. If growth rate peaks exist, they may occur at much older ages in areas where ponderosa pine is dominant. There is also the possibility that growth peaks in these areas are never

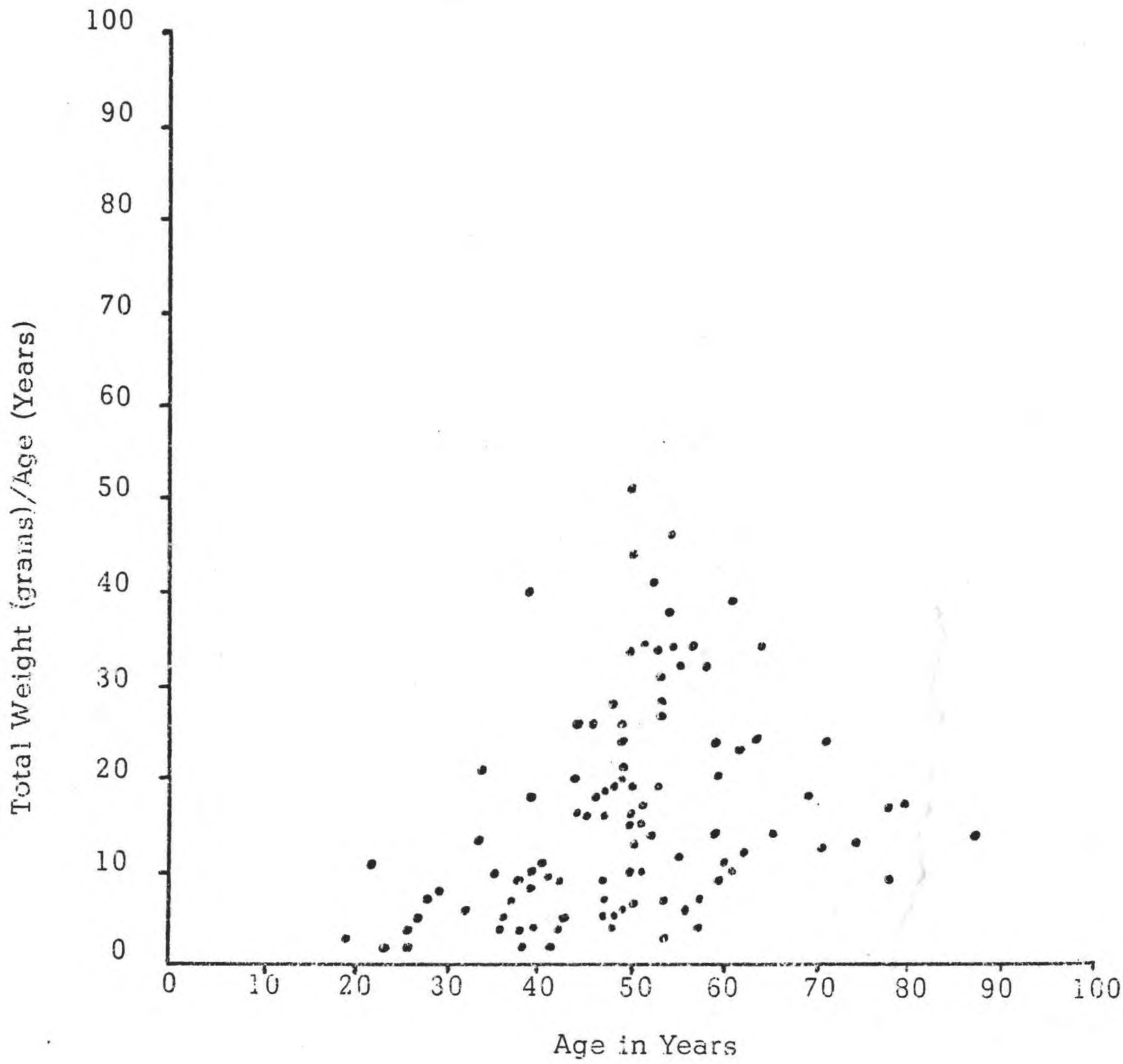

Fig. 4. Scatter diagram of total weight/age and age on study area two.

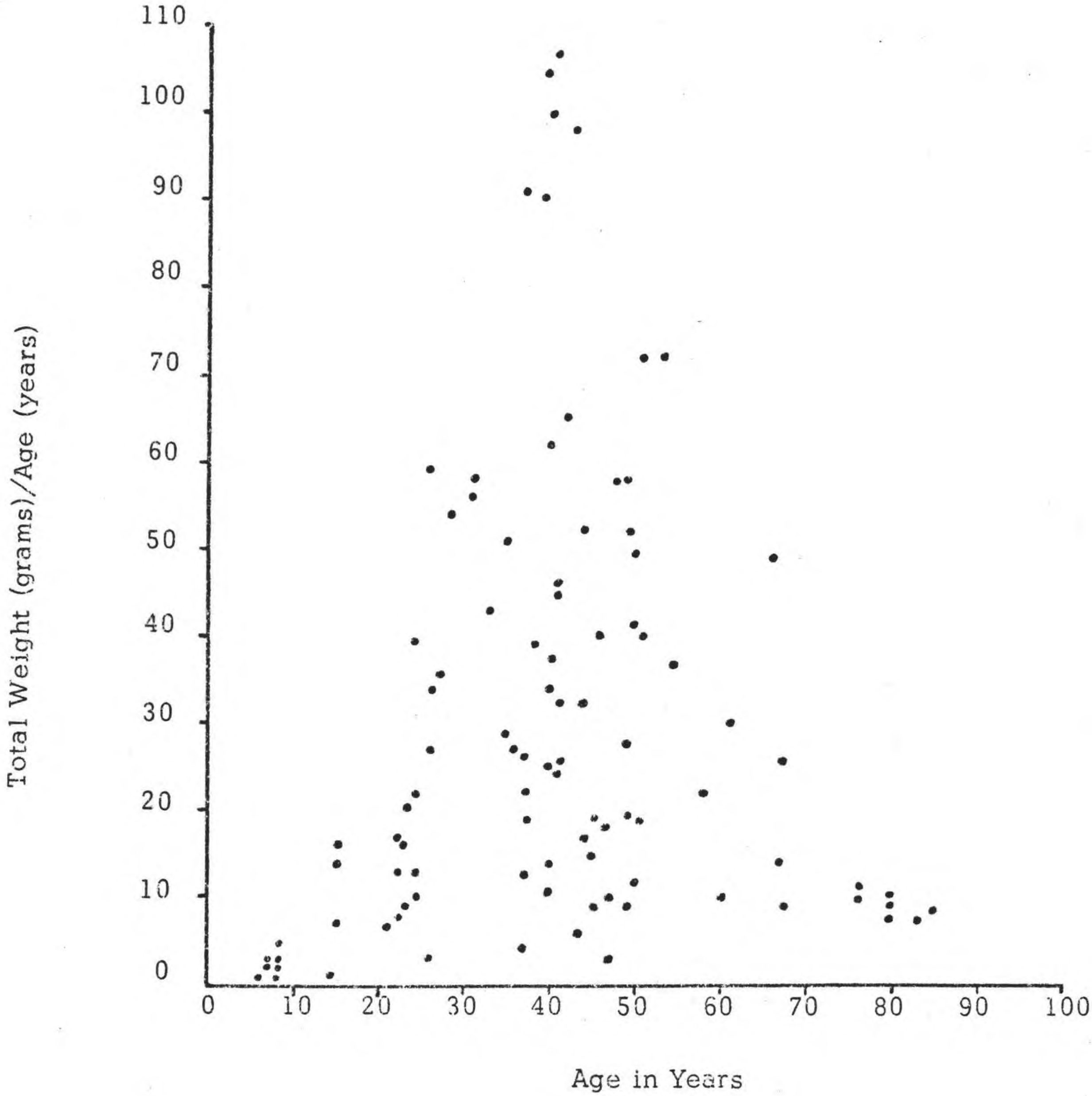

Fig. 5. Scatter diagram of total weight/age and age on study area three.

reached. Shrub death may occur before a peak is attained. However, it then becomes exceedingly difficult to attribute any shrub death to exclusively plant-ecological causes.

Regression analysis of total weight on age resulted in similar regression coefficients, with the exception of study areas four and six (Table 15).

Table 14. Linear regression analysis of total weight/age on age of 100 bitterbrush plants on each of six study areas.

Study Area	Standard Error of Estimate	Constant Term	Regression Coefficient	Correlation Coefficient	Mean Growth[1/] Rate (grams/year)	SE
1	14	-1.7	0.43*	0.48	14	1.6
2	11	-3.8	0.43*	0.44	17	1.3
3	29	14.8	0.44*	0.25	30	3.0
4	13	8.6	0.12*	0.11	14	1.3
5	11	-4.7	0.55*	0.54	11	1.2
6	5	-2.6	0.16*	0.47	5	0.6

1/ Computed from $\frac{\text{total weight}}{\text{age}}$ on individual plants.

Table 15. Linear regression analysis of total crown weight on age of 100 bitterbrush plants on each of six study areas.

Study Area	Standard Error of Estimate	Constant Term	Regression Coefficient	Correlation Coefficient	Mean Growth[1/] Rate (grams/year)
1	628	-656	36*	0.70	17
2	626	-784	35*	0.50	18
3	1034	-58	35*	0.50	34
4	590	-166	18*	0.36	14
5	487	-586	35*	0.65	14
6	331	-379	15*	0.58	8

1/ Computed from mean $\frac{\text{total weight}}{\text{mean age}}$.

If regression coefficients are used as an index to growth rate, study area four appears very low in this respect. However, the more sophisticated technique of considering growth rate as a constantly changing value, indicates that this is a fallacious conclusion.

Comparisons of results in Tables 14 and 15 reveals an apparent inflation of growth rate, if one does not consider the variable nature of this characteristic. In addition, the relativity of the two sets is somewhat distorted. Area four possesses a moderate growth rate, not as high as in areas of negligible ponderosa pine cover, but still greater than in study area six.

Examination of the analyses presented here indicates that a simple regression of total weight on age is a relatively insensitive tool for determining growth rate of bitterbrush. Furthermore, evidence suggests that growth rate is not a constant value, rather it is a changing parameter, that may reach a peak or plateau during the lifespan of a shrub. The location of such peaks is most likely a function of the type and amount of other vegetation present. Analysis of growth rate is not very meaningful unless these factors are put into proper perspective.

Comparisons with Ponderosa Pine

Ponderosa pine influences growth of bitterbrush primarily through competition for light and moisture. Reid (1964) stated that crown cover of ponderosa pine forests is inverseley related to browse production. This suggests that light is the limiting factor with respect to growth. Stanton (1959) found that, although bitterbrush reproduction was high under a canopy, growth rates were significantly lower than in open stands. Comparing a mixed bitterbrush-sagebrush community with a pine-bitterbrush community, he found that young bitterbrush on the mixed stand maintained a relatively slow growth rate until overtopping of sagebrush began to occur. At that time, a pronounced spurt of growth became evident, suggesting a release from shading. No growth spurt was apparent in the forested stand. He also found that mature plants tended to be smaller for any given age class, when a canopy was present. Since it is generally acknowledged that herbaceous vegetation is more effective as a competitor for moisture than trees, it is probably a safe assumption that light is the more growth limiting factor under a canopy. However, the same cannot be said in the case of seedlings.

Three criteria of ponderosa pine abundance were used during my study. Basal area, canopy cover, and density were measured in the hope that at least one would show a relationship with bitterbrush growth. Pase and Hurd (1957) studied the effects of silvicultural thinning of Black Hills ponderosa pine on understory yield. Understory was divided into grasses, forbs, and browse. All three goups showed a positive response to thinning, but grasses and forbs accounted for the majority of increase. Browse plants were relatively slow responding to a competition release. In spite of this, shrub understory experienced a 16-fold increase in production on clear cut areas. Total herbage yield was inversely related in a curvilinear manner to basal area and canopy cover. McConnell and Smith (1965) in a similar study, found negative linear relationships with canopy cover and basal area. Levels of thinning, as measured by density proved nonsignificant. Results obtained during my study were definitely negative, but whether the relationships are linear or curvilinear remains to be seen.

Average growth rates of bitterbrush and the three pine measurements are given in Figures 6, 7, and 8 to illustrate the overall effect of ponderosa pine. To obtain an adequate range of values, these data were compiled from all six study areas. All three graphs reveal an inverse relationship with growth rate that approaches curvilinearity. Basal area and density are apparently the factors most strongly related to growth rate. A plausible explanation might be that measurement techniques for these two variables were considerably more accurate than for canopy cover.

Disregarding growth rate for the moment, a comparison of mean total weights on the six study areas confirms the hypothesis that bitterbrush plants are larger in open stands than in forested communities. Table 16 arranges the study areas so that mean total weights appear in ascending order. Basal area corresponds inversely to this arrangement.

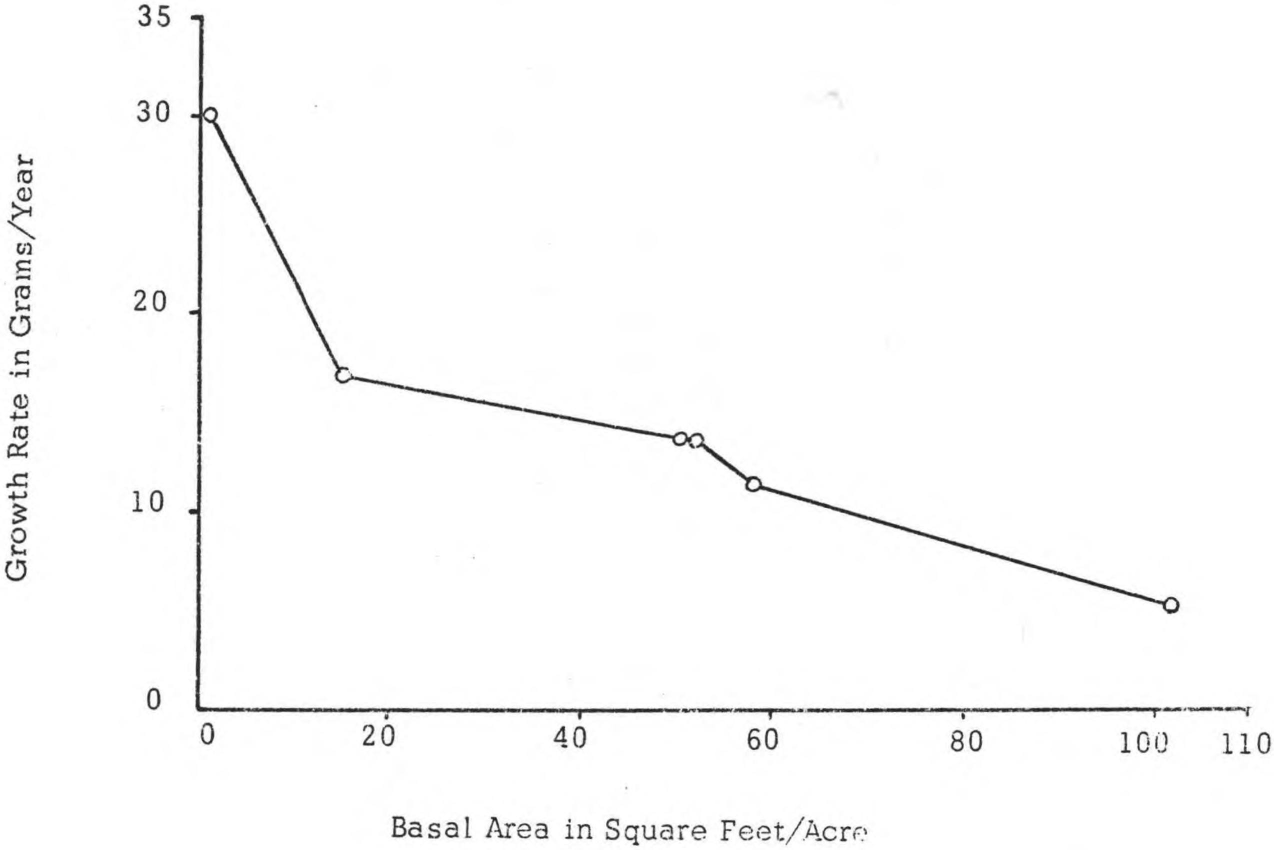

Fig. 6. Growth rate of bitterbrush compared with ponderosa pine basal area.

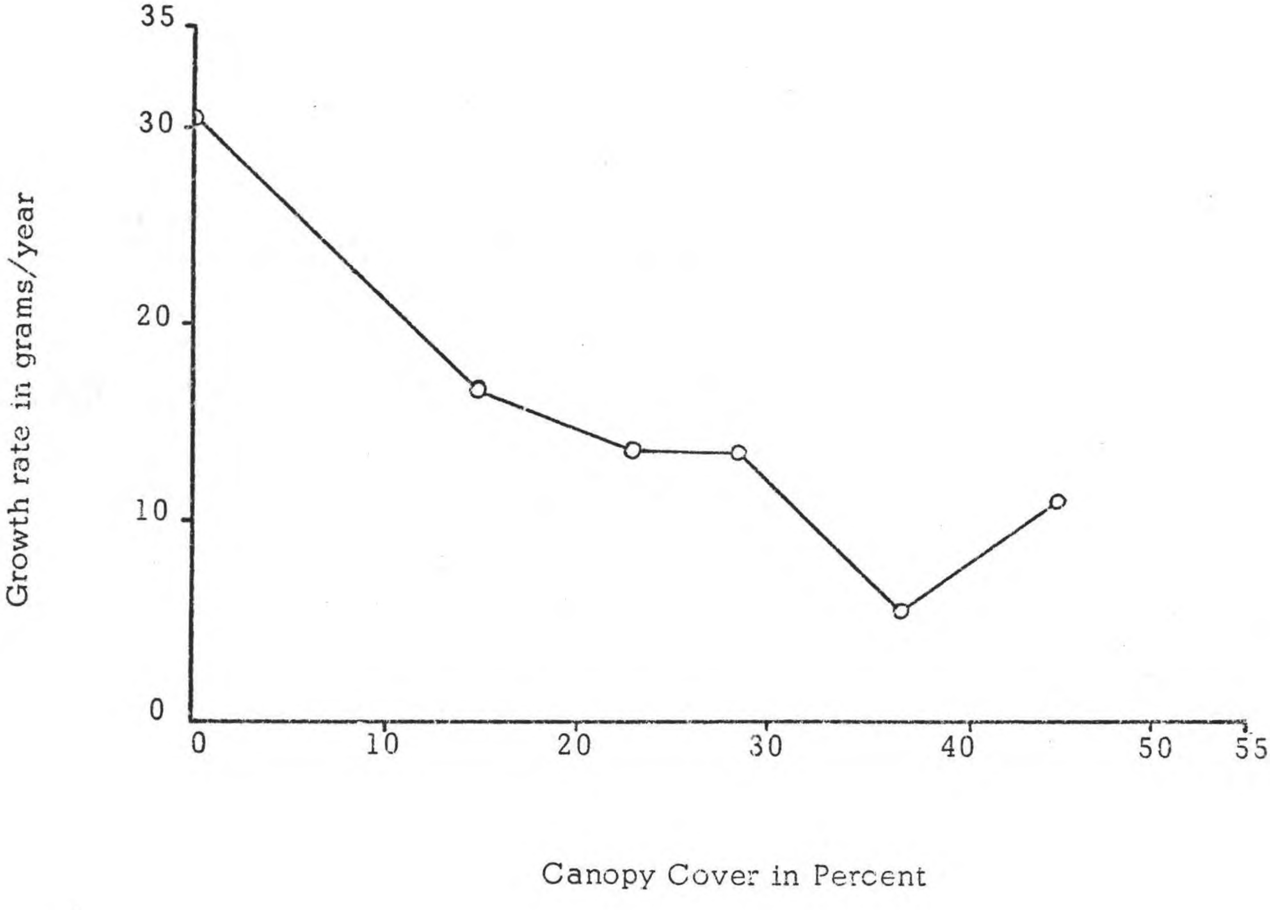

Fig. 7. Growth rate of bitterbrush compared with ponderosa pine canopy cover.

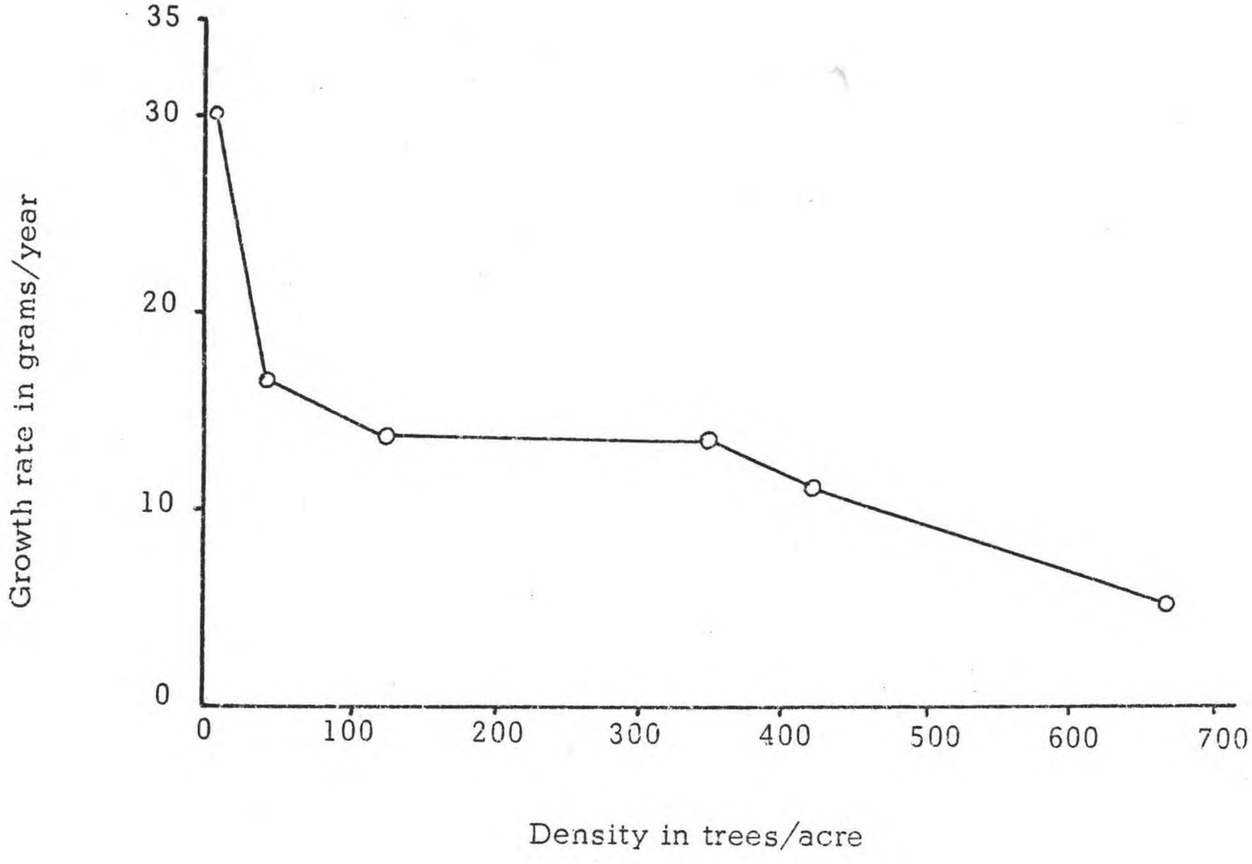

Fig. 8. Growth rate of bitterbrush compared with ponderosa pine density.

Table 16. Mean total weight and basal area on six study areas.

Study Area	Basal Area (ft^2/acre)	Total Weight (grams)
6	102	312
5	58	393
1	47	619
4	46	626
2	15	874
3	1	1178

An analysis was made utilizing total weight per plot as the dependent variable and with five independent variables (Table 17). Herbaceous cover and shrub cover will be discussed later. The standard error of estimate for the multiple regression equation was 2939 grams and 54 percent of the variation was accounted for.

Basal area is by far the best predictor of total weight in bitterbrush. Possibly this is because basal area is a composite of both size and density. Therefore it is a more accurate index to the relative dominance of pine. In contrast, canopy cover largely neglects density, and the latter gives no indication of size.

In the analysis presented in Table 17, partial regression coefficients were significant for both canopy cover and basal area. Relating bitterbrush growth rate to these two variables results in only basal area being significant (Table 18). A possible reason is

Table 17. Multiple regression analysis of plot totals for bitterbrush total weight on indices of ponderosa pine abundance, herbaceous cover and shrub cover.1/

Factor	Partial Regression Coefficient	Standard Partial Regression Coefficient	Simple Correlation	Partial Correlation
Tree density	2	-0.27	-0.53	0.07
Canopy cover	-57*	0.09	-0.62	-0.28
Basal area	-66*	-0.59	-0.07	-0.43
Herbaceous cover	-16	-0.07	0.41	-0.07
Shrub cover	40	0.10	0.43	0.12

1/ The constant term for the equation was 10,470.

Table 18. Multiple regression analysis of plot means for total weight/age of bitterbrush on basal area, canopy cover, and herbaceous cover.1/

Factor	Partial Regression Coefficient	Standard Partial Regression Coefficient	Simple Correlation	Partial Correlation
Basal area	-0.16*	-0.56	-0.69	-0.45
Canopy cover	-0.12	-0.23	-0.59	-0.23
Herbaceous cover	-0.03	-0.04	0.44	-0.05

1/ The constant term for the equation was 25.81.

that height growth of ponderosa pine is generally more rapid than diameter growth. Thus, 20 years ago basal area may have been nearly the same as now, but canopy cover could have been significantly less.

In addition to the two variables already named, herbaceous cover was a third independent variable in the regression involving growth rate. The coefficient of determination for this analysis was 50 percent and standard error of the estimate was 7.5. Very little difference between standard partial regression coefficients for basal area is evident when one compares the two analyses. Presumably because growth rate is a function of total biomass production.

Comparisons with Herbaceous Cover

Both herbaceous vegetation and ponderosa pine limit the growth of bitterbrush. Pine competes for light and soil moisture, while herbaceous vegetation asserts its effect, primarily, on soil moisture in the upper horizons (Horton 1950).

The lieterature suggests that herbaceous vegetation is primarily limiting to establishment and survival of seedlings (Holmgren 1954; Hubbard 1956b). Effects on the growth of mature plants are less well known, but it is likely that herbaceous vegetation is not nearly as growth-limiting as trees. If this were not true we could expect that bitterbrush growing in study areas one and six to be at least as large as in areas two and three. Hubbard and Sanderson (1961b) found that removal of perrennial grasses from bitterbrush plots resulted in significant growth increases. Average leader length on their sample plants increased approximately 0.8 inches as a result of weeding. Number of leaders increased by approximately four per main branch. A quick computation of total herbage increase reveals that this is certainly not equal to the 16 fold increase that resulted from clear-cutting pine (Pase and Hurd 1957).

Herbaceous cover did not significantly influence bitterbrush growth (Table 17 and 18). Scatter diagrams of herbaceous cover, total weight, and growth rate show no recognizeable pattern. If there is a relationship, it could be masked by the confounding effect of ponderosa pine. However, multiple regression analysis should have eliminated this.

Crown Die Back and Vigor

Age and Living Crown Weight

Total biomass production is useful information for evaluating competitive relationships, but it is a relatively poor index for evaluating forage production. The weight of the living or productive portion of the crown may be more useful in this respect. Such a measurement when compared with total weight and age, will provide some indication of vigor status. It is generally accepted that vigor profoundly affects forage production. However, in the past, vigor has too often been categorized as either poor, fair, good, or excellent simply on the basis of subjective judgment. If a reliable quantitative measure of vigor can be ascertained, it would be a real contribution to present game range menagement.

The most logical conception of browse vigor is that it is a composite of several factors. Some of the more likely measurements relating to vigor are age, living weight, percent of dead crown material, crown area or volume, and the ability to produce forage. Living weight in combination with age makes up what we might call an "effective growth rate". It is a measure not only of the ability to produce biomass in a given community, but also an index to the environmental resistance acting upon the plant.

Linear regression analysis of living weight on age was uniformly significant on all study areas (Table 19). Since it is crown death which results in living weight being less than total weight, it may be that linear regression is not the proper method. Crown die back should accelerate with increasing age. Evidence presented later confirms an increase, but not necessarily a constantly changing one. There may be a curvilinear relationship of age and living weight, but the variability of the data precludes positive determination.

Comparison of mean age and living weight on the six study areas suggests that shrub age is not directly important in determining living weight (Table 20). This is because age was not a factor with respect to total weight production. More likely, it is the external environment which controls this. Although growth rates may vary with increasing age, it is unlikely that age alone is responsible.

Dead Crown Material as a Vigor Index

Essentially two criteria are available to game range managers for estimating browse vigor. The first is growth potential, made evident

Table 19. Linear regression analysis of living crown weight on age of 100 bitterbrush plants on each of six study areas.

Study Area	Standard Error of Estimate	Constant Term	Regression Coefficient	Correlation Coefficient
1	465	-430	25	0.69
2	350	-349	19	0.56
3	556	36	16	0.43
4	372	-47	9	0.30
5	279	-221	17	0.59
6	208	150	7	0.47

by current leader production. Although leader growth is strongly related to yearly climatic variation, relativity of growth should remain constant between poor and good vigor plants. The second characteristic is proximity to death, recognizeable by the amount of dead material in the crown.

Table 20. Bitterbrush crown die back as related to other growth parameters.

Study Area	Total Weight (grams)	Growth Rate (grams/year)	Living Weight (grams)	Effective[1/] Growth rate (grams/year)	Dead Crown Material (%)
6	312	5	178	4	37
5	393	11	257	9	19
1	619	14	473	13	13
4	626	14	369	8	37
2	874	17	544	11	29
3	1178	30	592	17	40

[1/] These figures based on a calculation using study area means (living weight). All others are derived from 100 individual observations.
age

Few papers have been concerned with the rationale for using percentage of dead crown matter as a vigor index. In spite of this, it has been widely used in management. An unpublished report outlining procedures for standard big game range analysis, considers that browse plants with more than 1/4 dead material in the crown must be rated decadent. This report has seen wide circulation among western game and fish departments. Many have used it as a guide for game range analysis. Stanton (1959) noted that in one particular bitterbrush stand he studied, many of the plants had large percentages of dead material in the crown. He concluded that vigor was very low overall and that the community was probably not maintaining itself.

Stickney (1965) studied winter crown kill of buckbrush (Ceanothus velutinus) and found that snow depth at the time of a sudden freeze following a warm period was a critical factor. Exposed branches were generally killed when these conditions were met. In the case of bitterbrush, I doubt if snow depth and temperature are important factors. If this were true, some locational pattern of dead branches should be evident. Bitterbrush exhibits no such pattern. Often dead portions occur on the lowest branches of the plant.

Rodent and insect activity may cause some crown die back, but their importance is unknown. Clark (1956) reported that the Great Basin tent caterpillar (Malocosoma fragile) periodically defoliates bitterbrush, and under certain conditions causes death. Hubbard and Mckeever (1961) studied a population irruption of Microtus montanus of sufficient magnitude to cause a movement of mice out of their normal habitat into adjacent bitterbrush range. The result was a five percent bitterbrush kill and a 15 percent damage rate. The mechanism was stem girdling.

Another possibility is unusual climatic variation. If two or even three extremely good growth years are followed by a drouth period, there may be crown die back rather than thinning of the stand.

Six factor multiple regression analyses were used to relate bitterbrush age, some shrub-to-tree distances, and pine stem diameter to the percent of dead crown material. Results were inconclusive. On six study areas, only age proved to be consistently significant.

A second multiple regression listed canopy cover, basal area, tree density, herbaceous cover, and shrub cover as independent variables. None of these showed a significant regression on percent dead material, although basal area and canopy cover approached significance.

Table 20 presents mean percent dead material as it relates to some other growth parameters. At present, this seems to be the only way to visualize crown death. Certainly it doesn't appear to be a function of other vegetation. Perhaps the machanisms involved are not primarily biotic, but rather climatic or even genetic. Also, relatively little is known concerning the past history of these areas, particularly as it relates to browsing or grazing animals. Surely deer and elk have a profound influence on vigor, but the exact effect is difficult to assess unless the investigator can date the time and intensity of use and afterwards follow shrub growth for a period of years.

The almost total failure of this study to establish causes for crown die back is at first disappointing. However, even negative results provide some information. Namely, that factors other than those studied may exert a much greater influence. It is apparent that future investigations will require more sophisticated measurements. Although research projects of this type are bound to be complex and difficult, I believe their potential merits perserverance.

Production of Leaders

Effects of Age and Vigor

Current leader growth is a vigor criterion not yet fully examined. Most past studies have used length of leaders as the principal measurement. Stanton (1959) did not attempt to relate leader length to vegetative portions of the environment, but he did find significant correlations with current year precipitation. This is confirmed by a number of other authors. It is one of the aims of this thesis to relate leader growth to age and other growth characteristics of bitterbrush and some measures of pine and herbaceous abundance. To achieve this, leader growth is expressed in several ways. In this section all plant weights are in oven-dry terms, instead of the green weights used previously. Table 21 lists study area means of the various measurements employed. Study area one is omitted because of a failure to collect the needed data.

Attempts to correlate current growth parameters with age were generally unsuccessful. Partially this was the result of small sample size. One study area, did however, show a significant relationship. On study area three it was found that percent leader weight declined with age (Fig. 9). Similar analyses, using number, total weight, and length of leaders proved uniformly nonsignificant. It is apparent to me that bitterbrush age is not a crucial factor determining current

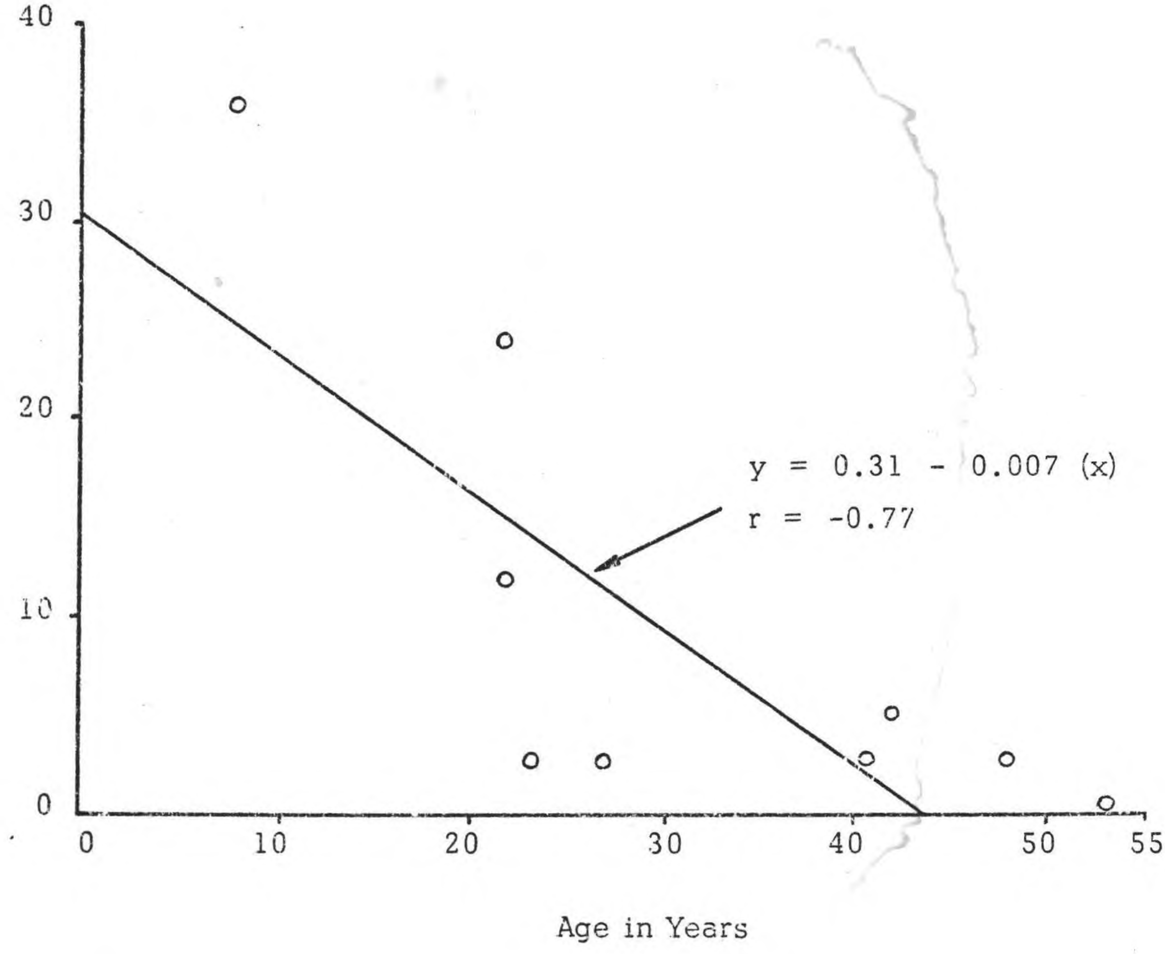

Fig. 9. Linear regression analysis of leader weight expressed as a percent of living crown weight on bitterbrush age on Study area three.

forage production. The fact that there was a regression on study area three could be coincidence.

That leader growth is a criterion of vigor is illustrated by a regression analysis of percent leader weight on percent dead crown material (Table 22). There should be an inverse relationship, and this is precisely the case. Five study areas were grouped together for the analysis. Two plants had to be eliminated because of zero observations. Thus, the effective sample size was 48 individuals.

Table 21. Characteristics used to describe current leader production.1/

Study Area	Number of Leaders/bush	Mean Leader Length (cm)	Total Leader Weight/bush (g)	% of Living Weight
2	98±21 2/	3.8±0.4	7±1.7	3±1
3	134±30	4.3±0.4	9±2.4	10±4
4	113±42	4.3±0.3	8±3.2	7±2
5	95±23	4.6±0.3	5±1.3	12±3
6	131±50	5.0±0.5	11±4.9	8±1

1/ Based on a sample of 10 bushes per study area.
2/ ± Standard error of the mean.

Table 22. Linear regression analysis of percent of living weight composed of leaders on percent dead crown.

Standard error of Estimate	Constant Term	Regression Coefficient	Correlation Coefficient
0.07	0.15	-0.19*	-0.48

The above analysis suggests that dead material and leader growth are indeed indicators of vigor. The problem, however, is to delineate the factors which cause crown die back and leader production. If this can be accomplished, management practices can be devised that would favor maintenance of good vigor bitterbrush.

Effects of Competition

Competitive effects of herbaceous vegetation on bitterbrush growth have been well documented. The foremost effect is a shortening of the growing season. Holmgren (1956) found that when soil moisture is exhausted early, seedlings usually die and further growth of mature plants is sharply inhibited. He also found that the severity of competition is directly linked to current precipitation.

If production of leaders is primarily a product of precipitation, it may be that moisture competition was minimal during this study. Reference to Chapter 3, Table 2, reveals that 1967 was a wet year, particularly during the critical May to July period. Since it is generally acknowledged that moisture competition is most severe during drouth periods, the relative abundance of moisture during the growing period of 1967 suggests that perhaps competition was much less a factor than it normally is. Herbaceous cover can compensate for increased moisture by an increase in density. Ponderosa pine cannot quickly do this, and must rely on an increase in growth rate. The end result is an increase in available moisture for bitterbrush growth, particularly where herbaceous cover is at a minimum.

A tabular comparison of herbaceous cover, tree basal area, and some current growth paramenters may be helpful in understanding competitive influences (Table 23).

Table 23. Bitterbrush current growth parameters as related to ponderosa pine and herbaceous abundance.

Study Area	Mean Leader Length (cm)	Number of Leaders/bush	Herbaceous Cover (%)	Basal Area (ft^2/acre)
2	3.8	98	41	15
3	4.3	134	44	1
4	4.3	113	38	46
5	4.6	95	27	58
6	5.0	131	3	102

Looking closely at Table 23, Leader length seems inversely related to herbaceous cover. Basal area has no apparent effect. Number of leaders seems independent of either ponderosa pine of herbaceous abundance. The conclusion is, that if surrounding vegetation exerts any influence upon current annual growth in bitterbrush, it is the herbaceous component which has the greatest effect.

Crown Area of Bitterbrush

Estimating Living Weight

Frequently during the course of ecological investigations, it becomes necessary or desirable to estimate the amount of biomass occupying a given area. A number of techniques have been used to estimate herbaceous yields. Double-sampling as described by Wilm, Costello, and Klipple (1944) is an accepted method still in use today. Tree volumes can be calculated with the aid of wedge prisms (Grosenbaugh 1952). Shrubs have not received much attention. Lyon (1968) devised an accurate method of estimating twig production on serviceberry (*Amelanchier alnifolia*), that was quick and easy. Fitting crown volumes and twig production into a linear regression design, he was able to assign over 80 percent of the variation in twig production to crown volume. Similar techniques may hold promise for bitterbrush, if environmental variation can be held constant or accounted for.

During this study, it was found that living weight could be accurately estimated from two simple measurements. Measuring crown width at its widest point and again at right angles, resulted in two lengths from which area could be calculated.

The same data were also used to describe shape or eccentricity of crowns. Mean minimum-maximum ratios varied from 0.70 to 0.74 over five study areas. A two-way nested analysis of variance was used to test two null hypotheses. First, that eccentricity was equal between study areas. Second, that eccentricity was equal between plots, within study areas. Both of these hypotheses were accepted. Thus, it seems that crown shape of bitterbrush is essentially elliptical, under almost all conditions.

Regression analysis revealed that a curvilinear relationship existed between crown area and living weight (Table 24). Logarithmic transformation was used to straighten out the curve.

Table 24. Curvilinear regression of living weight on crown area on five study areas.[1]

Study Area	Standard Error of Estimate	Constant	Regression Coefficient	Correlation Coefficient
2	0.15	-0.7	0.99*	0.92
3	0.18	-1.4	1.17*	0.97
4	0.14	-1.2	1.08*	0.95
5	0.18	-1.3	1.08*	0.94
6	0.20	-1.1	1.02*	0.94

[1] Regression equation follows the form: $\log y = a + b (\log x)$

All of the analyses were significant, and correlation coefficients confirm that living weight can be estimated with considerable accuracy by this method.

Effects of Competition

Multiple regression analysis of bitterbrush crown area on herbaceous cover, canopy cover, and basal area was similar to previous analyses using total weight as the dependent variable (Table 25). Standard error of the estimate was 1031 and 34 percent of the variation was accounted for. Basal area was the best predictor of shrub crown area, just as it was for total weight.

Table 25. Multiple regression analysis of plot means of crown area on herbaceous cover, basal area, and canopy cover.[1/]

Factor	Partial Regression Coefficient	Standard Partial Regression Coefficient	Simple Correlation	Partial Correlation
Herbaceous cover	-18	-0.3	0.22	-0.23
Basal area	-25*	-0.7	-0.55	-0.50
Canopy cover	2	0.0	0.03	0.03

[1/] The constant term for the equation was 4429.9.

Recommendations for Future Research

This study was essentially an exploratory investigation about a very broad area of knowledge. During the data gathering and analysis, numerous opportunities for further research have become apparent. To be successful, followup studies must have more specific objectives and more closely controlled experimental designs. Listed below are some recommendations for research.

1 Investigations should be initiated that will evaluate effects of small rodent populations on sexual reproduction of bitterbrush.

2 The significance of asexual reproduction to selected bitterbrush communities should be studied. This is a subject about which very little detailed information is available.

3 Further age structure studies of bitterbrush populations could be of considerable value. Age must have a profound influence on such things as vigor, forage production, and seed production. The problem is to detect these effects. A more controlled experiment than the present one, might be more successful.

4 Comparisons of bitterbrush age structures with climatic records and history of an area would do much to explain some of the differences existing in community age structures.

5 A series of studies need to be started that will investigage various facets of bitterbrush growth and vigor. First, these are terms which need more precise definition. Only then, can the factors which influence growth and vigor be properly evaluated.

CHAPTER V

SUMMARY AND CONCLUSIONS

The objectives of this study were to study possible effects of ponderosa pine and herbaceous vegetation on the growth and vigor of bitterbrush. More specifically, it was desired to investigate and identify important coactions.

Field work was accomplished during the summers of 1966 and 1967. Study areas were located approximately 30 miles due west of Fort Collins, Colorado. Exposures were generally southeasterly and elecvation ranged from 3700 to 8400 feet. Six sites representing various combinations of bitterbrush, ponderosa pine, and herbaceous vegetation were chosen for study.

Ten randomly located points on each study area provided a basis for selection of bitterbrush plants, ground cover estimates, and measurements of ponderosa pine abundance.

Soils on all six sites were characterized by shall A horizons and B horizons from 13 to 17 inches deep. Texture was sandy, organic matter content was less than 10 percent in the upper horizon, and organic content decreased with depth.

Bitterbrush plants were measured for height, crown diameters, and shrub to tree distances. Then the stem was severed at the root crown and the living and dead portions weighed separately. A stem section was collected for laboratory determination of age by direct ring count.

Herbaceous vegetation was classified according to total cover on a 100 ft^2 circular plot. Species were identified and relative abundance and grazing intensity estimated. Grasses proved to be the most important herbaceous component on all study areas.

Sexual regeneration of bitterbrush was extremely rare during the period of the study. Vegetative reproduction by layering was common. These limited data suggest that bitterbrush is more successful at sexual reproduction when ponderosa pine is present. Perhaps this is due to shading, reduced herbaceous competition, or a combination of both. The occurrence of multiple seedlings groups indicates that small rodents may play an important role in seed dispersal.

Age structure varied significantly between study areas, although no relationship with ponderosa pine or herbaceous vegetation was evident. Study area means of age varied from 28 to 49 years. On the basis of age structure, three of the study areas appear to have declining bitterbrush stands.

Growth studies of bitterbrush revealed that growth rate is a dynamic parameter, at least partially related to age. Growth rate and biomass production of bitterbrush were responsive to different levels of ponderosa pine basal area. Herbaceous vegetation did not limit growth, except during the seedling stage. Bitterbrush plants of equal age are almost invariably larger in open stands.

Adequate methods of measuring shrub vigor were not developed. The percent of dead material in the crown was an unsatisfactory index because of extreme variation between plants. Percent dead crown was not a function of pine or herbaceous cover.

There is some evidence that herbaceous vegetation is the factor most directly influencing current annual growth in bitterbrush. Leader production, expressed as a percent of living crown weight was inversely related to percent dead crown.

Correlation coefficients between living weight and crown area were from 0.92 to 0.97.

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APPENDIXES

DATA SHEET FOR STUDY AREAS

Investigator(s) ______________________________

Project Number	Project Code	Data Year	Study Area No.	Slope %	Exposure	Elevation	Dist. to Permanent water	Distance to salt grounds	Depth A	Depth B	Depth C	% sand A	% silt A	% clay A	% Organic Matter A	% sand B	% silt B	% clay B	% Organic Matter B			Data type
XXXX0XXX	XXXX	X	XX	XX	XXX	XXXX	XXXX	XXXX	XX	XX	XXX	XX	XX	XX	XX0XX	XX	XX	XX	XX0XX			
																						1
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DATA SHEET FOR PLOTS

Investigator(s) ______________________ Dates collected ______________________

Project Number	Project code	Data Year	Study Area	Plot Number	number of seedlings	% Bare Ground	% Litter	% Rock	% herbaceous cover	% Under Canopy	% Shrub Cover	Trees/0.2 Acre	Basal Area	% Canopy Cover		Data Type
XXXXOXXX	XXXX	X	XX	XX	XX	XX	XX	XX	XX	XX	XX	XXX	XXX	XX		X
CAES 315	1817															2
CAES 315	1817															2
CAES 315	1817															2
CAES 315	1817															2
CAES 315	1817															2
CAES 315	1817															2
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CAES 315	1817															2
CAES 315	1817															2

DATA SHEET FOR HERBACEOUS VEGETATION

Investigator(s) ______________________ Date(s) Collected ______________________

Project Number	Project Code	Data Year	Study Area No.	Plot Number	Species	Relative Importance	Grazing Class		Data Type
XXXXOXXX	XXXX	X	XX	XX	XXXX	XXX	XXX		X
-CAES 315	1017								3
									3
									3
									3
									3
									3
									3
									3
									3
									3

DATA SHEET FOR PUTR SEEDLINGS

Investigator(s) ______________________________

Project Number	Project Code	Data Year	Study area	Plot Number	Seedling Number	Height	Weight	Litter Weight	% Herb. cover	Distance to tree canopy	Distance to tree bole	Distance to shrub	Age		Data type
XXXXOXXX	XXXX	X	XX	XX	XX	XX	XXX	XXX	XX	XXX	XXX	XXX	XX		X
CAES 315	1817														4
															4
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															4

DATA SHEET FOR BITTERBRUSH PLANTS

Investigator(s)______________________________

Project number - CAES 315
Project code - 1817
Card columns - 1 through 12

Data year	Study area number	Plot Number	Shrub Number	Height	Max. Crown diameter	Mim. Crown diameter	Distance to canopy	Distance to bole	DbH of nearest tree	Dead green wt.	Living green wt.	Wt. of old live growth	Wt. of current growth	Oven dry wt. of current growth	Oven dry wt. of old live growth	Oven dry wt. of dead growth	Leader length	Age	No. of Leaders	No. of Stems		Type
X	XX	XX	XX	XX	XX	XX	XXX	XXX	XXOX	XXXX	XXXX	XXXX	XXXOX	XXOX	XXXX	XXXX	XXXX	XXX	XXX	XX		X
																						5
																						5