ECOLOGICAL STUDIES OF THE GROWTH OF PONDEROSA PINE ON THE EAST SLOPE OF THE ROCKY MOUNTAIN FRONT RANGE IN BOULDER COUNTY, COLORADO

by

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Ecological Studies of the Growth of Ponderosa Pine on the East Slope of the Rocky Mountain Front Range in Boulder County, Colorado

Thesis directed by Associate Professor John W. Marr

The purpose of this study was to describe in some detail the initiation, rate, and cessation of growth in ponderosa pine, and to correlate these three features of growth with certain environmental factors.

It is the first such growth study of ponderosa pine which has been made in this region utilizing both dendrometer and tissue-section methods. In addition to describing for the first time the gross features of growth at the one-meter level in the Front Range ecotype of this species some major correlations of this growth pattern with certain environmental factors have been pointed out.

The diameter growth in five individuals of <u>Pinus ponderosa</u> Laws. variety <u>scopulorum</u> was measured at the one-meter level for two consecutive seasons, at an elevation of 7,500 feet in the Lower Montane Zone in Boulder County, Colorado. Diameter measurements were made externally with a dial-gauge dendrometer. These diameter measurements were supplemented by microscopic study of tissue cross-sections taken from the cambium and adjacent tissues. Measurements of the external environment of the pine stand were made with standard United States Weather Bureau equipment supplemented by special apparatus for the measurement of soil moisture.

Growth was initiated early in May in the trunk cambium at the one-meter level. This initiation of growth is correlated with the attainment of a 50° F. mean air and soil temperature. Fifty percent of the diameter increase was completed within thirty days. This is a more rapid growth rate than is found in other ecotypes of ponderosa pine. Growth rate was constant and apparently unaffected by the seasonal trend of rising temperature and decreasing soil moisture. Three rows of phloem parenchyma were produced in a single season in contrast to the white pine which produces only a single row of phloem parenchyma. Crushing of new sieve elements occurs as early as the latter part of June. Cessation of diametral growth is difficult to determine exactly but by the end of August growth seems essentially complete and cambial activity at an end. This cessation of diameter growth does not appear to be directly correlated with soil drought or lowering temperatures, and is apparently autogenous in its onset.

This abstract of about 350 words is approved as to form and content. I recommend its publication.

Signed John W. Marr
Instructor in charge of dissertation

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[illegible] Date of Completion of [illegible] 50 and [illegible]
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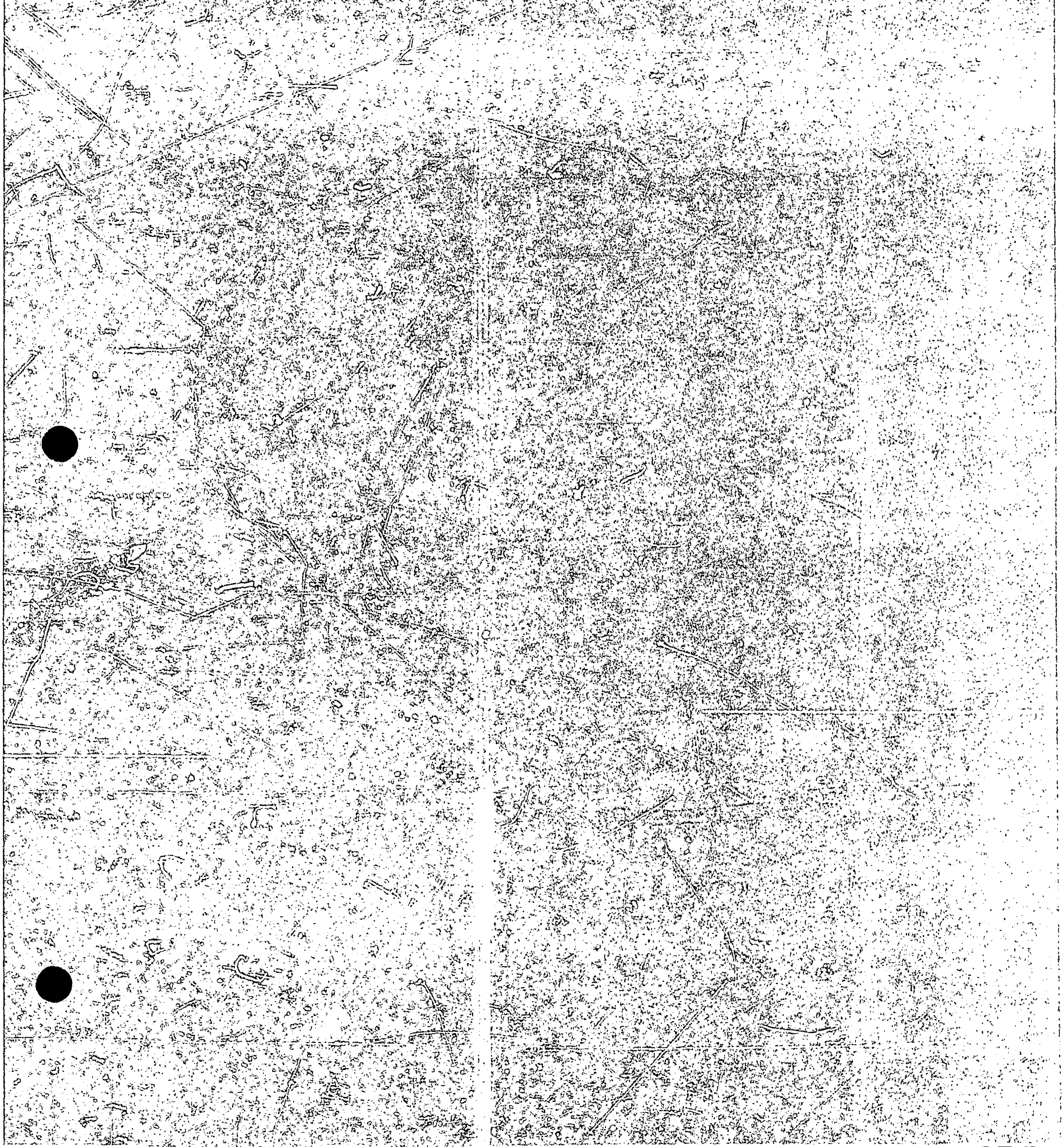

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INTRODUCTION

Pinus ponderosa Laws. is one of the most abundant and widely distributed trees in the western United States (Betts, 1945). It is found in a wide range of regional climates (Pearson 1951) occurring on a wide variety of sites in both pure and in mixed stands. The principal objective of this study, extending uninterrupted through two consecutive years (1957-1959), was to measure the seasonal diameter changes of this species at the one meter level and to compare its growth pattern at this single level with seasonal changes in the physical environment. The results discussed in this paper are based on data for the 1958 growing season.

In this investigation of diameter increment, two methods were used: periodic measurements of diameter with the dial gauge dendrometer, and microscopic measurements made on cross sections prepared from tissue samples taken from the cambium and adjacent regions. Dendrometer studies of diameter growth in ponderosa pine in the northern Rocky Mountains have been published in a series of papers by Daubenmire (1950, 1945) and Daubenmire and Deters (1947); however, they did not supplement their measurements with tissue studies. Numerous accounts of tissue studies made for the purpose of following the inception and cessation of growth in the conifers have been published, principally on two species, Pinus strobus L. and P. rigida Mill. (Brown 1912, 1915; Abbe and Crafts 1932). Lodewick (1928) published a very thorough study on the hardwoods and a few of the conifers of the northeastern United States. In only one instance, that of Fraser (1952) on white pine, have such growth studies been made utilizing both the dendrometer and tissue-section methods. The present investigation is the first such study of ponderosa pine growth which has been made in this region. It is also the first time that continuous measurements have been made of air and soil temperatures, precipitation, and soil moisture, in close proximity to the trees during the entire interval of the study. Thus, in addition to describing for the first time the gross features of growth at the one meter level in the Front Range ecotype of ponderosa pine, some major correlations of this growth pattern with certain environmental factors will be pointed out.

DESCRIPTION OF THE REGION

Topography

The Colorado Front Range is a north-south trending mountain uplift 30 to 35 miles wide extending north from Canyon City, Colorado, to the southeastern corner of Wyoming, where it merges with the Laramie Range. It rises sharply from the undulating surface of the Great Plains which lie to the east, and while its western slopes are precipitous, their exact boundaries are indistinct, often merging with other mountain systems of different geologic origin. The central portions of the range rise to elevations of 12,000 to 14,000 feet; however, individual peaks seldom extend more than 3,000 feet above the underlying mountain mass. The Continental Divide passes along the crest of the range. Most of the breadth of the range is taken up in its eastward extension which descends from the divide to the plains in a series of five gently sloping and much dissected benches (Lovering and Goddard 1950).

These benches are ancient erosion surfaces, each of which has been subjected to uplift and subsequent erosion at different times, and are deeply dissected in an east-west direction by narrow valleys, ranging in depth from 500 to 1,500 feet, and the larger ones of which have permanent streams flowing through them. The study site is on a spur of one of the ridges associated with the Bergen Park surface, one of the lowermost of these old erosion benches. To the west of the site this broad ridge rises at a rate of 400 feet per mile to the base of Sugarloaf mountain. After a similar rise to the north it drops steeply 1,500 feet into Fourmile Canyon. To the south and east the spur drops about 200 feet to the bottom of the very narrow Bummer Gulch, which after winding southeast for another 2 miles and losing 500 feet in elevation empties into Boulder Canyon. Reference to Figure 1 will make these relationships clear.

Vegetation and Cultural Influence

The Lower Montane Zone (Marr 1956), which is roughly equivalent to the Ponderosa Pine Zone (Daubenmire 1943), ranges from 6,000 feet to 7,700 feet at this latitude, although ponderosa pine extends beyond these limits. Below this, extending down to the hogbacks and mesa tops at 5,300 feet, is a transition zone composed of ponderosa pine and plains grasses, with some douglas-fir occurring on north-facing slopes.

Ponderosa pine is the dominant woody vegetation of the Lower Montane Zone, occurring in open park-like stands on the steeper south-facing slopes, and in closed stands on the more gentle south and east slopes and the ridge tops. Mature stands

Fig. 1. Aerial photograph of the region.

The large square outlines Section 29 of Township 1 North, Range 71 West of the 6th principal meridian. The study area, A-5, is enclosed by the trapezoid, and the position of A-1 by a triangle. Other prominent features represented by letters are:

W	Fourmile canyon, near Wallstreet
C	Fourmile canyon, near Crisman
Smt	The eastern edge of the base of Sugarloaf Mountain
Ts	The village of Sugarloaf
B	Bummer Gulch road
Bo	Boulder Canyon and State Highway #119

1 Mile

are generally open, whatever the topographic aspect, while stands with closed canopies are either young pole stages or older trees in which growth has stagnated due to natural over-stocking. Pure stands of pine are limited to south- and east-facing slopes, while on north-facing slopes douglas-fir is a co-dominant with ponderosa pine at lower elevation becoming more abundant at greater elevation. Above 9,000 feet ponderosa pine is generally absent except on steep south-facing slopes up to 10,000 feet elevation.

Characteristic shrubby species of the Lower Montane Zone are Juniperus scopulorum Sarg. on the south slopes, and on the north slopes and shady ridges J. communis L. and Arctostaphylos uva-ursi (L.) Spreng. These species are in the shrub layer with such deciduous plants as Ceanothus fendleri Gray and Ribes species. Various species of willows and cottonwoods are abundant along the stream courses. Characteristic herbs and their blooming period are listed in Table I.

Examination of the aerial photograph (Figure I) shows a patchwork of forest stands of varying density, interlarded with meadows of all sizes. Whether all of these meadows are the result of previous clearing and cultivation, or are natural grassland areas has not been determined. Undoubtably some are natural, their presence antedating the advent of white men. Others, such as the small meadow which marks the western boundary of the study area, are known to be in a stage of secondary succession. One or two conspicuously conical piles of assorted sizes of stones indicate that the land was probably cultivated in the past, a field observation which lends credence to oral communications of several old residents in the region. At present the land is grazed during part of the year.

Settlers moved into the Front Range in large numbers after the Civil War. Later, in the 1870's, gold and silver booms brought in large numbers, while in 1900, 1915, and 1945, tungsten booms also caused temporary population increases. Population pressures on the natural resources were probably greatest in the decades immediately before and after 1900. Lumbering was almost as prominent an industry as mining, for these forests had to furnish wood not only for building cabins, rail fences, and mine timbers of the mountain settlers, but also firewood and construction material for the numerous towns of the plains. It has been estimated by some of the early settlers still living, and also the present district forest ranger, that as many as 500 head of cattle and 100 head of horses grazed in the region to the east of Sugarloaf mountain, whereas today only a few dozen horses and two or three score cattle are permitted by the Forest Service.

In the early days almost every cabin had a small garden plot, and some of the ranchers cultivated several acres of small grain for stock feeding. In general such agricultural activity was not profitable, and the fertility of the land was not sustained. Most of the area is now under the control of the Forest Service.

The Study Site

The study area is located in north-central Colorado, in the Ponderosa Pine Zone of the east slope of the Rocky Mountain Front Range. It is at an elevation of 7,500 feet above sea level and may be reached by traveling west from Boulder, Colorado, on State Highway No. 119 to the Bummer Gulch road and following the latter to the region east of Sugarloaf mountain. The site lies on a ridge just to the north of the road about one mile east of Sugarloaf village. The aerial photograph (Figure 1) gives the location precisely (Sec. 29, T. 1 N., R. 71 W., 6th principal meridian).

The site was arbitrarily delimited to an area of about five acres (Figure 1) surrounded by other pine stands and open meadows. The western boundary of the stand is a small meadow, while the southern edge is abruptly marked by an old fence to the other side of which is a very dense pine stand. North and east the study stand continues beyond the five acre limit. A transect 200 feet wide and 800 feet long was run east to west through the study plot and all pines and shrubs mapped. Grass and herb cover was noted qualitatively. A species list (Table I) of the most abundant herbs and their season of blooming was prepared.

TABLE I

REPRESENTATIVE HERBACEOUS SPECIES FROM THE STUDY SITE AND THEIR PERIOD OF BLOOMING

Species Name*	Month					
	Apr.	May	June	July	Aug.	Sept.
Claytonia lanceolata Pursh	x					
Thlaspi arvense L.	x					
Anemone patens L.	x	x				
Aletes acaulis (Torr.) C. and R.			x			
Crypthantha virgata (Porter) Pays.			x			
Erysimum asperum (Nutt.) DC.			x			
Penstemon virens Pennell			x			
Phacelia leucophylla Torr.			x			
Mertensia lanceolata (Pursh) A. DC.			x			
Tradescantia occidentalis (Britt.) Smyth			x			
Achillea lanulosa Nutt.			x	x	x	
Eriogonum umbellatum Torr.			x	x		
Geranium fremontii Torr.			x	x	x	x
Oxytropis lambertii Pursh			x	x		
Penstemon unilateralis Rydb.			x	x		
Sedum stenopetalum Pursh			x	x		
Campanula rotundifolia L.				x	x	x
Calochortus gunnisonii Wats.				x		

*Names taken from Weber (1953).

TABLE I (cont.)

REPRESENTATIVE HERBACEOUS SPECIES FROM THE STUDY SITE AND THEIR PERIOD OF BLOOMING

Species Name*	Month					
	Apr.	May	June	July	Aug.	Sept.
Gaillardia aristata Pursh				x	x	
Gilia spicata Nutt.				x		
Allium textile Nels. and Macbr.					x	
Aster bigelovii Gray					x	
Aster porteri Gray					x	
Liatris punctata Hook.					x	
Artemisia frigida Willd.					x	x

*Names taken from Weber (1953).

The pines comprising the body of the stand are approximately of the same age, averaging 55 years old in a range of 40 to 70 years. Average basal diameter is twelve inches and average height thirty-five feet. A few individuals range between 150 and 170 years old, fifteen inches in basal diameter, and forty-five feet high. Numerically they make up about two percent of the stand. The remaining eighteen percent of the stand is made up of trees in the pole stage, some of open growth habit, others more typically in clusters. The stand density based on the number of mature trees in the transect is fifty trees per acre. Stands of both greater and lesser density are found in the immediate vicinity. The density of the stand is intermediate between that of the very open stands of the steeper south slopes, and the dense stands of young growth. Grasses and herbs cover the woodland floor between trees. Under individual trees the duff and needle layer ranges from one to three inches deep, and the herbaceous cover is less, often lacking; however, in some instances, especially where the crown commences high up on the stem, a thick grass sod grows up to the very base of the tree. Ponderosa pine is the only tree species present in the area.

The trees on the study site are shallowly rooted, a fact significant in the discussion of soil moisture values. This shallow-rooted character was noted upon examination of trees on near-by road cuts and also by a partial excavation of the root system of a single mature pine growing on the site. This shallow-rooted habit is due primarily to the shallow nature of the soil, tree roots not penetrating the saprolite to any appreciable depth. At least ninety-five percent of the ponderosa roots in the study site are in the upper one to two feet of soil. These observations are substantiated by others made on ponderosa pine root systems in the granitic soil near Manitou, Colorado (Annual Report, Rocky Mountain Forest and Range Experiment Station, 1957).

STAND CLIMATE

The abrupt beginning of the mountains has already been described. Equally sudden is the appearance of open coniferous forests on the mesas and hogbacks abutting the foothills and extending westward over the Front Range. Stand density and species composition slowly change with the increasing elevation. Consequently one might expect a major climatic change from the plains below to the Montane Zone above. This is not so, however, and the climate of the Lower Montane Zone is similar to the plains climate, the overlying air mass at any given time being approximately the same.

Instrumentation

In order to describe adequately the montane climate as it appears within the pine stand, especially those atmospheric factors which might have a major effect on the growth of the trees, a field weather station, called "A-5", was installed (Figure 2). The equipment and procedures used in recording the data are those recommended by the United States Weather Bureau (Circular B, 1952, and Circular N, 1951).

The shelter housing the instruments was the standard Robinson type of louvered, wooden shelter, thirty inches by thirty-two inches, supported on wooden legs forty-eight inches above a grassy

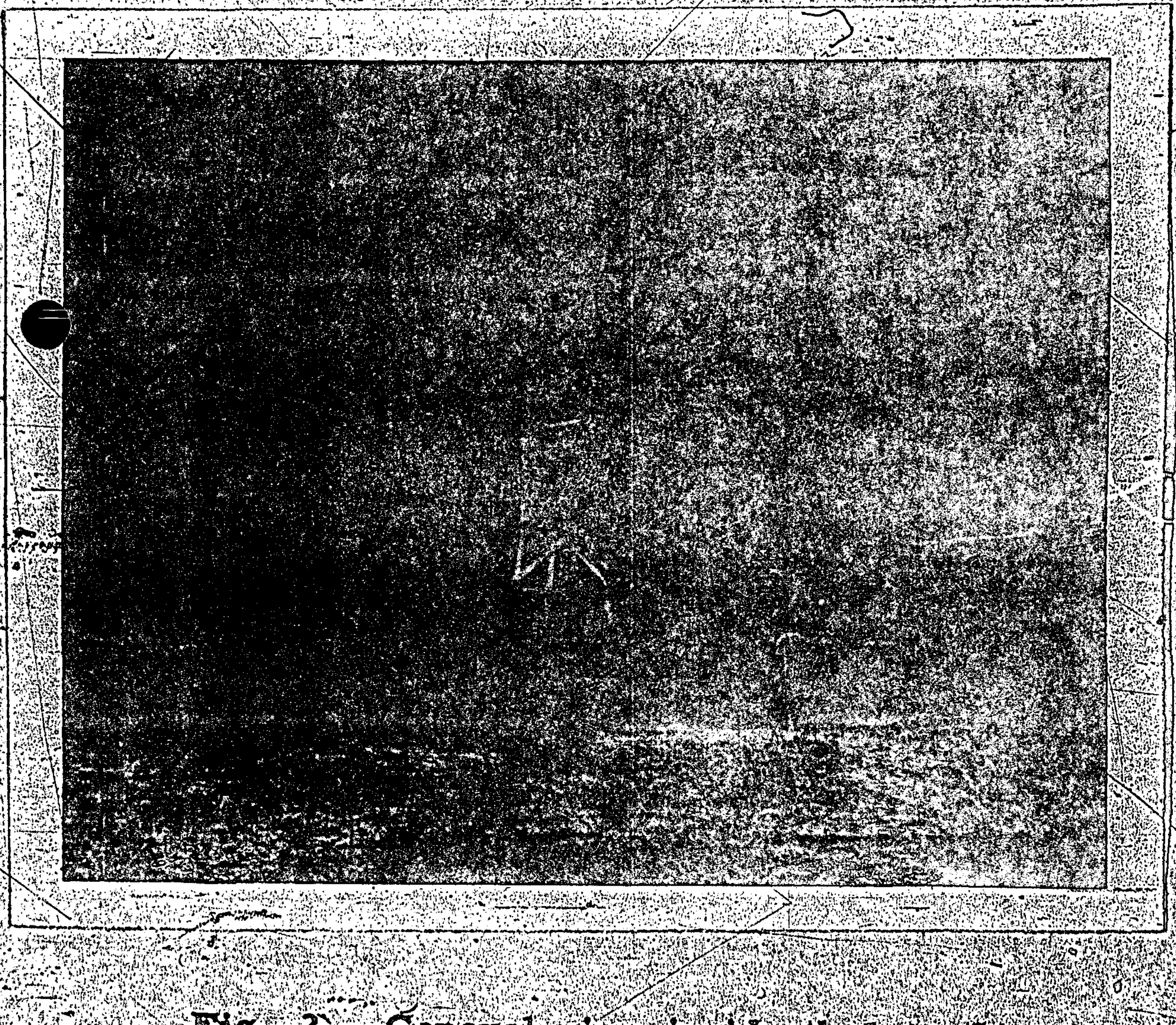


Fig. 2. General view inside the stand showing the instrument area.

surface. The door to the shelter opened to the north. Inside was placed one Friez hygrothermograph, one WB-type sling psychrometer, supported by a hook from the roof of the shelter, and one each of WB-type maximum and minimum thermometers properly positioned from L-hooks on a frame near the ceiling of the shelter.

The eight inch, WB-type of rain gauge was used for the measurement of precipitation. Two gauges were installed, one located within the pine stand, thirty feet from the nearest tree, the other in a nearby meadow, two hundred feet from any trees. According to Hayes and Kittredge (1949), a gauge is not affected by canopy interception if it is placed more than 3/4 the average height of the forest canopy from the nearest tree. The gauges were not mounted on a support, but set directly on the ground. They were prevented from tipping over by three iron bars driven into the ground around their periphery, and an encircling wire loop. Thus the mouth of the gauge was twenty-four to twenty-eight inches above the ground surface, depending upon whether or not the receiving funnel was in position. During the summer the entire apparatus was used, while during freezing weather, or when the likelihood of snow was great, the receiving funnel and the inner cylinder were removed and the outer cylinder alone used. During these periods this cylinder was charged with a two to four inch depth of concentrated calcium chloride solution to prevent freezing and to melt any snow. A thin layer of oil was added to prevent evaporation.

Electrical units buried in the ground gave values of soil temperature and soil moisture at the site. The details of installation will be described in the section on soil moisture.

The station was serviced an average of once every seven days, the interval ranging from five to nine days. At the time of servicing, the ambient temperature was noted from the minimum thermometer and also from the dry-bulb thermometer, as a check on the accuracy of the hygrothermograph temperature record. As there was generally a one degree difference, plus or minus, between the two thermometers, the dry-bulb value was arbitrarily designated as the standard of comparison, and the hygrothermograph was kept adjusted in comparison to it. A 2° F., plus or minus, difference was allowed before any adjustment was made. Degree and type of cloudiness, wind speed and direction, and snow cover, if any, were all estimated and recorded.

At the beginning of the study, which was in the late summer of 1957, a second instrument shelter containing the instruments enumerated above was installed in the small meadow to the west of the stand. The differences in relative humidity and temperature between the two sites was so slight, if any actually existed, that the instrumentation did not reveal it. Consequently, this second installation, except for the rain gauge already described, was discontinued after two and one half months.

Supplementary climatic data, which will be used in the discussion section of this report, were obtained from a similar type of station on an adjacent ridge 1/4 mile south across Bummer Gulch (Figure 1), also located in a pine stand but some 200 feet higher in elevation. This station, designated as "A-1", was established in 1951 by the University of Colorado Institute of Arctic and Alpine Research and has been in continuous operation since. Its records also include maximum and minimum soil temperatures at the six and twelve inch levels and total miles of wind, in addition to the standard data previously noted.

Results

Temperature

Complete and continuous records of air temperature were obtained from the hygrothermograph trace at the study site, and in addition the records from the adjacent ridgetop station, "A-1", have been made available by the Institute. These latter records cover a seven year period beginning with 1952 and continuing through 1958. These data, along with those of "A-5", are presented for comparative purposes in Table II.

The annual trend in rise and fall of soil temperature follows closely that of the air, though the relationship between the two is not always a direct one. At the "A-5" site soil temperatures were

TABLE II

Air Temperatures at Station A-1 from 1952-1958, and A-5 (1958)

MAXIMUM

Month	1952	'53	'54	'55	'56	'57	'58	A-5 '58
Jan.	50	60	60	61	61	53	59	56
Feb.	55	58	70	55	56	48	65	60
Mar.	57	71	61	59	71	60	58	54
Apr.	71	74	75	76	69	64	72	66
May	78	78	88	78	80	74	85	79
June	91	95	100	91	94	93	92	85
July	95	96	99	92	92	97	91	88
Aug.	94	91	95	88	88	93	95	90
Sept.	88	88	84	91	90	85	89	86
Oct.	79	82	76	78	87	76	82	78
Nov.	70	69	67	66	64	60	69	61
Dec.	61	53	62	61	59	64	57	55

MINIMUM

Month	1952	'53	'54	'55	'56	'57	'58	A-5 '58
Jan.	-1	-3	-4	9	7	-5	5	3
Feb.	0	-1	10	-2	-8	12	5	3
Mar.	1	10	-6	-7	0	9	3	1
Apr.	17	6	21	19	17	9	18	17
May	28	19	13	30	29	26	32	32
June	44	43	27	34	44	36	35	33
July	37	51	45	50	45	49	45	42
Aug.	42	46	45	45	37	47	47	47
Sept.	36	33	28	31	34	32	29	29
Oct.	18	25	12	23	27	23	18	18
Nov.	-3	8	13	-2	-1	6	2	0
Dec.	2	1	1	4	9	10	9	6

MEAN

Month	1952	'53	'54	'55	'56	'57	'58	A-5 '58
Jan.	30	36	34	34	28	34	26	30
Feb.	28	29	39	26	26	37	37	33
Mar.	28	39	30	31	36	34	28	25
Apr.	41	36	48	44	44	37	39	36
May	50	47	51	53	57	47	58	53
June	66	66	63	57	70	61	63	58
July	68	70	72	70	67	70	66	62
Aug.	68	66	67	68	65	69	70	68
Sept.	62	63	60	60	64	58	61	58
Oct.	51	51	46	51	54	47	51	50
Nov.	31	40	41	33	36	32	39	37
Dec.	31	28	34	33	36	37	34	32

obtained from instantaneous readings of the thermistors in the Colman moisture units, while at the "A-1" environmental station maximum and minimum thermometers at six and twelve inches in a metal-lined soil pit gave a measure of the soil temperature. Thus, there can be no direct comparison of temperatures between the two sites, but inspection of the thermistor values show that the maximum and minimum values obtained at "A-1" are generally comparable to those of the study site. Since such daily extremes are more meaningful for a climatic description than are random values, the "A-1" monthly means and extremes are presented in Tables III and IV as being representative of the study site. On the basis of this tabular material the annual trend of air and soil temperature is described below.

March is a wintry month. Though the sun's angle is steadily increasing and though daily air temperatures may occasionally reach as high as 70° F., they are more usually in the high 50's and low 60's. Minimum values drop to zero and below, while the monthly mean ranges from 25° to 35°. The soil surface alternately freezes and thaws, the six inch depth remaining much of the time below freezing. The twelve inch horizon is generally still frozen or thaws only briefly from below. Puddles of snow melt are common during the day but re-freeze at night.

During April, nightly values may still drop below freezing while the daily maximums are in the mid-60's or 70's. The

TABLE III

6" Soil Temperatures at Station A-1

MAXIMUM

Month	1952	'53	'54	'55	'56	'57	'58
Jan.	—	32	33	32	34	32	33
Feb.	—	33	36	31	31	41	39
Mar.	—	52	46	44	48	50	34
Apr.	—	52	64	62	53	52	52
May	57	68	70	66	69	66	68
June	69	76	81	76	82	80	74
July	72	80	85	80	84	86	78
Aug.	72	79	83	80	81	88	79
Sept.	67	76	77	80	75	77	74
Oct.	61	62	64	64	67	71	63
Nov.	50	49	44	47	44	47	46
Dec.	32	40	34	36	34	32	35

MINIMUM

Month	1952	'53	'54	'55	'56	'57	'58
Jan.	—	25	28	24	21	26	18
Feb.	—	28	30	25	23	25	30
Mar.	—	30	14	29	28	32	32
Apr.	—	32	33	32	34	32	33
May	43	36	36	42	39	34	35
June	56	50	48	44	51	44	52
July	56	56	55	55	54	56	57
Aug.	56	53	53	52	50	55	57
Sept.	53	51	42	42	48	42	50
Oct.	45	37	36	33	34	33	39
Nov.	31	34	30	28	33	26	34
Dec.	27	32	22	27	29	21	31

MEAN

Month	1952	'53	'54	'55	'56	'57	'58
Jan.	—	30	31	27	28	29	27
Feb.	—	31	32	28	28	32	32
Mar.	—	37	34	34	33	38	33
Apr.	—	40	48	45	43	38	40
May	50	50	54	54	54	48	53
June	61	62	65	58	66	61	64
July	64	68	70	68	69	70	68
Aug.	64	66	67	67	65	71	68
Sept.	59	62	62	61	62	59	62
Oct.	51	50	49	51	51	48	52
Nov.	39	38	38	35	37	34	40
Dec.	30	34	30	32	31	27	33

TABLE IV

12" Soil Temperatures at Station A-1

MAXIMUM

Month	1952	'53	'54	'55	'56	'57	'58
Jan.	—	34	35	34	37	32	34
Feb.	—	34	35	31	32	37	32
Mar.	—	44	42	37	42	40	34
Apr.	—	48	54	51	48	42	46
May	—	56	59	56	58	53	61
June	61	64	68	63	66	64	66
July	64	68	71	68	67	68	69
Aug.	68	67	71	68	68	71	71
Sept.	61	66	68	66	64	64	67
Oct.	57	60	58	56	60	60	58
Nov.	48	47	42	44	46	45	44
Dec.	35	38	36	35	36	34	36

MINIMUM

Month	1952	'53	'54	'55	'56	'57	'58
Jan.	—	29	30	26	28	28	26
Feb.	—	30	32	28	27	26	30
Mar.	—	30	16	30	29	32	32
Apr.	—	33	34	34	36	34	33
May	—	40	38	41	42	38	36
June	54	53	54	51	56	50	55
July	56	60	60	60	60	60	59
Aug.	57	61	61	60	58	60	60
Sept.	55	58	50	52	56	50	54
Oct.	44	44	41	42	44	41	42
Nov.	32	37	35	33	37	33	34
Dec.	30	33	30	32	30	27	33

MEAN

Month	1952	'53	'54	'55	'56	'57	'58
Jan.	—	32	33	30	32	30	30
Feb.	—	32	33	29	29	31	32
Mar.	—	35	34	33	33	36	33
Apr.	—	37	45	42	41	37	38
May	—	47	50	50	50	45	50
June	57	59	61	56	61	56	61
July	60	64	66	64	64	64	64
Aug.	61	64	65	64	63	66	66
Sept.	57	61	61	60	60	56	61
Oct.	49	52	51	52	53	50	52
Nov.	39	41	40	38	40	37	40
Dec.	32	35	33	34	34	31	35

monthly averages are now well above freezing. It is during late April that such growth phenomena as the expansion of the pine buds begin at this elevation, though such changes are not conspicuous until a month or more later. The warming trend continues. The soil has thawed completely, though the surface may freeze lightly at night. The monthly average of air temperature is now in the 50's, with nightly freezes uncommon.

By May even minimum temperatures are suitable for pine growth, the monthly minimum for this period being 34° but still dropping well below freezing upon occasion.

June may be said to be the first definitely warm month at the 7,500 foot elevation. Maximum temperatures into the 80's and 90's occur from June through August and even into September. Nightly minimums over a seven year period never dropped below freezing except for one year (1954) and generally averaged in the mid-30's and 40's.

July and August are summer months of very similar temperature characteristics. Mean air temperatures range in the 60's with minimums in the 40's and maximums of high 80's and 90's.

The first freezes of the fall come in mid-September; however, temperatures may remain mild through December. November through February are cold winter months differing little from one another in extremes.

Precipitation

In this climax region the precipitation comes both as snow and as rain. The relationship between precipitation and soil moisture will be discussed in another section of this paper. The first snows of the fall season come as early as late September and early October. Light rains and fog also occur during this period but the relative humidity is low most of the time and the total monthly precipitation is generally less than one inch during each of the two months. The fog is formed by low ceiling clouds over the plains abutting the mountains. At higher elevations the sky is generally clear and without precipitation, though high cloud cover may be present.

By November the soil surface has frozen, at least to a depth of one or two inches, and snow remains on the ground without appreciable melt in shaded areas. Snowfall is light, seldom more than two to three inches per storm. Precipitation recorded as inches of water for the month may approach a total of two inches but is generally less. Total accumulated snow seldom reaches a depth of one foot and this in drifts. Most is lost through evaporation. The average depth is from two to six inches.

There are the usual microclimatic differences due to north and south exposures. The study area is intermediate in snow accumulation between the 100 percent winter cover of the north-facing slopes and the usual complete absence of permanent snow on the south-facing slopes. The moderate density of the stand and resultant shading results in a fifty to eighty percent snow cover.

December, January, and February are cold and dry winter months with rarely as much as one inch of moisture falling during any one month (Table V). The ground is frozen to a depth of at least one foot. No snow melt occurs, but snow disappears both by evaporation and by sublimation. Drifts are permanent in shaded areas or where direct sun strikes only for an hour or so each day. In areal extent these drifts are sometimes large, especially in wooded areas and on north-facing slopes; however, the total depth is seldom more than twelve to eighteen inches.

In March extremes of soil and air temperature are almost as low as those of the preceding two months, though the daylight hours are increasing. There is a marked increase in precipitation as the first of the heavy spring snows arrive. Total precipitation for the month expressed as inches of water is from two to three times as much as for the preceding month (Table V), ranging from a total of one to three inches. April has slightly more precipitation than March, averaging a total of one-half inch greater. Much of this falls as wet snow mixed with rain.

On an annual basis, the month of May has the most precipitation, falling mostly as rain, though an occasional heavy

TABLE 5

Precipitation Measured as Inches of Water at Sites A-1 and A-5

Month	1952	'53	'54	'55	'56	'57	'58	Aver. 7-yr. pd.	A-5 1958
Jan.	0.30	0.55	0.40	0.40	0.35	1.10	0.90	0.57	0.70
Feb.	0.90	1.20	0.20	1.30	0.80	0.70	0.30	0.77	0.30
Mar.	3.00	1.95	1.50	2.50	1.20	1.30	3.05	2.07	2.65
Apr.	3.90	2.30	0.50	0.50	1.95	8.10	3.10	2.91	3.05
May	4.50	3.15	1.75	2.95	3.85	8.35	3.70	4.04	4.20
June	1.10	1.67	0.25	2.50	1.14	1.43	3.24	1.62	3.31
July	0.95	3.55	1.60	1.88	4.95	1.36	1.53	2.26	1.50
Aug.	2.17	2.76	0.84	2.96	2.35	1.81	3.08	2.29	3.45
Sept.	0.71	0.80	1.85	0.99	0.05	1.25	1.04	0.96	0.75
Oct.	0.35	0.74	0.70	0.35	0.15	2.61	0.99	0.84	1.53
Nov.	2.10	1.95	0.95	1.55	1.65	1.30	1.20	1.53	1.10
Dec.	0.50	1.15	0.60	0.80	0.70	0.30	1.40	0.75	1.40
Annual Total	20.48	21.77	11.14	18.48	19.14	29.61	23.53	20.61	23.94

snow can be expected. Most of the snow drifts have disappeared, and any fresh snow melts very rapidly. The average for a seven year period is four inches, ranging from a low of 1.75 inches (1954) to a high of 8.35 inches (1957), with the precipitation for most seasons being within one inch of the average value.

June shows but a slight decrease in rainfall over that of May, while in July there is no definite trend, the precipitation being greater in some years and less in others, than that of the preceding month. August shows the same characteristics. This may be due in large part to the nature of the summer rainfall pattern, all precipitation coming in the form of thundershowers, often of cloudburst intensity. Note (Table V) the difference in monthly total rainfall for 1958 at "A-5" and "A-1", for the months of June and August, though they are of similar exposure and less than half a mile apart. Hail also falls in some of the showers, sometimes in large quantities, but with stones never over one-fourth inch in diameter. Distribution is local and it contributes only slightly to the overall soil moisture pattern.

Soil Structure

As the present investigation called for a general knowledge of such soil properties as water holding capacity, water retentivity, and other features related to structure and depth, and as there are no published accounts of the mountain soils in this region, it was necessary to carry out a brief study of the soil on the site.

This entire region is underlain by a core of pre-Cambrian granite, the Boulder Creek batholith. It is a dark gray, faintly banded rock that ranges in composition from quartz monzonite to a sodic granite. Intrusive dikes of pegmatite and aplite varying from a few feet to many yards in width are common, and several prominent breccia reefs spaced at intervals of about one mile across the region, trending northwestward. These dikes, being more resistant to weathering, form small knobs, ridges, and conspicuous outcrops in the landscape (Lovering and Goddard 1950). Granite disintegrates readily in the climate of this region to a soil which is a coarse, light brown, loamy sand. Soil differences, if any, between the granitic mass and the areas of intrusives were not determined.

The soil of the ridge in the vicinity of the study site is residual and rather shallow. Boulders and rock outcrops occur, but there are no extensive areas of bare rock nearby. The slope is gentle and broken into knolls and broad shallow terraces.

The A horizon is generally from three to five inches deep, black in color, especially when damp, and high in organic colloids. Loss-on-ignition values were forty-two percent, while loss-on-acid-treatment yielded a value of forty-three percent organics. When treated with sodium hydroxide the supernatant is a dark tea color, a general indication of organic matter. Soil below six inches showed no color in the supernatant other than the light yellow of the clay fraction.

The B horizon is from twelve to fifteen inches thick and is sharply delimited from the A horizon by color change. The former is a light brown when dry, becoming a darker brown when wetted. It is not easily separated into a B_1 and a B_2 sub-division, though the upper six inches show slightly less clay (Table VI) than the lower part. The lower boundary of the B horizon grades indistinguishably into the C parent material, a brownish yellow, rotten granite, pervious to water but still a consolidated material, known as saprolite.

The amount of material greater than two millimeters in diameter is considerable throughout the profile. The largest proportion of this material is from two to ten millimeters in diameter and is composed of angular quartz gravel. Pieces larger than this are found in varying amounts. The amount of rock and the depth of a developed soil profile vary greatly within a few yards; however, the proportion and structure of soil segregates less than two millimeters is generally the same throughout this region of the Lower Montane Zone. The percentage of material from two to ten millimeters shows a gradual increase with increasing depth of profile. These values are shown below in Table VI. The percentages of sand, silt, and clay are computed from samples from which all material larger than two millimeters has been removed by sieving. Gravel was determined from another series of samples. For this reason the values in Table VI add up to more than 100 percent.

TABLE VI

MECHANICAL ANALYSIS OF "A-5" SOIL

Depth (inches)	Gravel (5-2.0 mm)	Sand (2-.05 mm)	Silt (.05-.002 mm)	Clay (below .002 mm)
1	23%	--	--	--
3	27%	76.2%	16.8%	7.0%
6	31%	74.6%	18.0%	7.4%
12	40%	74.4%	17.2%	8.4%
15	50%	--	--	--

Mechanical analyses were not run on soil at the one inch depth, which is quite similar in texture to soil at the three inch depth. At fifteen inches the material is saprolite, a rock-like material, rather than a developed soil, and though easily crushed, the separates obtained by mechanical analysis are not truly comparable to those of the upper horizons.

Soil Moisture Characteristics

A knowledge of the proportion of sand, silt, and clay as well as of the larger soil segregates is useful in determining the moisture characteristics of a given soil. If, in addition, certain volume properties of a soil are known, it is possible to calculate the amount of water necessary to bring up to field capacity a specified volume of soil.

Field capacity was determined from a series of samples taken in the field twenty-four to forty-eight hours after drainage had occurred from the saturated soil. The first of these samples were taken in the spring after the late snows and spring rains; the second series was taken during the summer after certain heavy rain storms. In addition, values approximating field capacity were determined from chunks of soil. These were wetted and allowed to drain on sand for three days, without allowing evaporation to dry the surface. When each chunk had reached a relatively stable moisture content, as determined by a series of successive weighings, it was assumed to be at field capacity. This method was developed by the author, but it is quite likely that similar methods developed by others are described in the literature. Results from the field and laboratory determinations were in close agreement, except in the case of the topmost three inches of soil, the A horizon. Both field and laboratory samples varied widely among themselves giving values ranging from seventeen to thirty-seven percent. On the basis of the few samples, and because of the wide variation in depth and amount of organic matter which causes the variation in field capacity, the lower field-determined values in the range of twenty percent were assumed to be the most representative of field capacity as the higher values were all obtained from the chunk laboratory samples; a method more subject to error than field sampling.

Volume-weight, also called bulk density was determined from weighed, oven-dry chunks of soil whose volume was measured by immersion in water after they had been lightly coated with hot paraffin. Values for field capacity and for volume-weight are presented in Table VII.

Another soil moisture constant, useful in evaluating plant-soil moisture relationships, is the wilting percentage, a measure of the lower limits of water available to a plant in a given soil.

TABLE VII

FIELD CAPACITY AND VOLUME-WEIGHT VALUES BASED ON TWENTY SAMPLES EACH

Depth (inches)	Horizon	Field Capacity (percent)	Volume-weight
0-1	A	20	1.55
1-3	A	15	1.60
3-6	B	12	1.71
6-12	B	10	1.80
Below 15	C	5	2.31

Though recently subjected to serious criticism (Slayter 1957) and being replaced by other values (Richards 1941), the wilting percentage is still a useful concept. In the present study, sunflowers were the test plant, and standard techniques were followed. Data are presented in the following table.

TABLE VIII

WILTING PERCENTAGES AND AVAILABLE WATER

Depth and Horizon (inches)	Wilting Percentage (percent)	Available Water (percent)
0-3 (A)	7.20	13
6-12 (B)	4.75	5
15-20 (C)	3.40	2

Available water values are obtained by subtracting the wilting percentage from the field capacity and represents that percentage of soil water readily available for plant growth. It should be regarded as only an approximate value. In the above table it should also be pointed out that the wilting percentage for the C horizon was determined on pulverized material. Under natural conditions this horizon is consolidated material and is not easily penetrated by roots, though it may contain as much as three to five percent water by weight.

Soil Moisture Measurements

As the amount of soil moisture available for tree growth was one of the more important factors studied in this investigation, the amount of water actually in the soil was determined in several ways: by gravimetric sampling, by electrical means using Colman units, by means of commercial tensiometers (Figure 3), and by measuring amounts of precipitation entering the soil. The first method determines the amount of water per unit weight of dry soil, the value being expressed as a percentage. The second method, the use of Colman units, is an indirect method whereby the electrical resistance through a mat of fiberglas in equilibrium with the soil moisture is determined. The ohms resistance is converted into moisture values from a calibration curve. The third method, the use of the tensiometer, gives in hundredths of an atmosphere the tension with which the moisture is retained by the soil. And lastly, by determining the depth in the soil to which a measured amount of precipitation penetrates, a volume measure of water in the soil is obtained. All these methods were used simultaneously during the 1958 growing season.

Methods

Gravimetric Samples

During the early months of the study, soil moisture was determined solely by gravimetric means, and such sampling was continued at intervals throughout the investigation. The values given by this method of moisture determination are the standard against which all other methods are compared as it is the only direct way of measuring soil moisture (Lull and Reinhart 1955). Most of such samples were of loose soil taken from small pits dug with a pick or from holes dug with the use of a posthole type soil auger. This latter instrument is a hollow metal tube four inches in diameter and six inches long mounted on a sectioned extension T-handle. At the lower end of the cylinder are two opposed cutting blades. When placed on the ground and rotated by hand like a drill bit it cuts a cylindrical hole, the loose soil filling the inside of the tube. As the bit fills each time, the auger is drawn to the surface and emptied. From this, a sample is taken or is simply discarded if the desired depth has not yet been reached. A relatively large

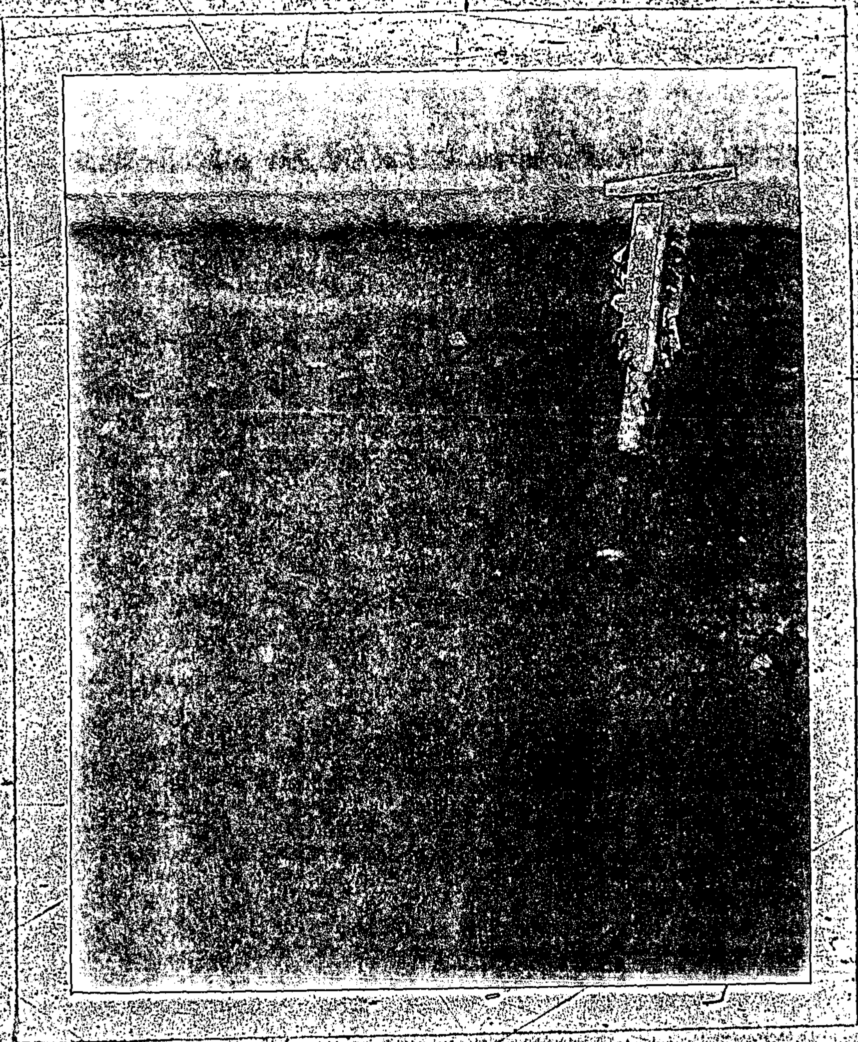


Fig. 3. Close-up of the soil moisture installation showing the Irrometers and the binding post for the Colman units.

sample is secured each time, up to one thousand grams, and progress is generally not impeded by small rocks. One difficulty encountered in using this apparatus in the sandy soils of this region, is that, at moisture contents of less than about five or six percent, the sample will not compact naturally and falls out of the auger upon being withdrawn from the hole. Bates (1924) encountered similar difficulties in sampling the granitic soils of the Pike's Peak region. This can be overcome to some extent by using a slender, blunt, wooden pole to tamp the loose soil in the cylinder before drawing it up.

Sample size ranged from one hundred to five hundred grams (air dry basis), and duplicates were taken at each soil depth. It was generally not feasible to sample below fifteen or twenty-five inches because of the saprolite. Soil samples were placed in sixteen-ounce, seamless tin cans closed with close fitting lids. After the samples had been returned to the laboratory they were weighed, oven-dried for twenty-four hours at 105°C., and then re-weighed; and the soil moisture was computed as a percentage of the oven-dry weight. Experience has demonstrated that further drying at this temperature does not remove a significant amount of water.

In taking gravimetric samples in the field, it is the general procedure of the Institute of Arctic and Alpine Research, as well as some other investigators, to first sieve the sample through a two millimeter screen to remove roots and large pebbles. This practice was not followed in the present case, primarily because when the soil was wet, i. e. generally above ten percent moisture, it could not be sieved properly, a large percentage of the fines being retained. Rather than to follow the dubious method of sieving samples during the drier seasons of the year and not sieving during periods of high soil moisture, it was decided that the majority of the samples should not be sieved. However, a small number of duplicate samples were screened under a variety of field moisture conditions in order to compare the differences in moisture percentage between sieved and unsieved samples. This comparison of results using different methods of gravimetric sampling was necessary in order to establish the range of variation between the different techniques. Water content of the soil expressed as a percentage, using gravimetric methods based on unsieved samples, was chosen as the standard in this study. Large pebbles and roots in the sample were removed by hand.

Differences in soil moisture percentages between sieved and unsieved samples is due to the fact that sieving a sample, whether wet or dry, removes that portion of soil fragments which have a high bulk density (i.e. weight), and contain little moisture either on their surfaces or internally. The effect of passing a soil sample through a screen is therefore to reduce the total dry weight of a sample, without removing a proportionate amount of water. It is the fines, clay and silt, which retain most of the moisture in a soil. At values of moisture above 9.5 percent (computed on an unsieved weight basis), many of these fines are retained on the surfaces of the discarded larger fragments, causing the sample to yield a moisture percentage from one to two percent less than a sieved sample. In a less moist soil, on the other hand, sieving yields a soil moisture from 0.05 to 5.0 percent higher than an unsieved sample. If the sample is first dried, then sieved the values run from 3.5 to 7.5 percent more than with unsieved samples. Data are presented in Tables IX and X.

This picture is further complicated by the fact pointed out above (Table VI) that the percentage of soil fragments from two to five millimeters in diameter almost doubles in going from the soil surface to a depth of twenty-five inches. Thus moisture values based on gross weight (unsieved) would show a spurious decrease in soil moisture with increasing depth. However, it was demonstrated that this difference amounts to no more than two or three percent. This may be verified in Table IX by a comparison between original and re-computed soil moisture values for the three inch and eighteen inch depths. The differences between sieved and unsieved samples at any one level run as much as 3.4 to 7.4

TABLE IX

SOIL MOISTURE YIELDED BY TWO SAMPLING METHODS

Depth (in.)	Percent Moisture Unsieved Basis	Percent Moisture Sieved Basis	Percent Apparent Increase	Percent Gravel Increase
		Forest Stand		
3	14.8	20.8	6.0	29.6
6	10.8	16.6	5.8	35.4
12	10.4	16.3	5.9	36.6
18	9.3	16.7	7.4	45.3
		Meadow Stand		
3	14.0	18.8	4.8	26.2
6	11.5	14.9	3.4	23.4
12	10.3	14.4	4.3	28.8
18	7.9	13.5	5.6	35.9

TABLE X

COMPARISONS BETWEEN SIEVED AND UNSIEVED SOIL MOISTURE SAMPLES. DIFFERENCES EXPRESSED IN TERMS OF THE UNSIEVED SAMPLES

Soil Moisture Content (Percent)		
Unsieved	Sieved	Percent Difference
47.2	37.3	-9.9
22.8	20.3	-2.5
17.5	17.4	-0.1
12.5	6.0	-5.5
9.5	13.5	4.0
9.5	12.0	2.5
8.4	9.7	1.3
7.8	9.0	1.2
6.5	7.4	0.9
6.5	8.2	1.7
5.8	7.8	2.0
5.0	9.0	4.0
4.5	4.7	0.2
3.6	4.5	0.9
3.4	4.4	1.0
2.8	3.8	1.0
2.5	3.0	0.5

percent while the error due to the increase in bulk density with increase in depth ranges only from 1.4 to 0.8 percent.

In summary, in the present study, the use of soil moisture values determined on the basis of unsieved samples is justified on the basis of ease, enabling more samples to be collected in a shorter period of time, and the usability of the same method at all soil moisture contents. In general the decrease in soil moisture with increasing depth, to be pointed out later, is due to a real decrease in water content because of increased bulk density and lessened pore space in the lower horizons. The values obtained from the unsieved gravimetric samples are the standard for all discussion of soil moisture in this paper.

Electrical Method

Seasonal changes in soil moisture can be followed by electrical elements buried in the soil. In the Colman electrical unit the resistance between two monel metal electrodes varies with the amount of moisture in a fiberglas mat separating them. The perforated monel metal case containing the fiberglas and electrodes also contains a thermistor, thus allowing electrical determination of the soil temperature. Both temperature and moisture values are read as amperes, using an alternating-current microammeter, and these values are converted to ohms resistance. The resistance values from the thermistors can be converted directly to temperature using a nomograph furnished by the manufacturer (Colman, Berkeley Division of Beckman Instruments, Richmond, California, 1947). The conversion of the resistance values to values of soil moisture is more complex and requires that each unit first be calibrated at various known moisture contents in the soil in which it is to be placed. Such calibration may be done in the greenhouse with the use of containers of loose soil samples brought from the site; or a field calibration may be done after installation by sampling the soil gravimetrically at points a few yard distance from the elements, at intervals throughout the season. Both methods are subject to error (Lull and Reinhart 1955), and subsequently both methods were used. The moisture values obtained from the greenhouse calibration curves tended to be higher by several percent than those obtained in the field from gravimetric samples. However, as the trends in seasonal changes revealed by the two methods corresponded, the Colman values were used as supplementary data for periods between gravimetric sampling dates to indicate a trend of increasing or decreasing soil moisture.

The Colman units were installed early in September of 1957, five units being placed at five different depths in a single hole. This hole was eight inches in diameter and twenty-eight inches deep. Five small horizontal slots, each just large enough to contain one of the monel metal units, were scratched into the side of the pit, at the following depths: 3, 6, 12, 18, and 24 inches. These were not directly in line, one below the other, but were offset slightly in a spiral. Each element had been dipped in a slurry of parent soil which was allowed to dry. Just prior to insertion this dried slurry was moistened slightly, and the unit with its casing of damp earth was pushed into a slot. Damp earth was filled in behind the unit flush with the side of the pit. The lead wires were dropped vertically down the side of the pit for a distance of two inches, then led horizontally around the wall one quarter of its circumference before being brought to the surface. The earth which had been removed was replaced in its natural sequence and tamped, about two inches being added at a time. After the hole was filled, the five sets of leads were soldered to individual Jones plugs, which were fastened onto a binding post half a meter offside from the hole. An area one meter square immediately over the units was cleared of grass and kept bare for the remainder of the study by occasional re-weeding (Figure 3).

Tensiometers

In June of 1958, four commercial tensiometers (Trade name: "Irrometer," manufactured by the T. W. Prosser Company, Arlington, California) were installed in the area. They were placed one in each corner of the square-meter plot described above. These instruments consist of elongated porous, porcelain tubes, two and one half inches long and three fourths inches in diameter (outside dimensions), connected through rigid plastic tubes, to Bourdon-type pressure gauges calibrated in hundredths of an atmosphere.

Two of the instruments had their porous cups located in the four to six inch zone, while the other two reached the ten to twelve inch depth. Each pair of the same length was placed in alternate corners of the plot. They were placed in holes which had been driven to the proper depth with a one-half inch lead pipe and sledge hammer. The pipe was rocked back and forth with a slight twisting motion so that the holes were enlarged just enough to give a snug fit to the inserted tensiometer stems. Fine sand and silt were poured around the stem at the ground surface and tamped to provide a seal to prevent rainwater from seeping ahead of the general soil moisture after a shower and thus indicating an erroneous depth of penetration.

Measured Amounts of Precipitation

Soil moisture at the study site was dependent almost entirely upon precipitation. Many factors govern the amount of precipitation actually entering the soil, such as type, intensity, and duration of precipitation, interception by vegetation, and degree of slope. Interception by the crowns of the stand was estimated to be from 17 to 28 percent of the season's precipitation, averaging about 0.04" (of rain) per individual tree. These estimates are based on the reports of several workers. (Kittredge, et al., 1941, Horton 1919, and Wilm 1943). Litter under the trees and grasses and herbs in the open area also intercept precipitation. The moisture profiles (Figures 4, 5, and 6) in this study are based on gravimetric samples taken in open areas between trees, where plant and litter cover was slight or lacking and interception at a minimum.

Depth of penetration of water finally entering the soil is dependent upon many things, including such factors as soil structure, porosity, organic matter, and existing moisture conditions. Using a formula method modified by this author from one used in a soils study under Dr. Coile of Duke University, it was possible to compute, at least to a first approximation, the amount of water necessary to bring to field capacity a given zone of soil. The formula is as follows:

$$\text{Water in inches} = \frac{(\text{F.C.} - \text{M.C.}) \times \text{V/W} \times \text{Th.}}{100}$$

where: F. C. equals the field capacity
M. C. equals moisture content already present
V /W equals volume-weight of the soil
Th. equals thickness of zone being measured .

These computed values ranged from 0.14 inches to 0.17 inches of water necessary to wet one inch of mineral soil. For the A horizon, high in organic matter, nearly twice as much water was needed to wet a one-inch layer, the value being 0.28 inches.

These computations were based on a hypothetical existing moisture content of two percent.

Empirical values may be obtained in the field by actual measurements of depth of penetration in a moderately dry soil twenty-four to forty-eight hours after a single storm. A series of gravimetric samples taken before and after a measured storm add refinement to the method. Such data are presented in Table XI. These empirical data yield values ranging from 0.12 to 0.15 inch of precipitation necessary to wet one inch of soil. The major weakness of the method is its inability to distinguish between the amounts of water necessary to wet the organic layers and the more mineral layers.

A few attempts to measure depth of snow-melt penetration were not successful as it was impossible to take into account the amount of evaporation, a variable greater with snowfall than with rain, where the snow lies an appreciable length of time.

TABLE 11

MEASURED AMOUNTS OF PRECIPITATION AND THE DEPTHS TO WHICH THEY PENETRATED

Inches of Rain	Depth of Penetration (Inches)	Percent Soil Moisture					
		1 inch		3-6 in.		12-15 in.	
		Before	After	B	A	B	A
1.50	10-12	2.0	14.0	2.5	7.5	4.0	4.0
1.19	8-10	--	24.0	10.0	--	5.5	5.5
0.98	6-8	2.0	17.5	2.0	9.0	5.0	5.0
0.75	5-6	7.5	17.5	4.0	8.5	4.0	4.0

The correlation between inches of rain and depth of penetration is remarkably constant, but the correlations between the rainfall value and the soil moisture conditions before and after are not positive. Due to the smallness of the sample little more can be said. The complexities of infiltration and resulting moisture conditions have been very well reviewed by Meinzer (1942).

Soil Moisture Results

From a maximum in April and May when the soil is frequently saturated, the soil moisture reaches its lowest values during October when it averages no more than two or three percent at all depths. As one would expect, the surface of the soil is dusty dry during the early fall season. Rains are generally light during this period, and though the total accumulation of water in the rain gauge for any one period may show half an inch or more of precipitation, this has usually fallen as more than one shower. These showers contribute little to the soil moisture as they never penetrate beyond the first inch of litter and soil. Rains during this season are not of the thunderstorm type but are of light intensity, falling gently over a period of hours.

After the summer drought, the early snows of September and October begin to replenish the soil reservoir. The soil temperatures are still well above freezing and the snow melts, rather than evaporating, and contributes significantly to the soil moisture supply. By the time the upper layer of the soil has frozen, thus preventing any more water from entering, the soil moisture has risen to values of twelve to fifteen percent in the upper three inches, eight to ten percent in the B horizon, and still remains as low as three to five percent in the saprolite. During the winter there is a slight redistribution of the moisture to lower levels.

Winter moisture conditions are depicted in the curve for January to March in Figure 4. The soil is frozen at least to a depth of six inches and often deeper, depending on the snow cover and the length of cold snaps. Surface thaw begins in March, but the melt puddles on the ground surface because of the still-frozen subsoil.

April and May (Figure 4) are the wettest months of the year, precipitation falling as heavy wet snows which melt rapidly and as rain. Patterns in soil moisture which might have resulted from late-lying snow drifts and canopy interception, thereby decreasing the amount of snow about the bases of the trees (Jaenicke and Foerster 1915), are wiped out by the relatively large amounts of rain and snow which saturate the soil even under dense stands of pine.

By the middle of June (Figure 5) the surface layer, though still near field capacity, is beginning to lose water to drainage and to new herbaceous vegetation. The lower levels of the soil are still gaining moisture from above. July and August plots (Figure 5) illustrate summer conditions. The trend of increasing soil dryness is shown by the curves labeled A, while the curves labeled B show the effect of single summer thundershowers of moderate intensity. These B curves seem to show the anomalous effect of decreasing soil moisture at the lower horizons after a thunderstorm. This is not so and is due solely to the time lapse of fifteen days between the data for the A curves and the B curves. If intermediate soil conditions were plotted, the family of curves would show a continuing trend of decreasing soil moisture. This season drying trend is occasionally interrupted by a thunderstorm, the water from

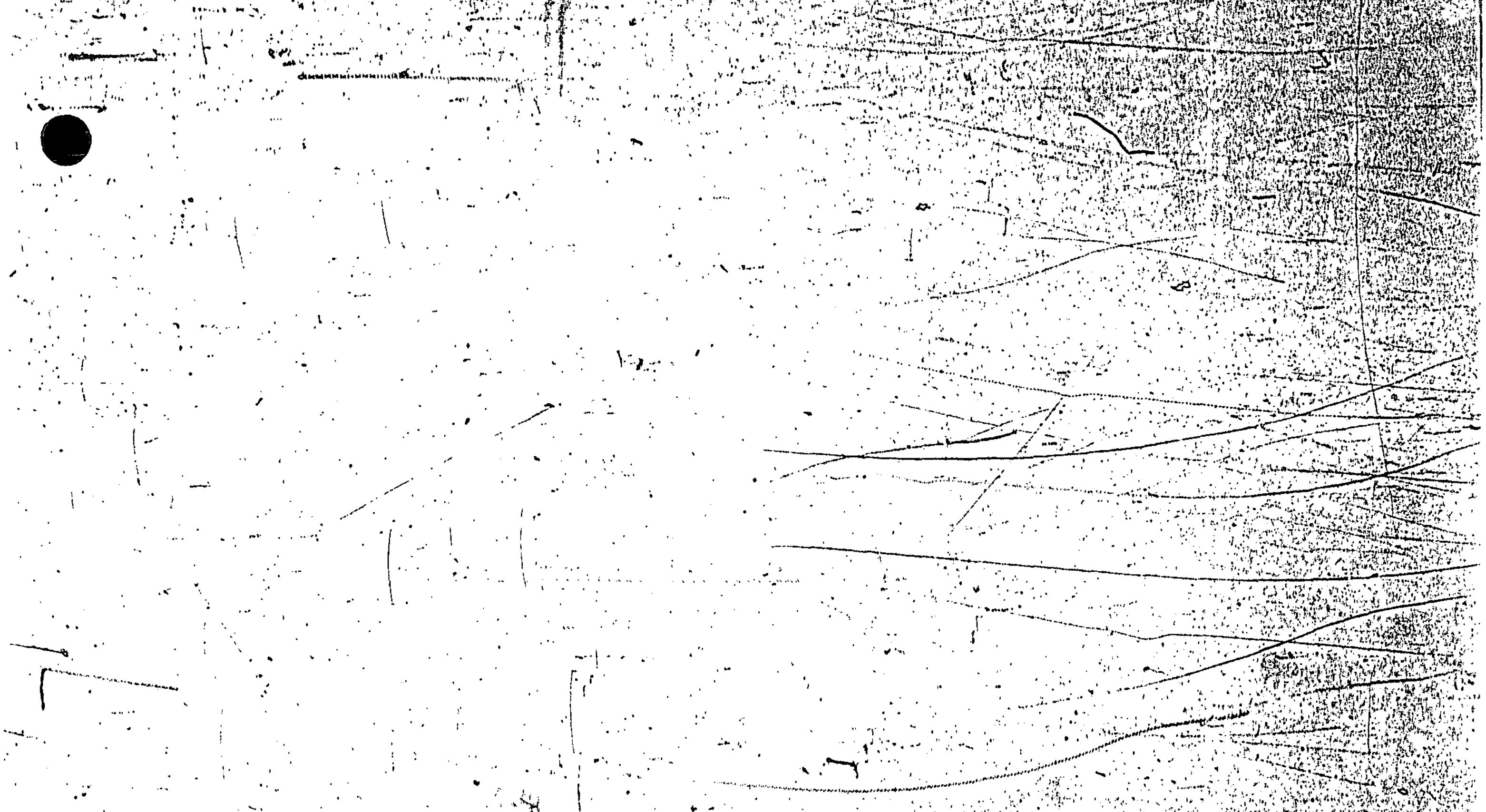


Fig. 4. Soil moisture profiles from January to May of 1958. The curves represent average conditions and are based on weekly electrical determinations and 12 sets of gravimetric samples.

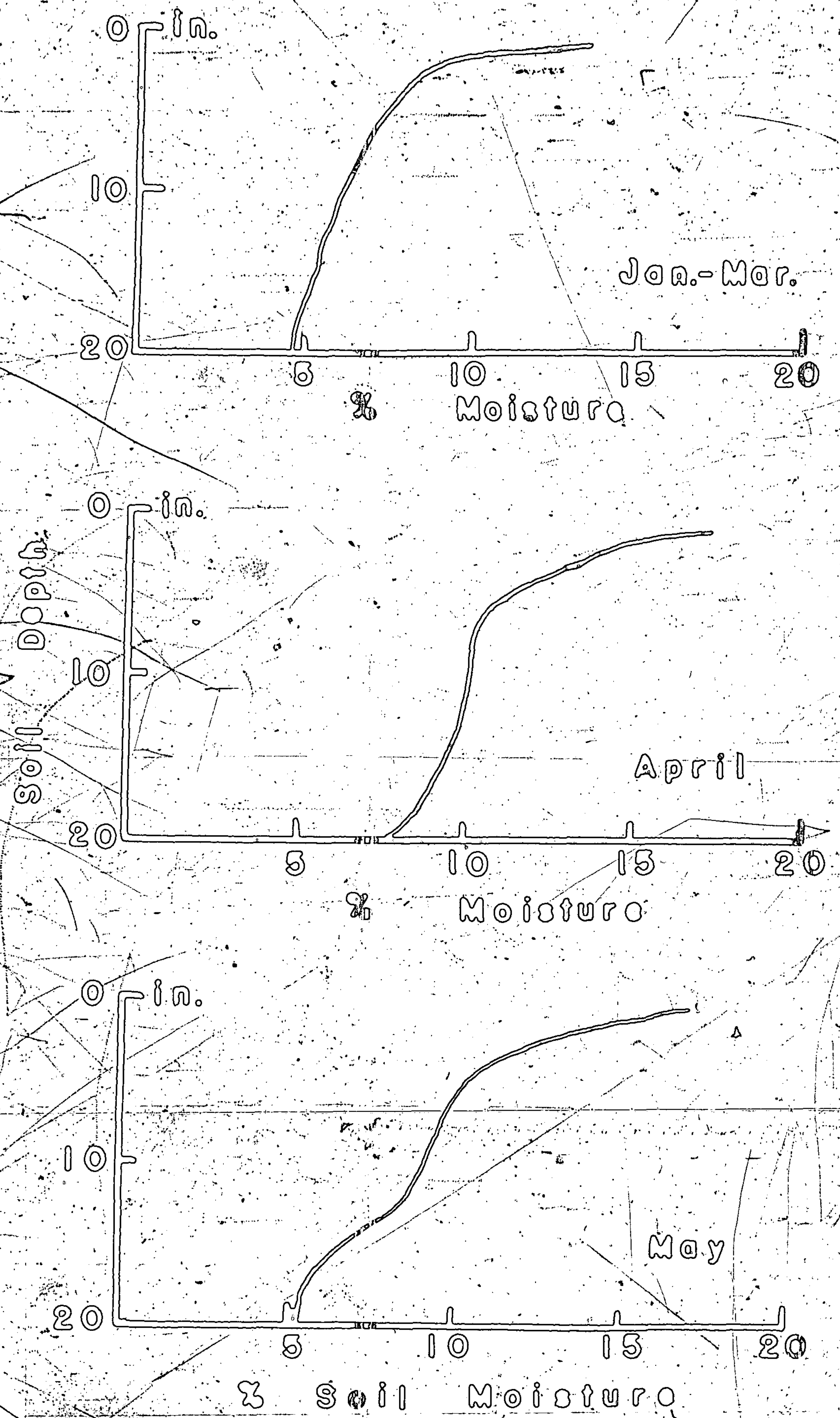
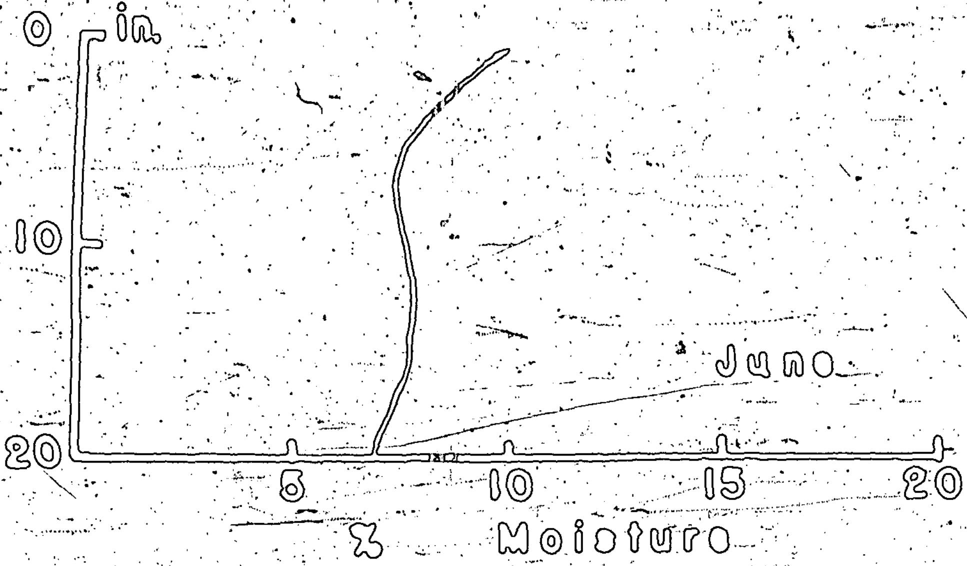
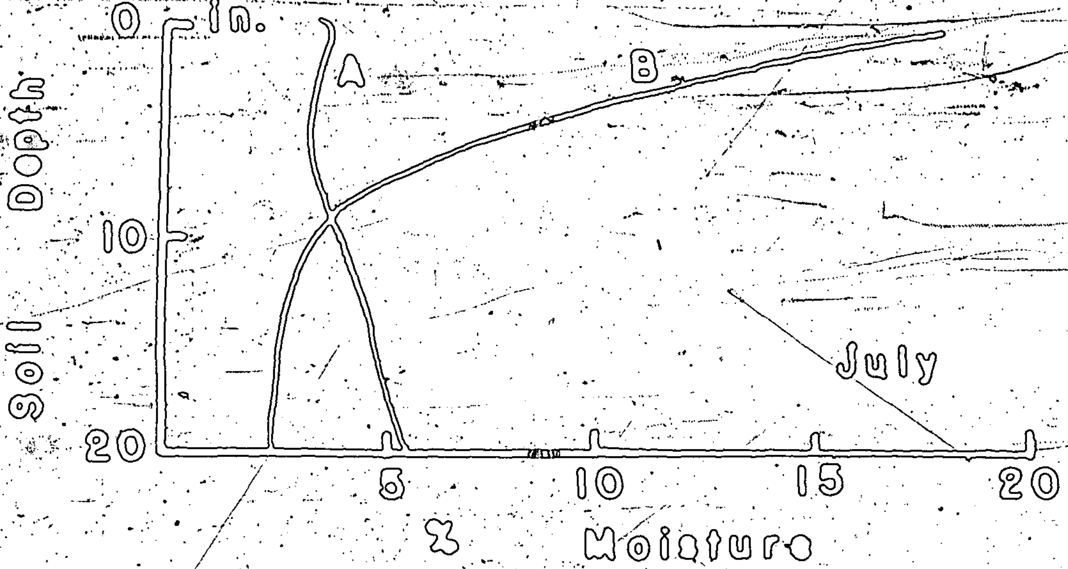
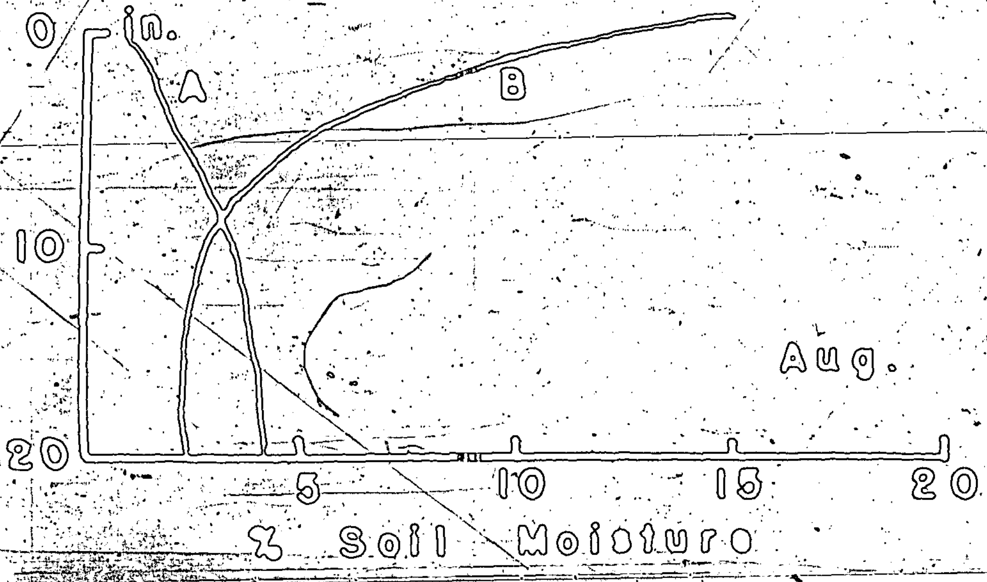

0 in.
10
20
5
10
15
20
% Moisture
Jan.-Mar.
0 in.
10
20
Soil Depth
5
10
15
20
% Moisture
April
0 in.
10
20
5
10
15
20
% Soil Moisture
May

Fig. 5. Soil moisture profiles for June, July, and August. The curves represent average conditions and are based on weekly electrical determinations and 33 sets of gravimetric samples. The trend of increasing soil dryness is shown by the curves labeled A, while the curves labeled B show the effect of single summer thunder showers.


0 in.
10
20
5
10
15
20
% Moisture
June


0 in.
10
20
Soil Depth
A
B
5
10
15
20
% Moisture
July

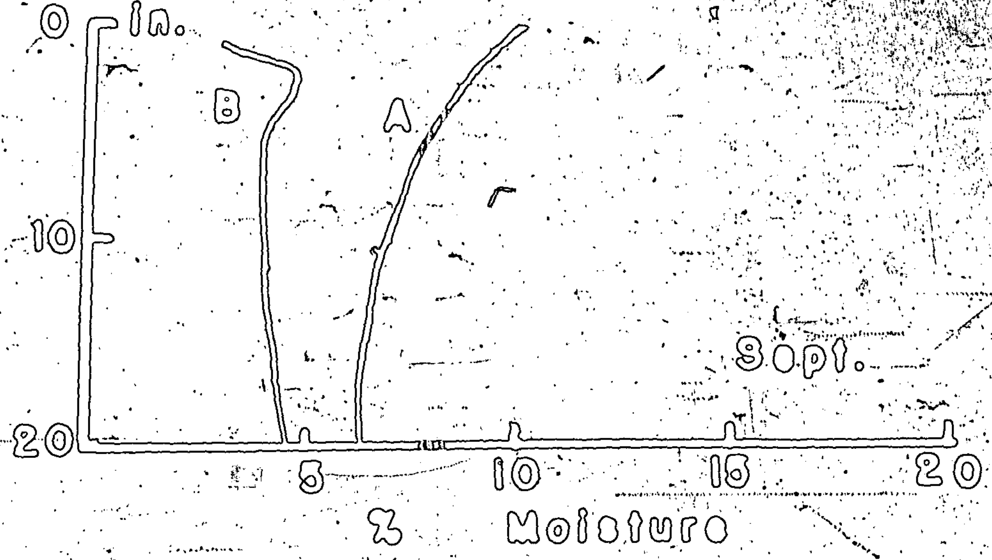

0 in.
10
20
A
B
5
10
15
20
% Soil Moisture
Aug.

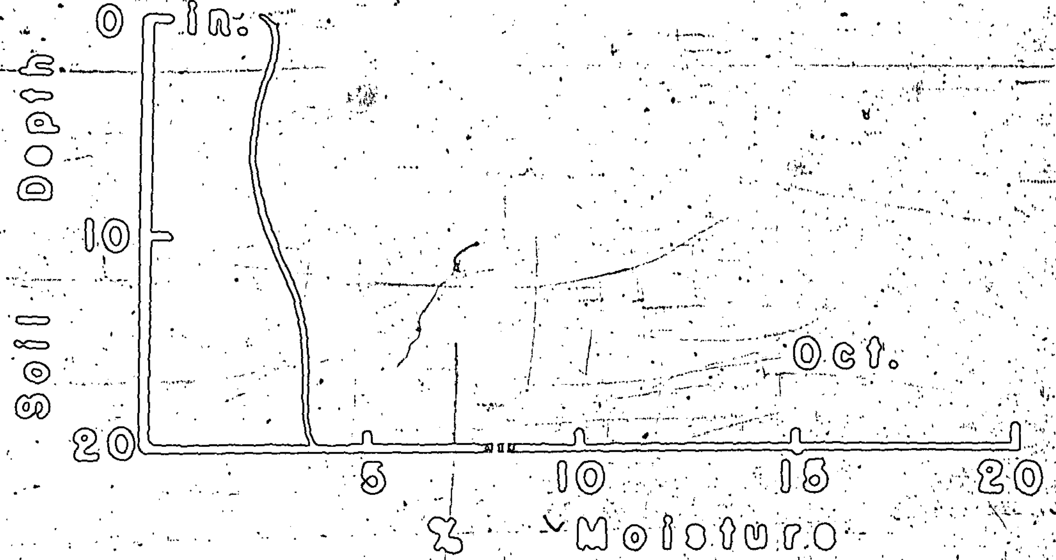
which while saturating the upper horizons never penetrated below about ten inches. A similar situation is shown for September (Figure 6). The curve for October shows the lowest moisture values reached during the entire year, while in November (curve A) and in December (curve B) there is a slow winter replenishing of soil moisture (Figure 6).

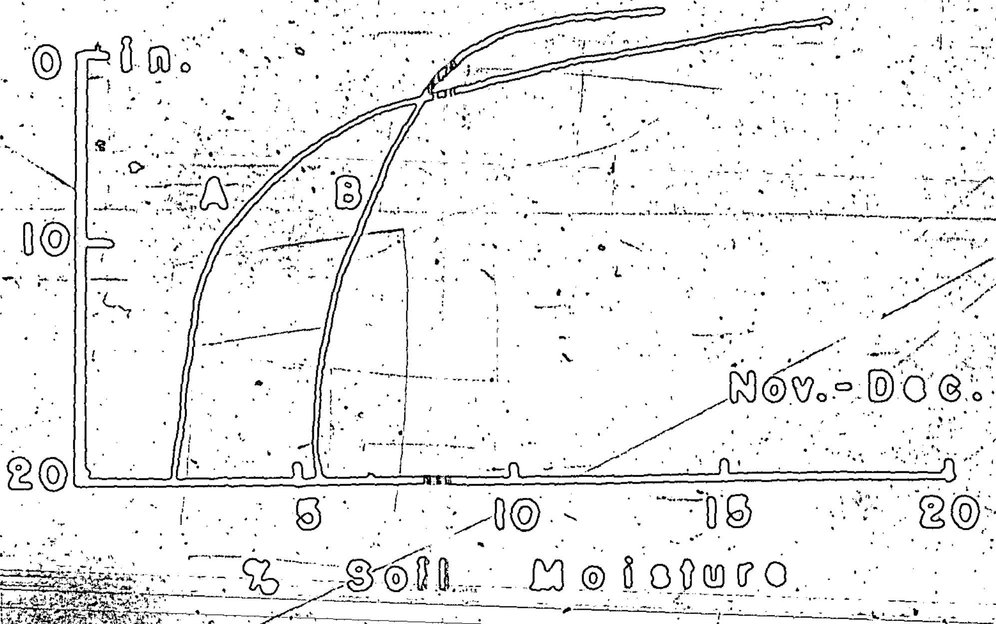
All of the curves and other soil moisture data presented are based on soil within the study site but not directly under any tree crown. Sampling was done under trees as well and not until late summer is the soil beneath and around the edges of tree canopies appreciably drier than the surrounding soil, and then by no more than two or three percent.

The soil moisture stress, as measured with paired tensiometers, is shown in Figure 7 in relation to the amount of precipitation. In interpreting the chart it must be borne in mind that the precipitation is measured cumulatively, and that a week's reading of 1.5 inches of rain, for example, may have fallen as a single storm or as several showers. The pattern of rainfall affects the pattern of soil moisture and the depth to which the soil is wetted. Periods of greatest moisture tension were in the middle of July, the last week of August, and the latter part of September.

Fig. 6. Soil moisture profiles for September through December. The curves represent average conditions and are based on weekly electrical determinations, and 9 sets of gravimetric samples. Curve A in September represents soil moisture conditions after a storm. On the lower chart curve A represents moisture conditions in November, curve B conditions in December.


0 in.
B
A
10
Sept.
20
5
10
15
20
% Moisture


0 in.
Soil Depth
10
Oct.
20
5
10
15
20
% Moisture


0 in.
A
B
10
Nov.-Dec.
20
5
10
15
20
% Soil Moisture

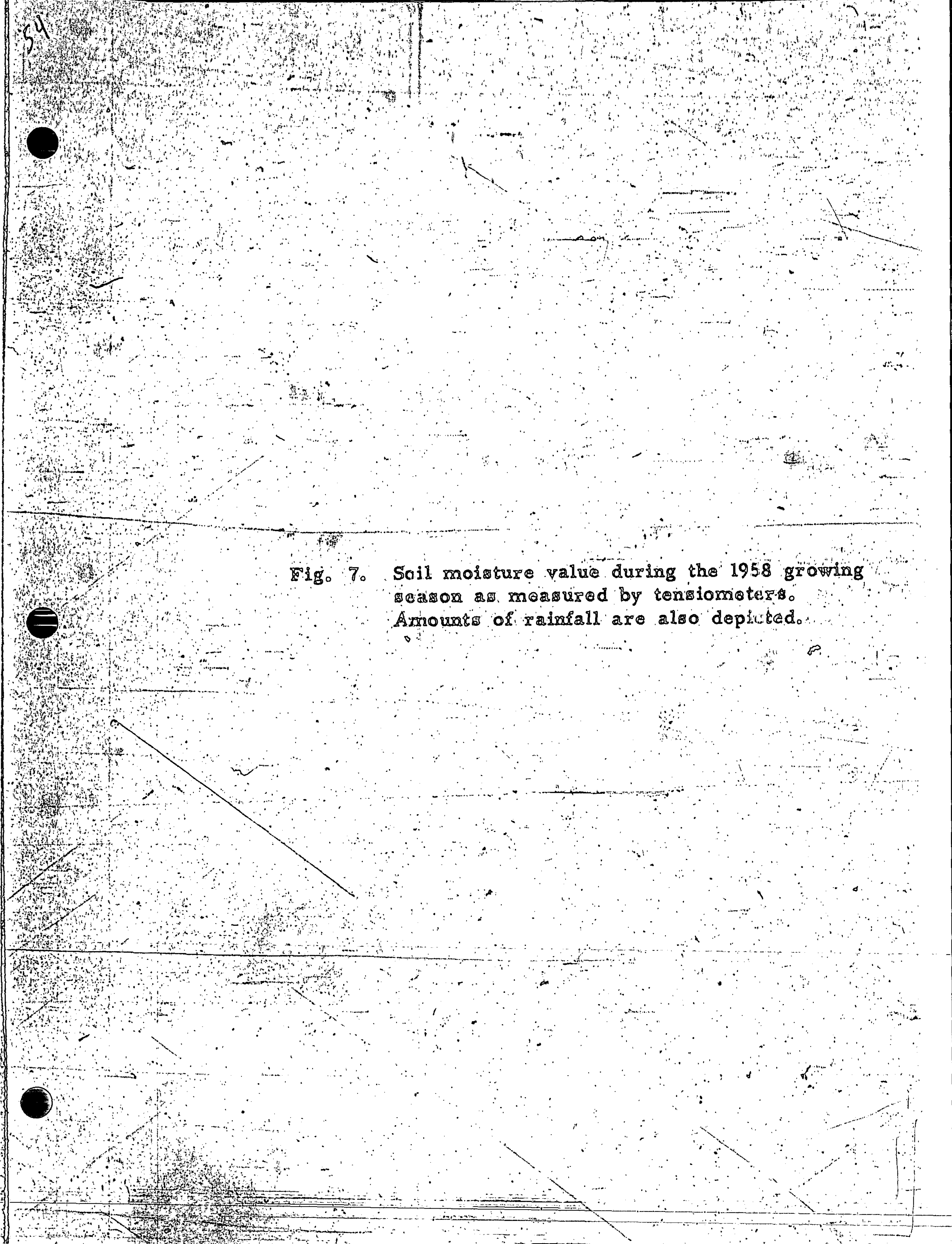
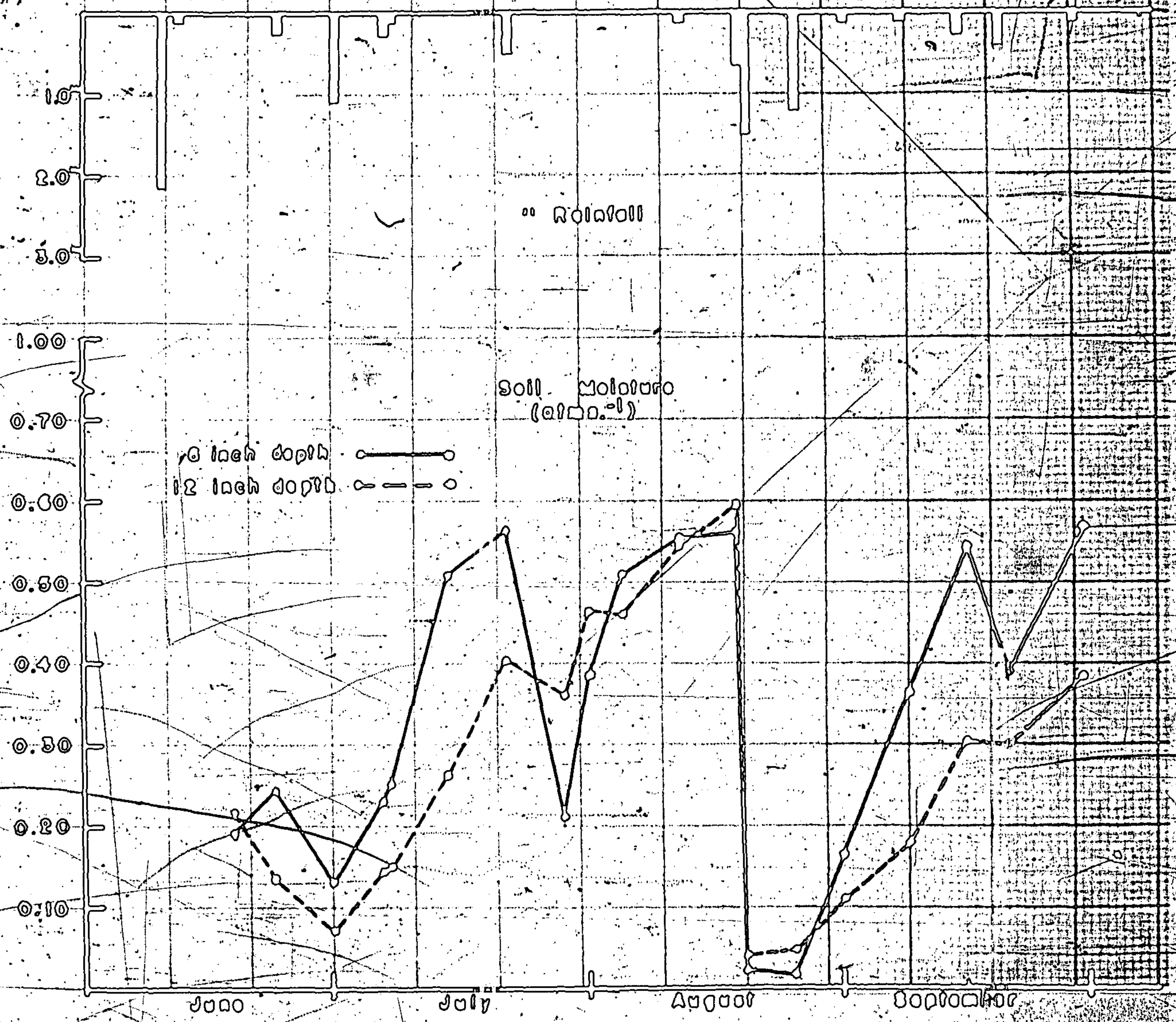


Fig. 7. Soil moisture value during the 1958 growing season as measured by tensiometers. Amounts of rainfall are also depicted.


1.0
2.0
3.0
" Rainfall
1.00
0.70
0.60
0.50
0.40
0.30
0.20
0.10
Soil Moisture
(atmos.$^{-1}$)
6 inch depth
12 inch depth
June
July
August
September

DENDROMETER MEASUREMENTS

Methods

As one of the principal objectives of this study was to measure as accurately as possible the diameter increase in a selected number of trees, the dendrometer which was employed will be described in some detail. It consists essentially of a dial gauge micrometer attached to a mounting. This mounting when engaged against fittings mounted to the side of a tree, enables the observer to read a value of linear distance with the micrometer. This reading when compared with a value taken on a previous date gives a measure of increase or decrease occurring in the outer layers of the bole during the intervening period. The device was originally designed by Reineke (1932) and later modified by Daubenmire (1945). In one form or another it has been used by several subsequent investigators. It is simple in construction, easy to operate, and relatively inexpensive.

The dendrometer used in the present study is essentially of the same design as that of Daubenmire's, with some slight modification. A. D. C. Ames (Waltham, Massachusetts) model No. 262-M, metric series, dial indicator was used. The face of this instrument is divided into 100 divisions each representing 0.01 millimeter. Mechanical accuracy is stated to be within one division plus or minus. The total range of measurement possible is 12.50 millimeters. Two small counter dials are mounted on the face of the main dial; one counting the number of complete revolutions of the main dial hand, the other totaling the revolutions of the first counter. These greatly facilitate reading the instrument.

To construct a dendrometer the dial gauge is fastened, by means of a bracket, at right angles to the center of a metal plate with the measuring arm (spindle) of the gauge protruding through a hole in the plate. The dimensions are not critical. The plate in this particular instrument was a rectangle of aluminum three-sixteenths of an inch thick and six inches long by four inches wide. A small spirit level was fastened to the upper edge of the plate, directly above the protruding spindle of the gauge (Figure 8).

To measure the changes in diameter of a tree trunk with this instrument, one must drive three screws into the tree around the point which is to be measured. Wood screws at least three inches long are used and are driven in until one to two inches of shank and the head remain protruding. These three screws should outline a triangular area on the trunk and their heads should form an imaginary plane surface tangent to the circumference of the tree. On the bark, equidistant between the screws, a plastic sequin or similar small plaque is mounted. This plaque serves as a single moving point, advancing or retreating from the plane defined by the screw-heads, depending upon the expansion or shrinkage in the

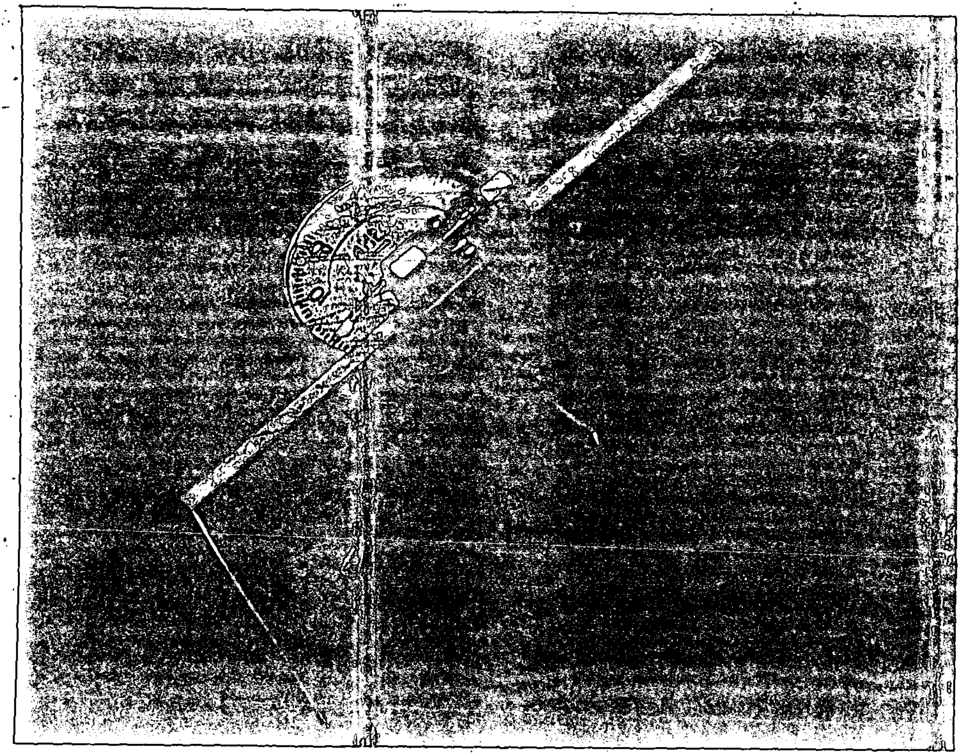


Fig. 8. Photograph of the dendrometer used in measuring tree diameters.

tissues directly beneath. The position of the screws is fixed since they are mounted in the inactive xylem below the current growth. The thermal expansion of the screws due to diurnal and annual temperature changes is slight, amounting to about 0.025 millimeters total change from zero to 100°C.

As the outer bark of mature ponderosa is quite thick and deeply furrowed, some preliminary preparation is necessary before the screws and sequin are mounted. A sharp hand-ax is used to smooth an area approximately eight inches square by cutting away most of the bark to within about three millimeters of the cambial region. This distance must be estimated. If a cut accidentally exposes the cambium and underlying wood a new area should be prepared several inches to the side. Once the region has been roughly smoothed with the ax, a small area in the center of this is given a final preparation of the placement of the sequin. In this particular species the bark "shingles off" quite readily in large smooth flakes. These flakes are picked away with a pen-knife until one is reached which seems anchored just exterior to the phloem and has a smooth bark surface. The sequin is attached with a small amount of Duco cement or other weather-proof adhesive. The sequin serves two purposes, one, as a hard, non-wearing surface where the micrometer spindle strikes, and two, as a fixed point in one plane of reference, necessary for the proper positioning of the dendrometer. The three screws are then driven in equidistant about the sequin. The final step is to spray the entire area of smoothed bark, sequin, and the exposed parts of the screws with a clear enamel to retard weathering and rusting.

In order to obtain a dendrometer reading, the end of the spindle is placed against the sequin and the plate held firmly against the three screw heads, care being taken to keep the instrument level. The spirit level controls this horizontal orientation and is essential, since the heads of the screws generally do not define a true tangent to the surface of the tree and any rotation of the instrument about the point of measurement causes the values obtained to vary. The dial reading is noted and the apparatus lifted away from the tree. This sequence is repeated until the same dial value is registered three consecutive times. This value is then recorded. The sensitivity of the instrument, registering as it does, values as small as 0.01 millimeter (equal to 0.0004 inch), necessitates care in placing it for a reading. Consequently a series of consecutive trials insure a true value.

Five representative trees were selected on the site, ranging from nine inches to fourteen inches in diameter at the one meter level, and averaging thirty-five feet high. In age they ranged from forty to sixty-five years old and were spaced at almost even five-year intervals for the five trees, except that no age fifty was represented.

Results

The series of diameter increments as measured with the dendrometer, when plotted as growth curves, are striking in their uniformity (see Figures 9, 10, and 11). There are differences, however, between each tree, which, due to the smallness of the sample size cannot be definitely attributed to any particular factor such as age or exposure.

Trees T-3, T-7, and T-9 each had an installation on the east side of the tree and the plotted curves formed by these three are similar both in slope and magnitude. In all five trees there was a marked shrinkage between April 17, the date of installation, and May 3, the date of the first reading. From this date onward there was a period of rapid growth with no marked reversals (except in T-9) before reaching the upper portion of the curve, where the rate decreased noticeably during the first week in August. There were marked fluctuations in diameter, both positive and negative, during the fall and winter months, but with little or no net gain. In T-1 and T-6 the shapes of the curves are very similar to those just described, though the exposure was different. In the case of T-1 there was also a pronounced difference in total increment when compared with the other four trees.

During the late summer all the curves tended to flatten out and were characterized by irregular fluctuations. The first of

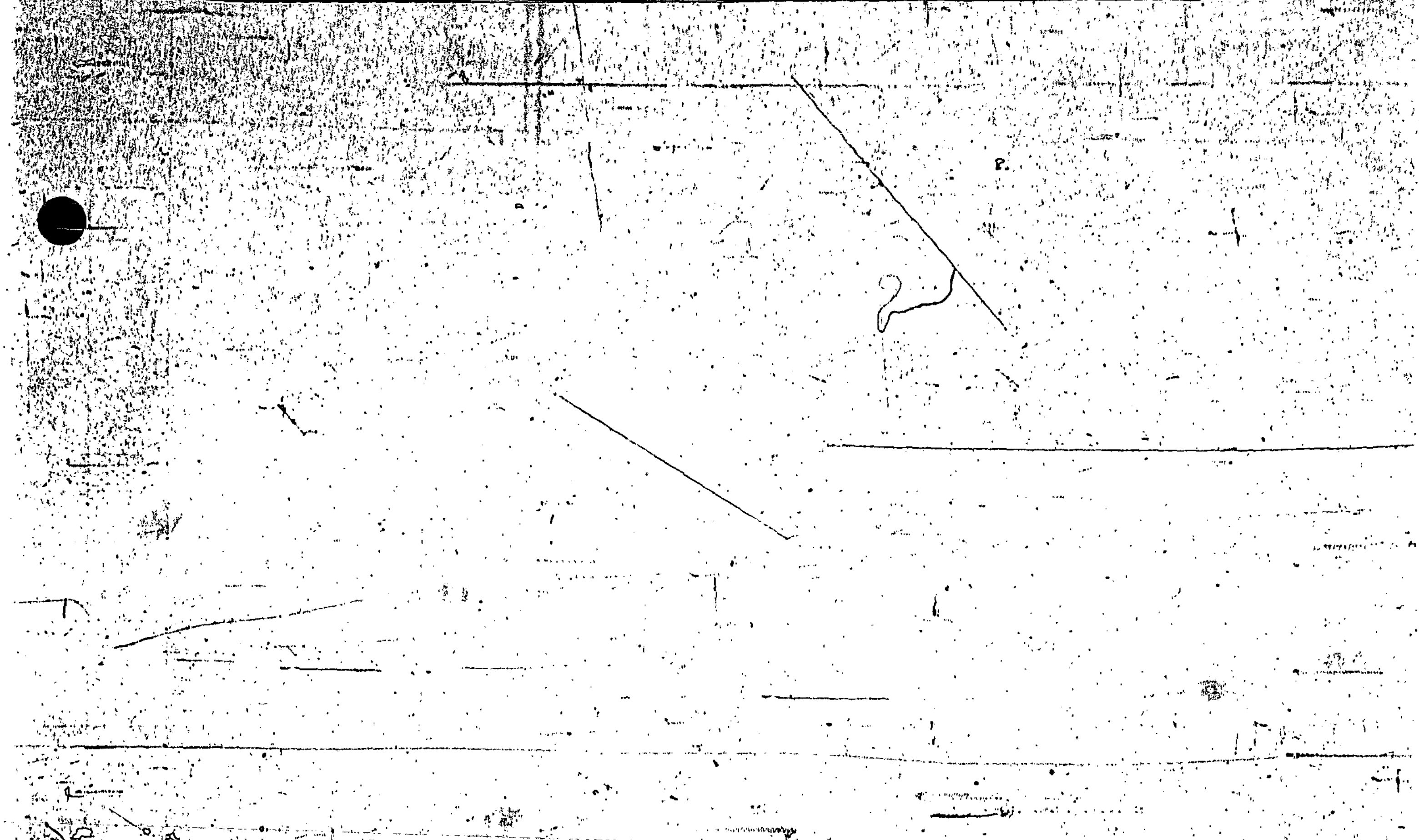
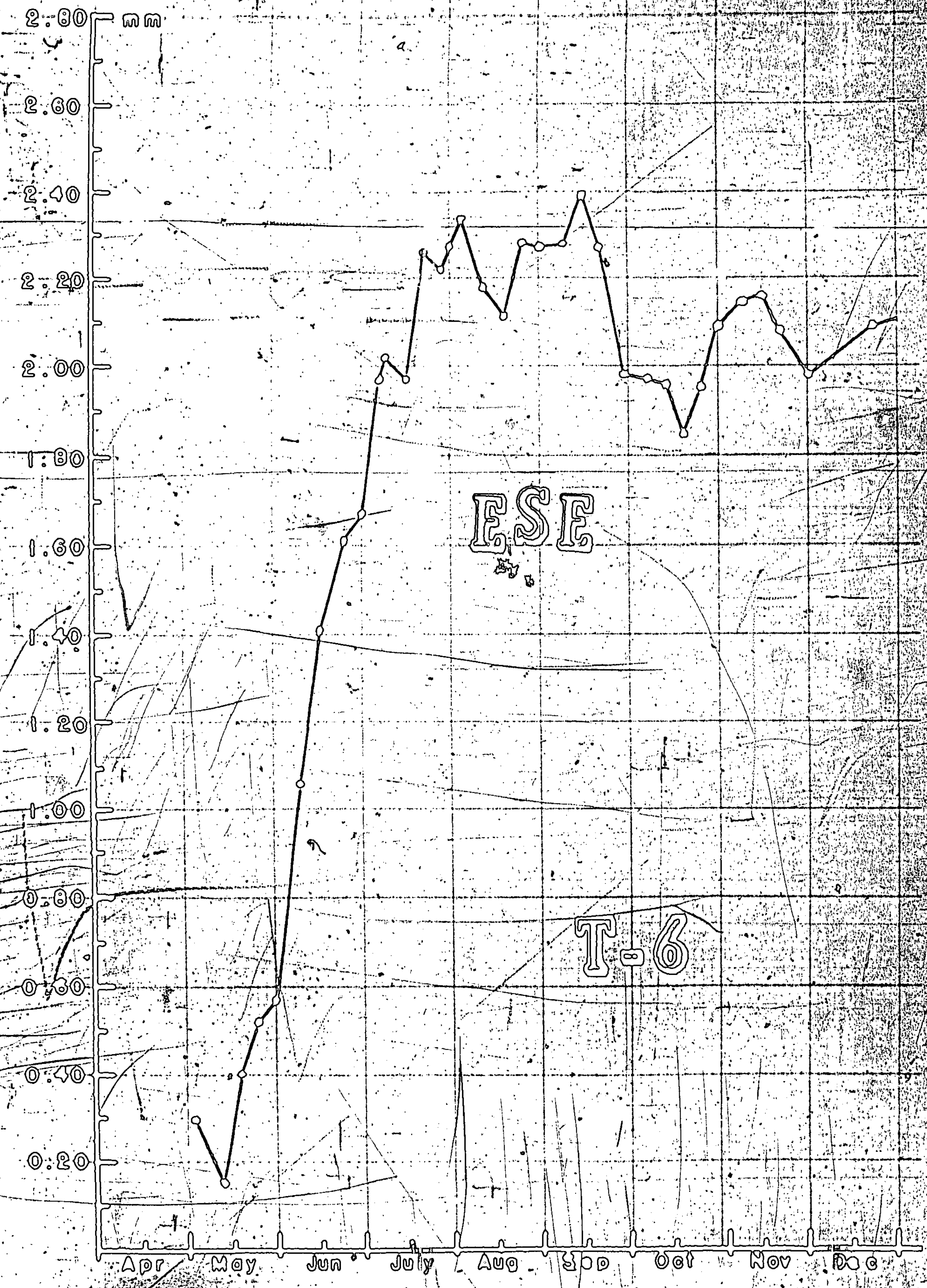


Fig. 9. Dendrometer curve for tree T-6. East-southeast exposure.


mm
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
Apr
May
Jun
July
Aug
Sep
Oct
Nov
Dec
ESE
T-6

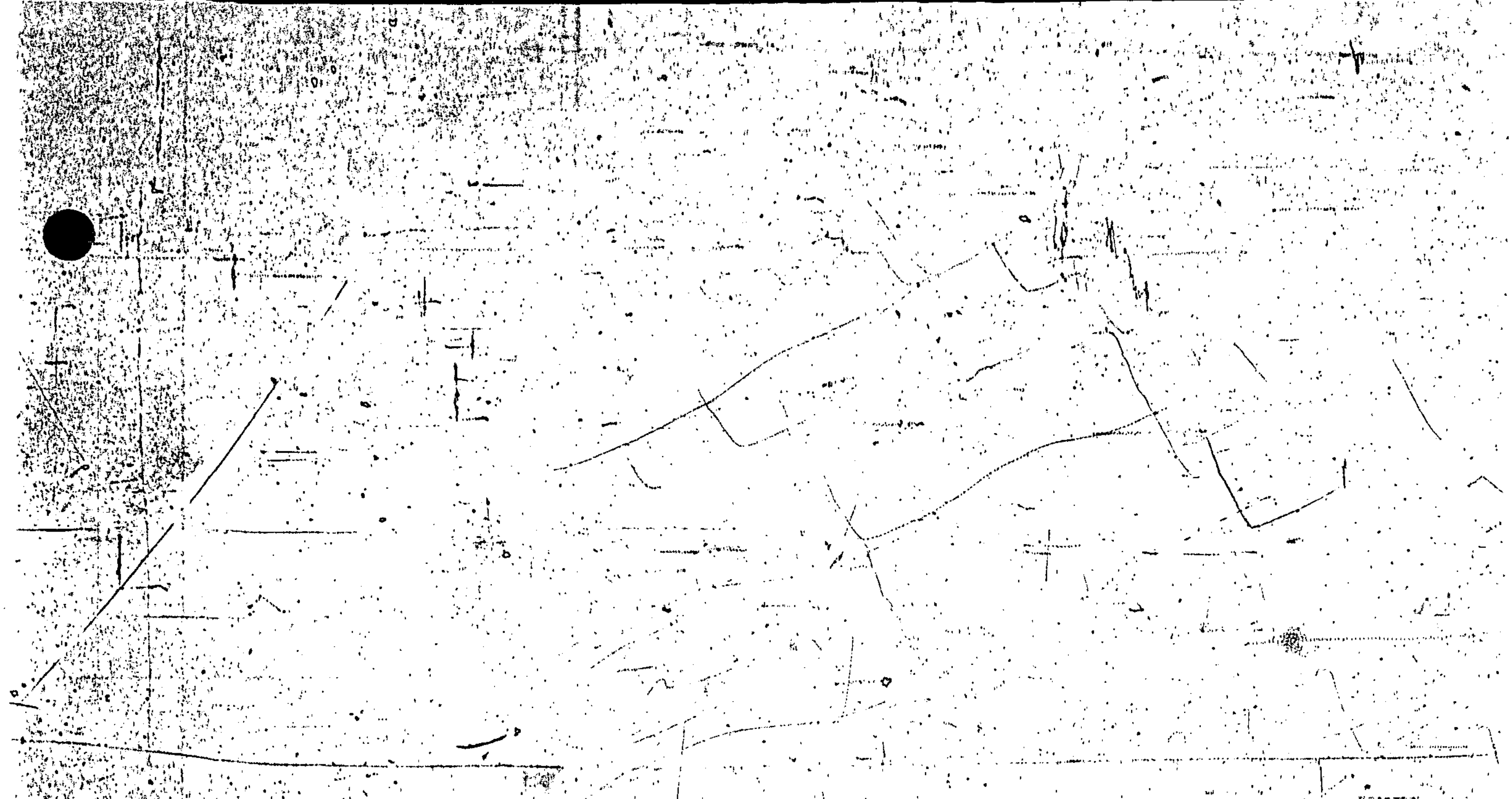
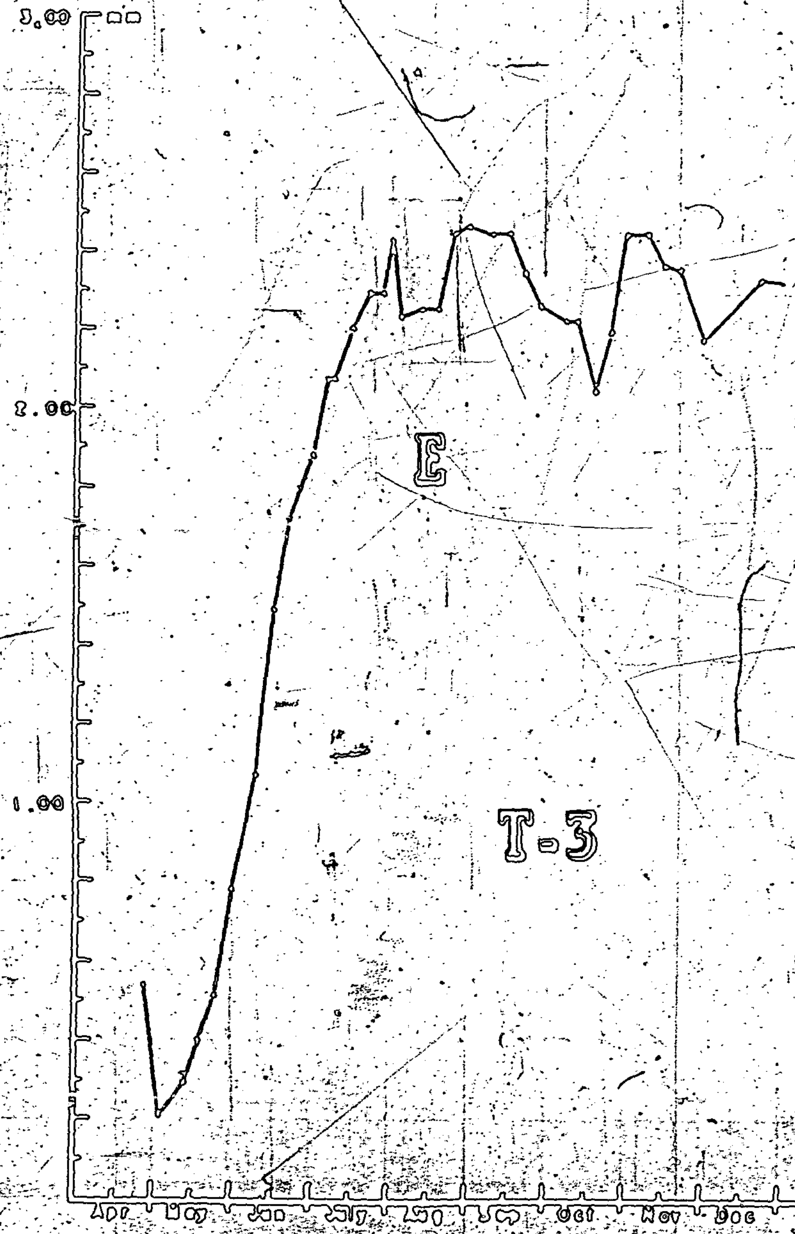
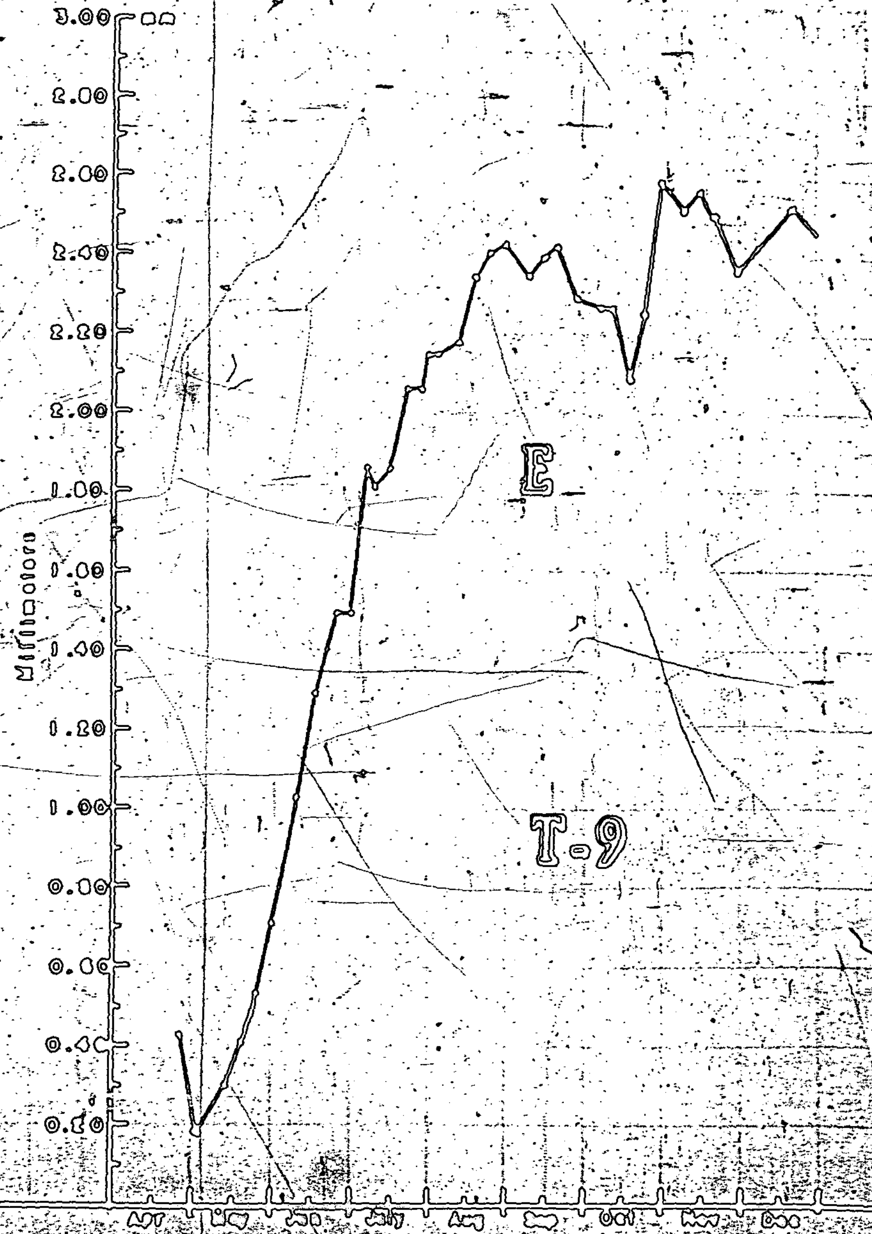


Fig. 10. Dendrometer curves for trees T-3 and T-9, both mounted on east exposures.


3.00
2.00
1.00
mm
E
T-3
Apr
May
Jun
July
Aug
Sep
Oct
Nov
Dec


Millimeters
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
mm
E
T-9
Apr
May
Jun
July
Aug
Sep
Oct
Nov
Dec

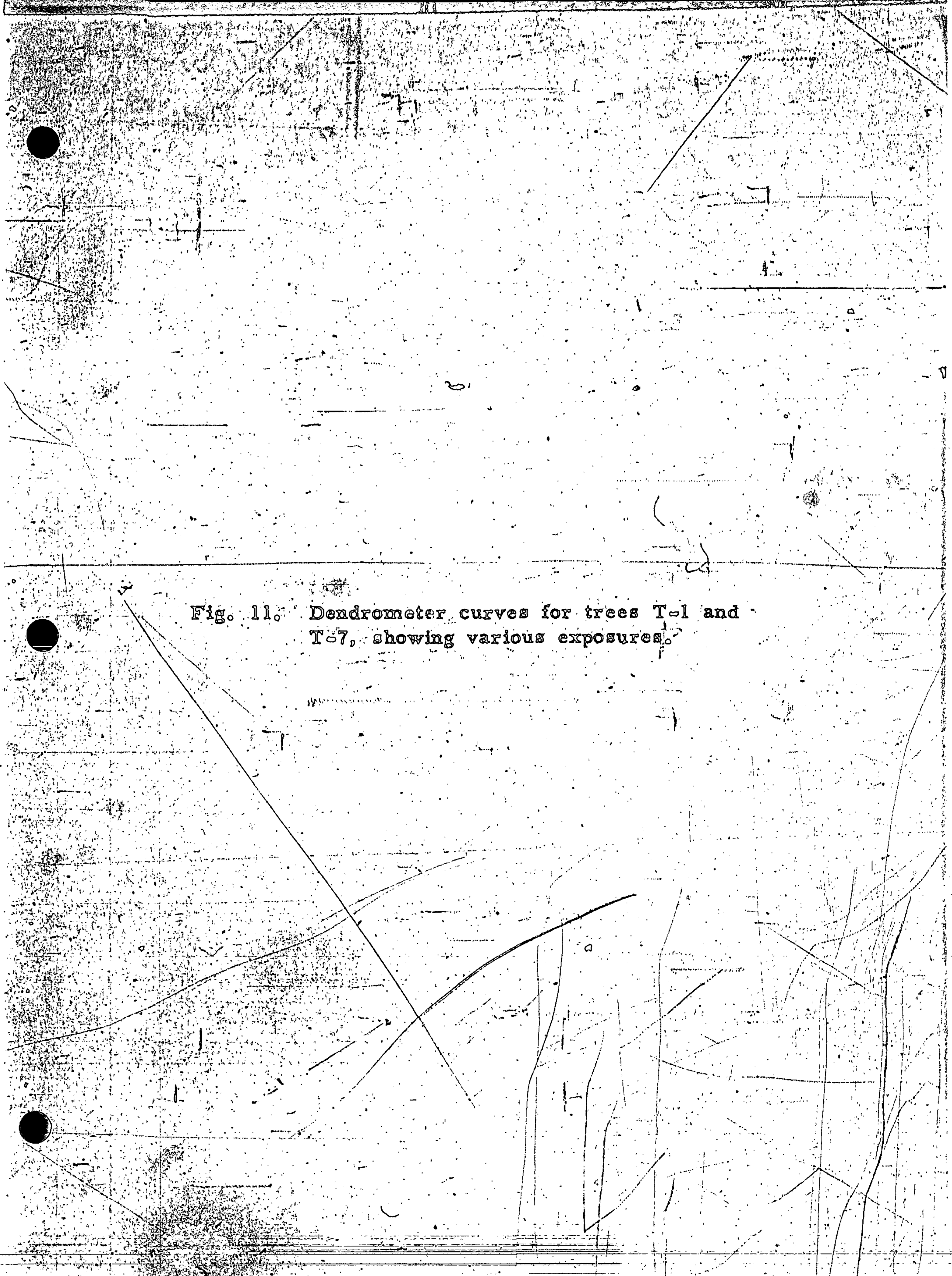
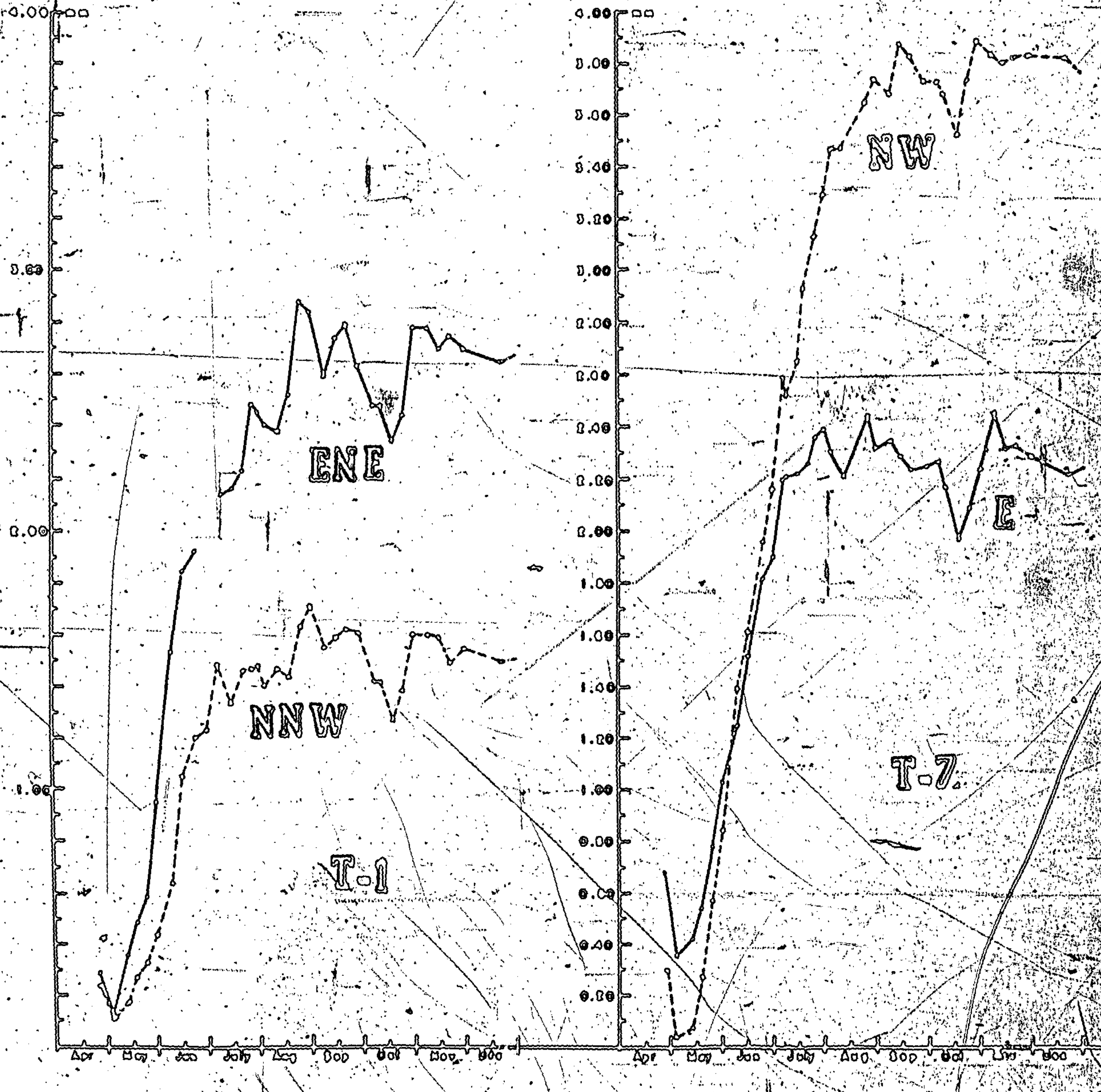


Fig. 11. Dendrometer curves for trees T-1 and T-7, showing various exposures.


ENE
NNW
T-1
Apr
May
Jun
July
Aug
Sep
Oct
Nov
Dec
4.00
NW
E
T-7
Apr
May
Jun
July
Aug
Sep
Oct
Nov
Dec

these fluctuations was a marked reversal occurring during the first half of August, after which there was an increase in diameter to slightly above the former high. This was followed by minor changes until the middle of november when there was again a very sharp decrease to a diameter corresponding to that of the first week in July for trees T-7, T-3, and T-6, and T-1 on the north-northwest side only. Since the July portion of the curve represents the very end of the grand period of growth, the sudden shrinkage in mid-November to this previous level can well be interpreted to mean that this late increment is due to other tissue elements than the rigid xylem which presumably could not show such a degree of shrinkage. These fluctuations can be followed by referring to Figures 9, 10, and 11.

In two trees, T-7 and T-1, two installations were made on approximately opposite sides of each tree. The most striking result of these paired observations is a difference in total growth between two sides of the same tree but a correspondence in the relative shape of the growth curves. For example (Figure 11) in T-7, while the east side reached its asymptote the first week in July, the northwest side continued uninterrupted its rapid rate of expansion until the first week in August. The same phenomenon is apparent in T-1 to a lesser extent, the north-northwest side being slow growing, while the rate of growth on the east-northeast side is much faster and the total increment greater, though both sides approach their season's maximum girth at about the same time.

CAMBIUM SAMPLING

Methods

The dendrometer does not distinguish between such factors as cell division, water uptake, xylem formation, phloem increase, and phellogen activity in measuring the increase or decrease in tree diameter. For this reason a series of small tissue sections were cut at biweekly intervals throughout the growing season of 1958 from trees adjacent to the dendrometer trees. One of the latter (T-9) was sampled intensively also. From the other four dendrometer trees only a single sample was taken at the end of the growing season, very near to the point of sequin attachment.

The method consists of removing most of the thickness of outer bark over a selected area, as described for the mounting of dendrometer screws, and then cutting out an elliptical section with a sharp pen-knife. These sections were about one inch long and one-quarter of an inch broad on the outer surface, slanting inward to form a keel half an inch beneath the surface and well into the 1957 xylem. The section was placed in a small vial containing formalin-alcohol-acetic acid (Johansen 1940) stoppered, labeled with date and tree number, and then returned to the laboratory and stored until sectioned for study. It is necessary to off-set consecutive samples about one inch from each other spiralling slowly around the tree, when sampling week after week.

All samples were stored until the end of the season and then sectioned at the same time. Free-hand sections made with a razor blade were adequate in revealing the major cellular changes of the season's growth. It is not anticipated that the more refined paraffin technique would alter the conclusions reached in the present study (Abbe and Crafts 1932, Fraser 1952, and Lodewick 1928).

Each section was cut about 0.1 millimeter thick. It was then placed for thirty seconds in a formalin-alcohol-acetic acid solution of methylene blue. From this it was transferred to ninety-five percent ethyl alcohol for one minute and then into toluene to remove the alcohol. From the latter it was placed on a slide in a drop of toluene-diluted Canada balsam and covered with a cover slip. The purpose of the stain was not to differentiate various tissues cytologically but rather to give a general background stain. It served quite well. The use of iodine-iodide solution on a separate series of sections aided in interpretation by distinguishing starch-containing cells.

Results

The first cambium samples were obtained in mid-March of 1958. Trees from which samples were to be taken were assigned numbers. Thereafter, from one to five of these selected trees, ten in all, were sampled every two weeks. After September the trees were sampled on a monthly basis.

Xylem increment in tissue sections is easy to measure and distinguish. Once the tissue is formed, it is permanent. Changes in phloem are less easy to follow. The cells are more fragile, especially in the undifferentiated zone, and sectioning usually destroys their true proportions. Once formed, sieve elements are readily measured, yet their subsequent fate of being crushed and later partially disintegrated (Abbe and Crafts 1932) makes increment studies difficult to interpret.

A decided aid in phloem studies in ponderosa pine is the periodic production of narrow rows, one or two cells in thickness, of naturally dark-colored phloem parenchyma. The color is due to stored tannins. These cells remain viable among the crushed cells of the inactive sieve zones and after several seasons may give rise to the external phellogen layers (Esau 1953). Since they are produced only periodically during the growing season they serve as convenient "markers" in the course of phloem extension.

The T-9 series served as the basis of the diagrams in Figure 12, supplemented by observations of tissue sections from the other trees. The following description gives the trend of one season's tissue development in the diametral increase of ponderosa pine.

Fig. 12. Each of the seven bars is a diagram based on a tissue section taken from T-9 during the 1958 growing season. The heavy black horizontal line at the base of each represents the terminal portion of the 1957 xylem. The cambium is represented by a dotted horizontal line. The stippled areas are phloem sieve cells, the horizontal lines between the stippled areas are phloem parenchyma. 1958 xylem is shown in cross hatching.

Bar

1. May 3. No growth. Cambium still a single line of cells (Ca) separating the 1957 xylem from the 1957 phloem (A).

2. May 31. New growth apparent. The cambium is a broad indistinct zone (CZ) composed of undifferentiated phloem and xylem lying to either side of an indistinguishable cambium. A new line of phloem parenchyma separates the 1957 phloem (still functional) from newly differentiated 1958 phloem. (X) represents 1958 xylem.

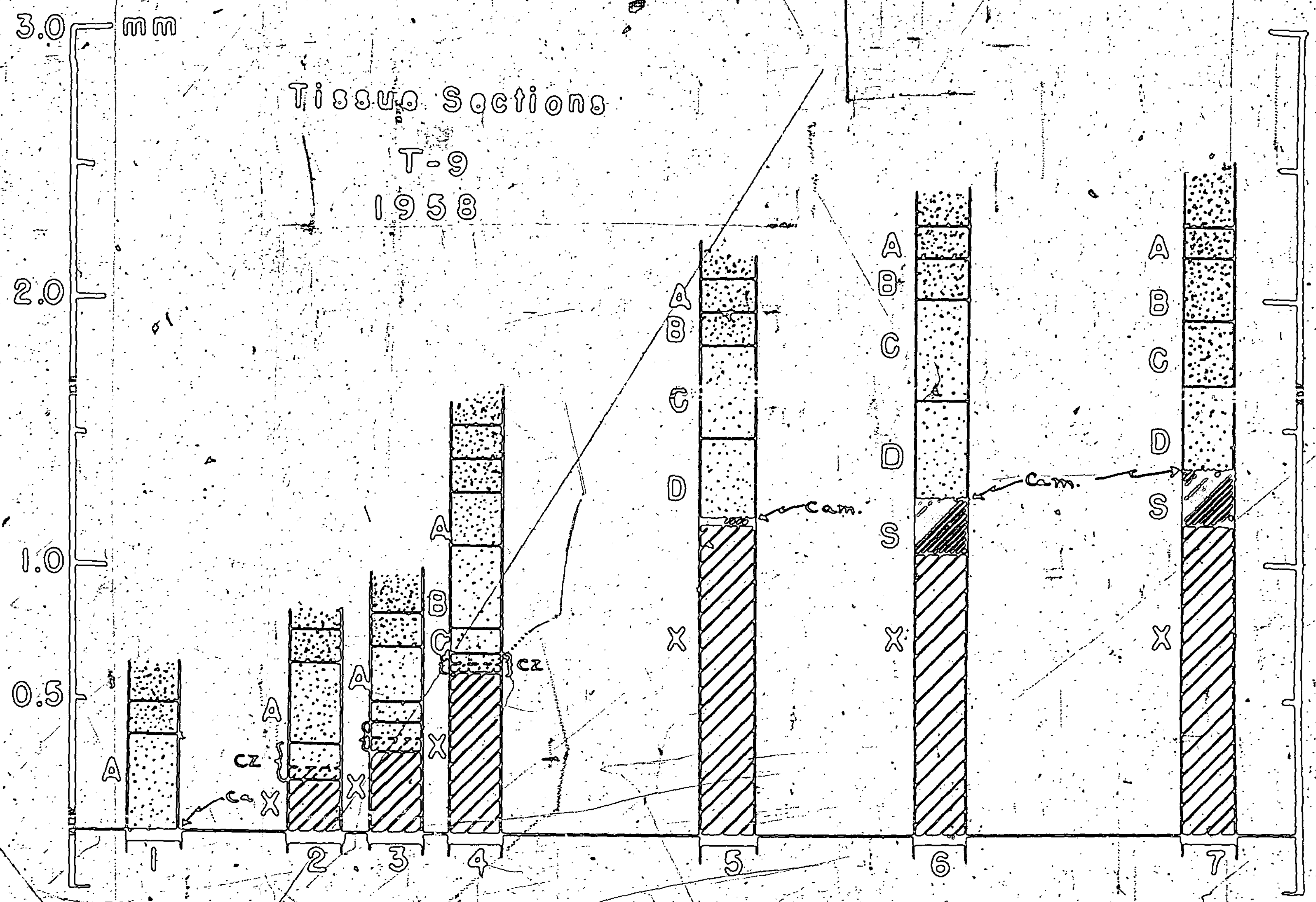
3. June 9. A second layer of phloem parenchyma has been produced. The "A" sieve zone is being crushed by new growth. The cambial zone of undifferentiated tissues is becoming more narrow.

4. June 16. Conditions similar to those of June 9, but growth more advanced. The third row of phloem parenchyma is just being produced.

5. July 28. Growth near completion. A narrow band of summer-type xylem is beginning to differentiate. The cambium is again a single row of cells. The 1957 ("A") sieve elements have been completely crushed, and also to some extent the 1958 ("B") zone; while sieve cells in zones C and D are still fully expanded.

6. Aug. 31. Season's growth essentially completed.

7. Oct. 11. Development appears little changed from that of August.


Tissue Sections
T-9
1958
3.0
mm
2.0
1.0
0.5
A
Ca
A
Cz
X
A
X
A
B
C
X
Cz
A
B
C
D
X
Cam.
A
B
C
D
S
X
Cam.
A
B
C
D
S
X
1
2
3
4
5
6
7

On May 3, 1958, the tissues were apparently the same as they had been the preceding fall. Spring and summer growth of xylem for the 1957 season were separated by a sharp boundary, the single layer of cambium cells, which was indistinguishable from the sieve cells. This layer of sieve elements, the last produced in 1957, was 0.36 millimeters wide and composed of twelve to sixteen rows of cells. It was bounded externally by a row of parenchyma. Beyond these were the usual bands of crushed sieve cells alternating with rows of the tannin-containing cells, about eight zones of each before the innermost phelloderm layer was reached.

Changes are quite apparent in the tissue section taken on May 31. A narrow band of newly differentiated 1958 xylem is visible. The active cambium is now somewhere within an indistinct zone of cells, crushed and torn in sectioning. Between this indistinct meristematic zone and the old 1957 sieve zone, now only 0.30 millimeters wide, is a newly formed row of parenchyma cells, as dark but only about half as large as they will be when fully matured. An undifferentiated newly-formed sieve cell layer, probably no more than two to three cells wide, forms a narrow zone 0.10 millimeters wide.

By June 9, the new phloem is distinctive, being a band 0.08 millimeters wide of mature elements, and the new xylem is now 0.24 to 0.35 millimeters wide. The cambium and undifferentiated xylem and phloem form a region 0.10 millimeters wide.

The last formed sieve elements of 1957, a band 0.36 millimeters wide at the beginning of 1958 have now been crushed to 0.200 millimeters. Figure 12 shows diagrammatically the development for the remainder of the season, while Table 12 gives the corresponding numerical data.

Three rows of parenchyma cells were produced during the season, each being separated one from the other by fifteen to twenty rows of sieve cells. By the summer's end the first-formed band of sieve elements had already been partially crushed, as had the second, with only the last-formed zone fully expanded, its outer boundary marked by the third row of parenchyma, its inner by a sharp line of demarcation from the summer wood of the xylem. As they first arise and are fully differentiated, sieve cells form a band about 0.35 millimeters wide, but they are then compressed by succeeding layers. The total increment in T-9 at the season's end due to sieve cell formation was 0.36 plus 0.38 plus 0.16 millimeters or a total of 0.90 millimeters rather than the 1.65 millimeters if there had been no crushing. The total width of the xylem on the other hand was 1.24 millimeters.

In attempting to compare growth as measured by these two methods, tissue sections versus dendrometer readings, several points must be borne in mind. Even in tree T-9, where a complete set of both measurements were taken, direct comparisons were not truly possible. The dendrometer installation was at a single

TABLE XII

XYLEM AND PHLOEM GROWTH MEASURED FROM TISSUE CROSS-SECTIONS (T-9)

Days from the Initiation of Growth	Total No. of Xylem Cells	Total Width of Xylem	Total No. of Phloem Cells	Total Width of Phloem
28	8	0.20 mm	1) 2-3*	0.10 mm
40	10	0.30 mm	1) 18 2) 5-10**	0.20 mm 0.08 mm
47	22	0.60 mm	1) -- 2) 20 3) --***	0.20 mm 0.30 mm 0.08 mm
89	45	1.14 mm	1) -- 2) 17 3) --	0.15 mm 0.34 mm 0.30 mm
123	54	1.24 mm	1) -- 2) -- 3) 18	0.16 mm 0.38 mm 0.36 mm
164	54	1.36 mm	1) -- 2) -- 3) --	0.24 mm 0.24 mm 0.32 mm

* 1) First zone of sieve cells produced in 1958
** 2) Second zone of sieve cells produced in 1958
*** 3) Third zone of sieve cells produced in 1958

point on the east side of the tree while tissue sections were cut as a series from the west side of the tree. Figure 11 showing the dendrometer values from two sides of the same tree reveal the large random differences which can be expected due to chance, and it is to be expected that such differences in total growth may exist between the east and west sides of tree T-9.

Even measurements made from two adjacent tissue samples cannot be directly compared due to random non-uniformity in the circuit of the growth ring. A comparison of sections Number 6 and 7 and Figure 12 will illustrate this. Nevertheless, cambium studies do produce valid results, when comparisons are made, because the random differences in width between two closely adjacent sections are always smaller than the total growth being measured.

A further complication in trying to compare growth measurements of a dendrometer with tissue sections are the changes due to phellogen activity and the shrinking and swelling of inactive of dead tissues in the outer bark. It was estimated that at least one and probably two or three phellogen layers lay between the sequin and the cambium. To what extent these outermost layers contribute to the characteristics of the growth curves of the dendrometer have not been fully evaluated. Observations on the tissue sections taken from the other four trees, though not as complete a series as T-9, agreed in all respects with those made on this tree.

DISCUSSION

Ecotypes

As is common in such a widespread species as ponderosa pine, a number of ecotypes have segregated. Munger (1947) and Mirox (1953) demonstrated that different ponderosa pine ecotypes, or regional races, occur in even short vertical distances or small geographical regions. It is, therefore, imperative that the ecotype of the trees on the present study site be identified. Most authors have used needle characteristics for delimiting these ecotypes. The trees in the present study show needles ranging from three to six inches in length, of mixed 3-needle and 2-needle fascicles, with the former predominating. Individual needles live from three to nine years. After a whorl is more than three years old, there is a pronounced autumnal needle cast and the older whorls lose from one-third to one-half of their remaining needles each fall. On the basis of the following brief survey of the literature it was concluded that these trees belong in the "scopulorum" ecotype, one of the most distinctive types in this species.

In 1911 the United States Forest Service, initiating a study designed to test the suitability of various races of Pinus ponderosa Laws. for forest planting, established a plantation at the Priest

River Experimental Forest in northern Idaho. Pine seeds were collected from twenty-two localities throughout its range. These were planted and established as nursery stock, then transplanted into contiguous plots of essentially identical environments. The first comprehensive report on the results of this planting was that of Weidman (1939). In it he demonstrates clearly the presence of racial strains in the twenty-five-year-old stand. These results are of particular interest to the present study, for they establish not only the existence of ecotypes, but give a measure of the degree of variability between the various populations of ponderosa pine. As one of the original seed sources was from Roosevelt National Forest, near Estes Park, Colorado, which is but a few miles north of the study site, some revealing comparisons are possible.

According to Weidman there are at least six races of ponderosa pine in the western United States, corresponding to six climatic provinces. One criterion of this racial difference is the ratio of 2-needle to 3-needle fascicles, and the change in this ratio from climatic region to region. Except in the eastern part of its range ponderosa is typically and frequently exclusively a 3-needled pine, but may range from two to as many as five needles per fascicle. The ratio between the two changes from region to region.

In the present study, needle counts revealed the preponderance of 2-needle fascicles over 3-needled ones, yet, as is demonstrated in Table 13 the variation from year to year, and from

TABLE XIII

TOTAL NUMBERS OF NEEDLE PER ANNUAL WHORL, AND THE RELATIVE NUMBERS OF 3-NEEDLE FACICLES, FOR THREE YEARS ON A SELECTED GROUP OF TREES

Sample Number	1958		1957		1956	
	Total	% of 3's	Total	% of 3's	Total	% of 3's
1*	86	12.8	127	52.0	91	59.5
2*	24	83.5	33	88.0	22	67.1
3**	71	7.0	128	18.7	107	22.4
4**	59	3.4	71	15.5	61	8.2
5**	52	23.1	47	83.7	32	72.0
6	42	0.0	19	0.0	88	0.0
7	36	100.0	44	47.8	41	24.0
8	55	21.8	74	98.7	68	78.0
9	34	8.8	16	0.0	19	0.0
10	40	12.5	23	78.0	22	18.2
11	35	85.7	22	100.0	16	50.0
Average	48	32.6	55	52.9	52	36.2

*Two samples from a single tree, No. 1 from a branch of the upper crown; No. 2 from a lower branch.

**Three samples from a single tree, Nos. 3 and 4 from the upper crown, No. 5 from a lower branch.

branch to branch on the same individual seems almost without pattern. The range was from zero to 100 percent of 3-needle fascicles for any particular whorl. Average values based on entire branches of eight different trees in which whorls for the years 1958, 1957, and 1956 were counted, show 32.6, 52.9, and 36.2 percent, respectively, of 3-needle fascicles. The average values given by Weidman for 3-needle fascicles in the Roosevelt population was twenty-two percent at the Estes Park site and eleven percent on the Priest River plot. It is apparent that Weidman's data are inadequate and that the spread of values in the present study also show that a proper study of needle ratios will necessitate a well-designed statistical study based on a large number of samples in order to yield reliable results. Some of the problems involved in adequate sampling of ponderosa pine needles (Baker 1948) and the morphological differences which exist within the various parts of the tree crown (Helmers 1943) have already been adequately treated.

In the transplants at the Priest River site the ratio of any particular ecotype remained the same as that of trees still growing in the parent locality. On the basis of this observation, Weidman states that the number of needles per fascicle is an inherited character and is not changed by the environment. To some extent this must be true since certain ratios are distinctive of particular populations. Shaw (1914) on the other hand, feels that while the heteromerous condition of the fascicle is characteristic in certain pines and heritable, it is in some degree dependent upon climatic conditions. The environmental control of the genetic expression is undoubtedly complex.

Ecotypic variation in the length of ponderosa pine needles is great, the maximum for this species over its range being over twice as great as the minimum. Maximum values are somewhat over seven inches, minimum values rarely less than three inches. The range of variation in the Boulder population was from slightly over three inches to almost six inches. Climate appears to have some influence on the hereditary mechanism, as boreal populations have shorter needles than stands in milder climates (Shaw 1914). This is also true of populations in regions of deep altitudinal spread, the higher trees having shorter needles and more compact whorls than trees only a few miles distant but at lower elevations.

Though needle length is primarily hereditary, with a slight susceptibility to environmental modification, the time of needle persistence (age) is almost entirely controlled by the climate (Weidman). Trees in the Front Range, both those in the present study site and those of Estes Park, show a foliage persistence of five to seven years, six years being the mode, and needle cast beginning after the third year. However, in the Priest River plots all ecotypes shed their needles uniformly after the third year.

Growth Characteristics

Trees on the study site began diametral increase at the one meter level between the first and the tenth of May during the 1958 growing season (Table XIV). The date of growth cessation at this level was more irregular than the date of its beginning and ranged from the first of August to the fifteenth of September, 1958. These dates, obtained from dendrometer measurements, are substantiated by measurements taken from tissue sections collected at the same one-meter level from several trees.

Some cytological characteristics of the tree's growth were revealed by microscopic study of tissue sections. Early in May, 1958, the cambium is a single row of cells sharply separating the 1957 xylem from the 1957 phloem. By the end of that month it has become indistinguishable within a zone 0.1 millimeter wide composed of new, undifferentiated, xylem and phloem cells. This broad zone of cambium and of xylem and phloem mother cells gradually narrows, and by the end of July a single row of cambium cells again sharply separates the summer wood of the 1958 xylem from the last-formed phloem sieve elements of 1958.

Three rows of phloem parenchyma (bast cells) were produced during the 1958 growing season. These tissues, not previously reported in the literature as three rows, were produced at seven to nine day intervals beginning the last week of May and ending in approximately mid-June. They were separated by zones of phloem sieve elements averaging 0.25 to 0.35 millimeters wide. The bands of phloem parenchyma were one to three cells wide, while zones of sieve elements were eighteen to twenty cells wide. A more detailed review of growth features and comparisons of the Boulder trees with those in other regions is presented in the following paragraphs. The initiation and cessation of growth in the five trees studied as determined by dendrometer measurements are presented below in Table XIV.

TABLE XIV
PERIOD OF DIAMETER INCREASE IN FIVE INDIVIDUALS OF PONDEROSA PINE ON THE BOULDER SITE IN 1958

Tree No.	Age (Years)	Compass Direction	Growth Began	Growth Ended	Total Days
1	60	ENE	May 3	July 28	86
		NNW	May 3	July 6	64
3	40	E	May 3	July 13	90
6	45	ESE	May 12	July 12	60
7	55	E	May 3	July 31	90
		NW	May 3	Aug. 31	120
9	65	E	May 3	Aug. 31	120

Daubenmire (1950) studied diameter increase in three ponderosa pines in the Priest River study described in the previous section. He made measurements on three trees of each of seventeen populations, at one and one-half meters above the ground over a period of two growing seasons. Most of the populations began growth in late May and ceased growth in late August. Table XV gives the growth period dates that Daubenmire found in the individuals from the Roosevelt (Estes Park) population. Comparison of the present data with Daubenmire's reveals that initiation of growth in the Boulder region began fourteen days earlier than those at the Priest River.

TABLE XV
PERIOD OF DIAMETER INCREASE IN THREE INDIVIDUALS OF PONDEROSA PINE ON THE PRIEST RIVER SITE IN 1950*

Tree No.	Compass Direction	Growth Began	Growth Ended	Total Days
1	N	May 20	July 18	59
2	N	May 28	July 20	53
3	N	June 1	July 28	58

Study of the termination of the growing season is complex because it is difficult to determine the time of that cessation of diametral increase which is caused solely by cambial activity and cell maturation. The dendrometer is not able to distinguish between diameter changes caused by growth and those caused by changes in water balance in the trunk tissues. Thus the end point of a season's growth is quite arbitrarily fixed by the investigator. In the present study the first pronounced reversal of diameter increase occurring after the grand period of growth was used as the end point. However, small permanent increases in diameter did take place during the fall.

The date of cessation of growth was quite irregular in the Boulder trees. The growing period ranged from sixty to one hundred and twenty days, some trees continuing growth for two months after others had ceased. Even the growing period on two sides of a single tree may exhibit a remarkable divergence. On tree T-1 this difference between an east and a west exposure was a span of twenty-two days between the two dates of growth cessation. Growth on two sides of T-7 ended thirty days apart (Table XIV). Daubenmire did not find such irregularity. The thirty-year-old trees in Idaho had a growing period of fifty to sixty days. Such a divergence between two groups of trees which are probably closely related genetically is difficult to explain. Differences in climate between the two seasons might be a possible explanation. The Priest River forest is nearly 500 miles farther north, though at a lower elevation. However, when climatic records (1941 Yearbook of Agriculture) are compared for such values as mean monthly temperature, annual range of temperature, length of frost-free season, and dates of first and last killing frosts, between the Priest River Experimental Station and the present site, the values are nearly identical. On the other hand, there is a difference in the amount and pattern of precipitation, the yearly average at the more northern station being 28.95 inches falling mostly from November through February, as compared with 17.94 inches falling mostly as spring and summer precipitation from March to October here in the Front Range. However, this difference in precipitation and the resulting patterns in available soil moisture have not been demonstrated as causative in time of growth between the southern and northern habitats.

Difference in growing period between the two might also be explained as an age difference between the two groups of trees as the trees measured by Daubenmire were of an even-aged stand thirty years old, while the trees in the present study were older, ranging from forty to sixty-five years old. Such an explanation is open to doubt because the extreme values of twenty-two days and thirty days difference in growing period occurred on different sides of the same tree in two instances, a difference greater than that between trees of the two populations.

Fraser (1952), working in the Chalk River district in Ontario, made a very thorough study of growth in the white pine. Dendrometer measurements were made on all four quadrants of each tree and at several heights extending from the base into the crown. These measurements were supplemented by tissue studies. First cambial activity at the one-meter level began in the ten day period after May 17, a date which corresponds well with those of Daubenmire's study at the Priest River. The two sites are in the same latitude. Though the comparison is between two species of the same genus, it is suggestive that the initiation of growth at the one-meter level corresponds so well between two populations of trees widely separated geographically but at the same latitude. At the same time this initiation is almost two weeks later than in a pine stand 600 miles to the south, the Boulder population. How does the initiation and cessation of growth in the trees of the Front Range compare with these phenomena in trees farther south?

Pearson (1924) reported on a one-year dendrographic study of two specimens of ponderosa pine in the vicinity of Flagstaff, Arizona. Though growing side by side there was a wide divergence in the growth activity between the two. One tree initiated growth on May 16 and ceased growth 117 days later on September 10. The other tree initiated growth on June 1 and completed growth 88 days later on August 27.

Later, Fowells (1941) published a seven-year record of dendrometer measurements of ponderosa pine and other conifers in the Sierras of California. His results, given below, are based on ten-tree samples at each elevation. All trees were growing on southeast and southwest slopes, which correspond with the slope aspect in the present study. Ages were not given. The table below shows the six-year averages for diameter growth at one meter.

TABLE XVa

INITIATION OF GROWTH AND PERIOD OF GROWTH OF PONDEROSA PINE IN THE SIERRA-NEVADAS OF CALIFORNIA

Elevation in feet	1800	3000	4000	5000	6000
Date of Initiation	Feb. 17	Feb. 25	Mar. 11	March 23	April 17
Days of Growth	241	148*	183	177	143

*The days-of-growth value for the 3000-foot level is anamolous due to a difference in exposure.

There is no 7,500-foot level in the Fowells study with which to compare the Boulder data, yet his general conclusions that both date of growth initiation and the total growth period are markedly delayed with each 2,000 feet increase in elevation allow significant comparisons to be made. Extrapolations from the values of these growth functions are permissible so long as it is remembered that conclusions drawn from them are still tentative. The trees in the present study commence growth during the first week in May, or slightly later. Their period of growth is quite variable and ranges from sixty to one hundred and twenty days. The California ecotype at 6,000 feet begins diameter growth on April 17 and grows for a period of 143 days. Thus, it begins growth nearly three weeks earlier and continues for three weeks longer than the Boulder group. However, if the differences between dates of initiation, and the periods of growth between 5,000 and 6,000 feet (Table XVa) are extrapolated for an additional 1,000 feet elevation, a close correlation of these values appears between the Front Range race and the Sierra race. Since the Sierra study site is about 200 miles south in latitude of the present stand, a greater disparity might have been expected in these extrapolated values. That is, it would be expected that of the two groups of trees, the group farther to the south would precede the other group in initiation of growth due to the normal increase in day-length and to the warming trend associated with the increasing angle of the sun.

Another very useful measure of diameter growth at the one-meter level is the rate of attainment of fifty percent of the total increment for the season. In 1958 the stand under study attained this value in thirty-one days, ranging from twenty-four to forty-one days (Table XVI). This compares favorably with Daubenmire's data of the Estes Park population which had a total growth period of fifty-six days, and thus a probable fifty percent value of about half this number of days. Fowells records an average of fifty-two days as being necessary to complete half the season's growth in the Sierras, a value which did not vary with altitude. Thus we find that the rate of growth of the ponderosa pine of the Front Range is much more rapid than that of the same species

TABLE XVI

DATES OF COMPLETION OF 5, 50, AND 95 PERCENT OF TOTAL GROWTH AS MEASURED BY THE DENDROMETER

Tree	Age	5% Amount (mm)	5% Date	50% Amount (mm)	50% Date	95% Amount (mm)	95% Date	Total
T-3 East	40	0.12	May 16	1.15	June 14	2.20	July 21	2.31
T-6 ESE	45	0.09	May 14	0.92	June 9	1.76	July 5	1.85
T-7 East	55	0.10	May 18	1.01	June 11	1.93	July 20	2.03
T-7 NW	55	0.19	May 17	1.91	June 27	3.64	Aug. 17	3.83
T-1 ENE	60	0.11	May 17	1.07	June 9	2.03	July 24	2.14
T-1 NNW	60	0.07	May 12	0.68	June 10	1.29	July 14	1.36
T-9 East	65	0.12	May 16	1.18	June 20	2.24	Aug. 18	2.35
Mean Values		0.11	May 16	1.13	June 14	2.16	July 26	2.27

in the Sierra Nevadas. And since Fowells found no growth rate change with the changing environmental conditions as related to increase in altitude we may assume that the variation between growth rate of the California and the Boulder trees are ecotype-specific. Further evidence, obtained from the present investigation, on the constancy of growth rate under changing environmental conditions will be presented in Section C which follows.

Correlations of Growth with Moisture and Temperature

Initiation of Growth

Diameter growth at the one-meter level commences early in May. This initiation of growth is strongly correlated with several environmental features. The air temperature has risen to a mean value of 50°F. or above. Night temperatures for May, 1958, were rarely as low as the mid-thirties and only once or twice dropped to 32°F. The soil mass has thawed completely and has reached a mean value near 50° F. both at the six-inch level and the twelve-inch level. This rise in soil temperature in the spring of the year is sharp, and it has an important bearing on the availability of soil moisture for plant growth. Daubenmire (1957) has demonstrated that a cool, moist soil will retain more water at field capacity than the same soil at a higher temperature. Thus the seasonal march of temperature results in raising the field capacity in the spring when soils are cool and lowering the wilting percentage in late summer. This gradual release of water in the soil due solely to seasonal warming may amount to as much as 0.5 inch of water readily available to the plant. Actually, under the climatic regime of the Lower Montane Zone of the Front Range, the soil mass is at, or above, field capacity during most of April and May. Consequently though the amount of soil water is not a limiting factor during the initial stages of diametral increase, its availibility may have some bearing on initiation of this growth. The author concludes, however, that both soil and temperatures must be near a mean value of 50° F. for this diameter growth at the one meter level to begin. Similar results and conclusions were offered by Friesner and Walden (1946) for white pine growing in Minnesota. After analyzing a five-year dendrograph record for each of two trees of this species, they concluded that temperature appeared to control the time of initiation of radial enlargement. The date of initiation varied plus or minus a few days before or after the air temperature was continuously above 50° F. This is a higher value than that necessary for growth inception in the Front Range but still within a comparable range of temperature values. They also found that the duration of radial enlargement between the two trees varied from 120 to 195 days and that the date of cessation of radial enlargement ranged over a period of 35 to 45 days.

It is well known that tree growth begins at the tips of the upper branches and progresses inward toward the trunk and downward as a wave of cambial activity. Fraser (1952) reviewed this subject of growth initiation briefly in his paper and on the basis of his own work substantiated that growth is initiated at the very tip of a (forty-foot-high) tree nearly a month before cambial activity is detected at the one-meter level. He also demonstrated with injections of auxin that this cambial activity is due at least in part to auxin concentration. In the present study this crown-induced control of cambial activity at the lower trunk levels is recognized. Consequently the correlations of growth at the one-meter level with climatic factors must be of a secondary nature; yet it is felt by this present author such correlations are valid, for if these certain climatic values are not attained then the auxin supplied by the crown will be ineffective in initiating growth.

Once growth was initiated in the Boulder stand, it continued at a constant rate until mid-June or July, depending upon the individual tree. This remarkably constant rate of growth, maintaining itself in a milieu of rising air temperatures and decreasing or fluctuating soil moisture, suggests a physiological control operating within a wide amplitude of such environmental factors. Fowells (1941) implied this when he noted that the growth rate was constant once diameter expansion began, and did not vary with the altitude at which the pines grow.

During this period of constant rate of diameter increase, the so-called grand period of growth, lasting from the first of May to mid-July, the mean air temperature rises 12° F., the mean soil temperature rises 15° F. in the upper horizons, and the soil moisture drops from field capacity to near the wilting point, except for fluctuations due to summer storms. However, such factors as air temperature may become limiting, as was revealed by a sudden cool period during the last week of June, 1958. Its effects were expressed as a slowed rate in the growth curves of T-6, T-1, and T-7 (east side only), and as a complete cessation of growth for a short time in the curve plotted for T-9; but, surprisingly, the cool period had no effect on the rate of expansion in T-3 and the northwest side of T-7 (Figures 9, 10, and 11). A similar cool, rainy period of two days duration in the latter part of the first week in July produced the same results. In this latter case, however, there was no return to the previous growth rate when temperatures rose and the skies became sunny again. The growth rate thus varies with time of season, and this variation must be subject to some sort of internal control, responding only secondarily to the external environment.

That soil drought also influences the total amount of growth has been clearly pointed out by Glock (1937), Friesner and Walden (1946), and many others, for this effect of lack of moisture in decreasing the season's increment, especially in arid regions, has been the basis of tree-ring analysis. However, the present investigation suggests that soil moisture stress does not affect the rate of diameter increase but that it may control the duration of such increase. A pronounced drought in July (Figure 7) during the grand period of growth had no visible effect, expressed either as a dendrometer curve or as revealed by cellular studies. Yet a dry period of similar intensity and slightly longer duration during the first half of August caused a five percent decrease in the diameter of all trees except T-9, which showed a slowing of growth rate. The ability of ponderosa to survive at soil moisture contents below the permanent wilting percent has been demonstrated by Stone (1957). The present investigation has demonstrated that a constant rate of growth can be maintained under low moisture conditions if these dry conditions occur early in the growing season and are not too prolonged. No appreciable permanent gain in diameter occurred after the August drought, but there was a series of fluctuations in diameter showing that the season's growth was essentially at an end.

Cessation of Growth

In the present study neither soil drought nor the approach of cold temperatures seem primary in the cessation of diameter growth at the one-meter level. Inspection of the tissue sections (data summarized in Figure 12) shows that by the first of August, 1958, growth as expressed by the production of new cells as well as the maturation of cells to their final dimensions, is at an end. Though the data show clearly that there is a slight increase in diameter during September and October amounting to two or three percent of the total for the season, this increase cannot be demonstrated to be the result of continuing cambial activity. As the grand period of growth ceased before any serious deficiency in soil moisture arose, and since there were no major increases in diameter after the grand period, even when the soil was re-wetted to field capacity, one is led to the conclusion that soil drought *per se* does not initiate the cessation of cambial activity at the one-meter level.

No one factor measured in this investigation seems definitely correlated with the ending of seasonal growth. These conclusions are in accord with those of Daubenmire and Deter (1947). In a dendrometer study of eight species of conifers of the Rocky Mountains, grown in the vicinity of Moscow, Idaho, they found that ponderosa pine alone of these species exhibited a pronounced autogenous retardation of growth that began early in the summer and apparently was related neither to temperature changes nor to soil moisture deficiency.

SUMMARY

1. The diameter growth in five individuals of *Pinus ponderosa* (Laws.) was measured at the one-meter level for two consecutive seasons in the Lower Montane Zone at an elevation of 7,500 feet in Boulder County, Colorado. Concurrent with these growth studies, measurements of the external environment of the pine stand were made with standard United States Weather Bureau apparatus supplemented by certain other instruments. Measurements were made of air temperature, relative humidity, soil temperature, and soil moisture. Degree of cloudiness, windiness, and amount and depth of snow cover were estimated. Rain and snow were measured directly as inches of water in a standard rain gauge.

2. A brief study of the ratio of 2-needle to 3-needle fascicles and of the length of the needles established that the trees under study were of the "*scopulorum*" ecotype.

3. Diameter measurements were made externally on the trees using a dial-gauge dendrometer, and the following results were obtained:

   a. Growth was initiated early in May in the trunk cambium at the one-meter level. Swelling of buds on the lowermost branches also occurred about this time. This initiation of growth is correlated with the attainment of a 50° F. mean air and soil temperature.

b. Fifty percent of the season's diameter increase was completed within about thirty days. This is a more rapid growth rate than is found in certain other ecotypes of ponderosa pine.

c. During the grand period of growth the rising trend of soil and air temperatures has no effect on the rate of growth, this rate remaining constant. However, a pronounced cool period has the effect of retarding the growth rate.

d. A widely fluctuating series of soil moisture values, at times below the wilting percentage, had no effect during the period of constant growth rate.

e. Cessation of diametral growth is difficult or impossible to determine with the dendrometer. The end point is generally fixed by the investigator. Positive and negative fluctuations, occurring after the grand period of growth, obscure the end point of enlargement due to cell division and maturation.

f. Cessation of diameter growth does not appear to be directly connected with soil drought.

4. Microscopic studies of the cambium and adjacent tissues were made on cross-sections prepared from samples cut at the one-meter level periodically during the growing season. Pertinent results are listed below:

a. These tissue studies were invaluable aids in interpreting the results of the dendrometer measurements, for example, such as fixing more precisely the end point of cambial activity.

b. Tissue sections collected before May 1, 1958 show no cambial activity. Sections collected later in the month show that cambial division begins the first or second week in May.

c. Three rows of phloem parenchyma cells were produced during the growing season of ponderosa pine, in contrast to only one row in the white pine, as reported by Abbe and Crafts (1932).

d. Crushing of new sieve elements occurs as early as the latter part of June. This is in contrast to Brown's report (1915) on white pine that crushing of current sieve elements did not occur until the first frosts.

e. These tissue studies show that by the end of August diameter growth is essentially complete and cambial activity at an end.

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