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1975

Effects of Temperature and Moisture on Productivity of Oryzopsis Hymenoides

L. C. Pearson

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Recommended Citation

Pearson, L.C. 1975. Effects of Temperature and Moisture on Productivity of Oryzopsis Hymenoides. U.S. International Biological Program, Desert Biome, Utah State University, Logan, Utah. Reports of 1974 Progress, Volume 3: Process Studies, RM 75-6.

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1974 PROGRESS REPORT [FINAL]

EFFECTS OF TEMPERATURE AND MOISTURE ON PRODUCTIVITY OF ORYZOPSIS HYMENOIDES

L. C. Pearson Ricks College

US/IBP **DESERT BIOME RESEARCH MEMORANDUM** 75-6

in

REPORTS OF 1974 **PROGRESS Volume 3: Process Studies** Plant Section, pp. 19-34

1971 Proposal No. 27609

Printed 1975

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> Citation format: Author(s). 1975. Title. US/IBP Desert Biome Res. Memo. 75-6. Utah State Univ., Logan. 16 pp.

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INTRODUCTION

In studies involving productivity and ecosystem dynam• ics, desert vegetation can be divided into four groups: shrubs, forbs, grasses and cryptogams. In general, shrubs make their greatest contribution to the annual energy budget during late fall and very early spring; forbs during the relatively early spring; and grasses during late spring and very early summer (Blaisdell 1958, Pearson 1965). During late sum mer and early fall and again during most of the winter, the vascular vegetation is relatively dormant. It is during this dormancy period that some of the cryptogams are most active and make their greatest contribution to productivity; however, in terms of total ecosystem production, the contribution of the cryptogams is seldom very significant. There are, of course, exceptions to these generalities. Evergreen shrubs, such as *Artemisia tridentata,* may carry on significant photosynthesis during the winter dormancy period, and some cryptogamic vegetation (e.g., algal crusts and soil lichens) reaches its greatest development during the spring and summer months. In earlier studies, I have attempted to obtain some overall measurements of desert area productivity and some somewhat refined measurements of shrub productivity (Pearson 1964, 1965, 1966, in prep.). In the present study, I have attempted to measure the ecological contribution of two grasses.

Desert grasses may be classified in the following categories: 1) annuals, such as *Bromus tectorum* and *Festuca octojlora;* 2) turf-formers, such as *Agropyron smithii* and *Bromus inermis;* 3) warm-season bunchgrasses, such as *Bouteloua gracilis* and *Aristida trfaetum;* and 4) cool-season bunchgrasses, such as *Stipa comata, Oryzopsis hymenoides, Agropyron desertorum, Agropyron trachycaulum, Agropyron spicatum, Poa secunda, Paa nevadensis* and *Sitanion hystrix.* In the northern Utah and eastern Idaho deserts, such as Curlew Valley and the area near Rexburg, the cool-season bunchgrasses are generally the most important grasses, from the point of view of both total productivity and of topgrowth production which can be utilized by range livestock and wild game.

Oryzopsis hymenoides (Indian ricegrass) is a relatively abundant cool-season species which is of greatest significance in midsuccessional stages in sandy areas. It is frequently associated with *Stipa comata* (thread and needle grass), but usually is less abundant than *Stipa.* It is highly palatable to livestock and wild game and is of anthropological interest because it was important to Indians as a food supply. It is a long-lived bunchgrass forming large clumps which eventually become "doughnut-shaped" as a result of the oldest culms dying. A preliminary survey of the vegetation of Curlew Valley (fall of 1969) indicated that *Oryzopsis hymenoides* was one of the major plant species in the valley; consequently, we chose this bunchgrass for our model of cool-season desert grasses. Other characteristics making it a desirable choice for this purpose are its high palatability and hence its actual or potential importance in food chains; the ease with which it can be positively identified, even at considerable distance; its anthropological

interest and presumed significance. Objectives for this phase of the project were 1) to obtain harvest data from which annual productivity could be calculated, 2) to develop nondestructive methods of estimating productivity, 3) to observe phenological changes, and 4) to observe the effects of water and temperature on productivity and on phenological patterns.

To reach the stated objectives, a total of 332 0. *hymenoides* plants and 49 S. *comata* plants were selected on the basis of uniformity (within replications) and proximity to each other at four sites in the Rexburg area. Design was a modified 7 x 8 factorial with five replications of 50 plants each. There were seven irrigation treatments and eight harvest dates (five dates for 1971 and three for later harvest, if desired) and/or observation. The irrigation treatments included every possible combination of 0, 4 and 8 cm of water and early and late application, viz., 0~0, 4-0, 8-0, 0·4, 0-8, 2.2 and 4-4 cm. For the first two harvest dates, only one irrigation treatment could precede harvesting and hence the total of 50 instead of 56 plants in each replication. At the time of selection, plants as nearly alike as possible on the basis of number of culms, crown diameter and height were placed in blocks of seven. Eight such blocks of seven were grouped together into replications. Within each block of seven, assignment to irrigation treatment was random and the seven plants were all harvested the same day. Irrigation was by hand, using buckets and an irrigation frame made of metal, 60 cm square and about 15 cm high. The frame was placed so that the plant was in the middle of the square formed and the frame was then driven into the soil just deep enough to form a dam. When 14.4 liters of water were poured into the frame, the equivalent of 4 cm precipitation had been applied to that area. Plants were irrigated about the last of May and the last of June. Weekly measurements of precipitation and soil temperature were also made,

Two kinds of data were obtained and analyzed. Every 10 days from about May 15 until August 5, 1971, each plant was examined and measurements were made of the number of culms per plant, maximum leaf length, the length of each leaf on each of five randomly chosen culms, average number of leaves per culm, three crown diameters-· 0, 120 and 240 degrees from north.south, maximum height of the seed heads, number of seed heads per plant and average number of seeds per head. In addition, soil temperature was measured at 20•cm depth on the north side of and adjacent to each plant, and subjective evaluations were made of the amount of grazing on each plant, and the percent weed cover adjacent to each plant. Additional measurements were made of many of the plants in June and July 1972 and in April and May 1973. The second kind of data involved excavation of plants using a shovel and taking care not to disturb the roots. This was done every 15 to 20 days from about May 20 to August 4, 1971. Thirty-five plants were excavated. We were confident that not more than 1 or 2% of the roots were lost because very careful screening of the soil around the plants never produced more than a few milligrams of roots when we checked this, although total root weight was around 7 or 8 g on the plants checked. The

plants \Vere brought into the laboratory and separated into root, crown, foliage and fruit-seed portions, which were carefully cleaned of soil and oven-dried at 65 C, and then weighed. Additional plants were harvested in June and July 1972; some of these plants were divided into individual culms and individual roots prior to weighing and measurements made of culm diameter, leaf width, leaf length, root diameter, number of branch rootlets per root and root length, as well as individual weights in milligrams.

Although *Ory:zopsls hymenoides* proved to be less important on the Curlew Valley sites than had originally been supposed, the results of the study to this point are significant because O. hymenoides is a typical cool-season grass and the information obtained by studying it should be easily applicable to other cool-season bunchgrasses. However, formulas and phenological patterns obtained from this study should not be expected to apply to annuals, turf-forming species, or warm-season bunchgrasses. The results of the study have been summarized, on the following pages, under the following headings: 1) production rates by phenological stage; 2) influence of water on productivity; 3) influence of temperature on productivity; 4) relationship between cover and productivity; 5) estimating productivity from linear measurements; 6) orientation of growth relative to compass directions; and 7) accumulation of root mass over a period of years.

Data for these studies are stored under the following DSCODES:A3UPC03 and 04, linear measurements and harvest data from Rexburg; A3UPC05 and 06, linear measurements and harvest data at Curlew Valley; A3UPC01, cover and density at Curlew and Rexburg.

PRODUCTION RATES BY PHENOLOGICAL STAGE

In cool-season perennial grasses there are four distinct phenological stages, some of which can be further subdivided and are indicated by the following outline:

- 1. Sprouting stage in spring as dormancy is broken
- 2. Vegetative growth stage
	- a. logarithmic phase
	- b. decelerating phase
- 3. Anthesis and maturation stage
	- a. weight increase phase
	- b. weight decrease phase
- 4. Dormancy stage
	- a, summer-fall phase
	- b. winter phase

During the sprouting stage, foliage weight increases but total plant weight decreases. The stage begins with the first sprouting of green foliage in the spring and continues until the compensation point is reached; that is, until daily photosynthesis equals daily respiration. At Rexburg, this stage began in 1971 and 1973 about April 4 (no observations

were made in 1972) and continued until about April 19. Judging from our 1971 data, the daily increase in foliage weight during this period of time at Rexburg averaged 28 mg per plant (Table 1). Observations made in 1973 and 1975 indicate that growth in the spring begins when the soil temperature at 15-cm depth reaches about 4 C and remains there for at least three or four days. According to Blaisdell (1958), the sprouting stage for *Poa secunda* begins while soil temperatures are about 0 C, or as soon as the snow disappears; for *P. nevadensis* and *Koeleria cristata* it begins slightly later, and for *Agropyron spicatum, A. dasystachywn* and *Stipa comata* it begins still later, or about the same time as for 0. *hymenoides.*

During the vegetative growth stage, which begins when the compensation point is reached and continues until the beginning of anthesis, there is rapid increase in foliage weight and also in total plant weight. In 1971, foliage weight in the Hcxburg area plants increased at an average rate of 69 mg per day for each gram of photosynthetic tissue (foliage dry weight) dming the first part of this stage, which lasted until about May 19. During the second part of the stage, from May 19 to June 15 at Rexburg, total plant weight continued to increase rapidly while foliage dry weight also increased, but less rapidly, at an average rate of 20 mg per day for each gram photosyrlthetic tissue less 2 mg for each gram photosynthetic tissue raised to a "time" power (Table !).

The anthesis and maturation stage begins when the first floret emerges from the boot and continues until the seeds mature and the plants become dry, During this period, foliage dry weight continues to increase at the same rate as in the second phase of the vegetative growth stage until just before seeds mature when it begins to decrease; the weight of the flowers, fruit and seeds increases very rapidly until just before maturation when it also begins to decrease, and root weight apparently decreases as flowers and fruit form and then increases as the tops approach maturity. According to Blaisdell (1958), the two species involved in this study, especially 0. *hymenoides,* mature more rapidly than other cool-season grasses. In 1971, the period lasted from June 15 to July 20 at Rexburg.

The dormancy period can very arbitrarily be divided into two phases; the summer-fall phase, characterized by relatively little litter accumulation which lasts until about December 15, and a winter phase characterized by the tops and leaves being battered down by wind and snow so that a relatively small percentage of the old seed stalks are still standing at the end of the stage. During the first part of the summer-fall phase, there appears to be some translocation of food substances and increase in root weight, but the stage is generally characterized by loss in weight of all plant parts. The major conversions are from living matter to standing dead during the summer-fall phase and from standing dead to litter during the winter phase. There is some overlap at the end of this period and the beginning of the new growth period inasmuch as many seed stalks do still stand until about May 15.

SEED GROWTH AND DEVELOPMENT

 $5,4$ (N=Anth to
N=365)

$$
s_{\text{Anth}} \max\limits_{\substack{m_{\max} \{0, Q(R_j+3F_j) (R_j-F_j)\} \\ S_{i+1} = S_i + 0S_i - HS_i^p \\ \text{where } p = N/(N-J) \\ \text{and } \text{Anth} = \text{beginning date} \\ \text{of } \text{anthesis} \end{cases}
$$

 $\mathbf{s}_{\texttt{Anth}}$ = .0552

$$
s_{i+1} = s_i + .5s_i - .18s_i^p
$$

where
$$
p = N/(N-45)
$$

and $\text{Anth} = \text{day } 72$

 $\mathcal{A}^{\mathcal{A}}$

Harvest data indicated rather smooth curves when 1971 dry weights were plotted against time (Fig. 1) for foliage, fruits and crowns; root weights changed more erratically. The estimates of weight increases given in previous paragraphs were obtained from these curves. Table 1 gives additional estimates for all locations.

The differences among sites indicated in Table 1 are probably due to differences in both environmental and genetic factors (McMillan 1959, 1961). The dates at which the different stages begin probably vary from year to year, depending on weather conditions. This latter expectation is borne out by studies by Blaisdell (1958) who observed that development during the early part of the season (stages 1 and 2a) is closely correlated with temperature while development during the latter part of the season (stages 2b) and 3) is more closely associated with precipitation.

INFLUENCE OF WATER ON PRODUCTIVITY

Seven different irrigation treatments were imposed on individual plants in each of 40 blocks in the Rexburg area and eight blocks in Curlew Valley. At each location, the seven largest plants (number of culms per plant x the maximum leaf length) in early May made up one block, the seven next largest made up the next block, and so on. Assignment to irrigation treatment within blocks was purely at random. The most sensitive comparisons, therefore, were

of the irrigation effects. Observations were made of productivity based on both the harvest method and the linear measurements method, increase or decrease in number of culms over winter, and change in time of maturation of plants.

Analysis of the data suggested that productivity was increased by irrigation; however, it made little difference whether with 4 cm or 8 cm or whether in one application or two (Tables 2 and 3). It appears as though the late irrigation was more effective than the early irrigation in increasing foliage dry weight, but the differences are not statistically significant. The Fremont County Sand Dunes plants varied considerably in beginning date of anthesis; the early irrigation seemed to delay anthesis, especially at the west site, but the late irrigation also had some delaying effect (Table 4). There was very slight, if any, variation in anthesis at any of the other sites. The irrigated plants at Ricks College produced more new shoots the following spring than did the unirrigated plants; at the other locations the number of shoots was not similarly increased by irrigation, possibly because of preferential grazing of the irrigated plants. One month after irrigation, the irrigated plants at Plano showed more evidence of grazing than did the unirrigated plants; this was most pronounced on the plants that had been irrigated twice although the amount of irrigation did not seem to make any difference (Table 5).

Figure 1. Patterns of growth in Oryzopsis hymenoides at the four sites in the Rexburg area of eastern Idaho. Each symbol represents the average of 35 harvested plants, or 20 at the two earliest dates, except the open circles and triangles which are averages of 140 estimated weights of foliage and root biomass, respectively.

*The linear regression eczponent of the foliage weight differences is significant at the 5% level of probability

 $\ddot{}$

Table 4. Influence of irrigation treatments on date of anthesis at the Sand Dunes site. This was the only site at which anthesis was measurably affected by irrigation

Total Irrigation	Specific Treatment	No. Days to	
(c ₂)	Early Late	Anthosis	
8	$4 - 4$	85 deys	
8	$8 - 0$	85 days	
8	$0 - 8$	77 days	
4	$4 - 0$	80 фаус	
4	$2 - 2$	75 deys	
4	$0 - 4$	70 days	
\circ	$0 - 0$	70 days	

Table 5. Effect of irrigation on grazing. Plants that showed evidence of having been eaten by rodents, insects or livestock on either July 22 or August 3 were subjectively scored 3 to 7, depending on severity of the grazing; plants that showed no evidence of grazing on either date were scored 0

*F value statistically significant at 5% probability lovel

Percent weed cover was estimated at 10-day intervals throughout the summer of 1971; on June 24 it reached 10.9% but had declined to 1.7% by July 14 and 0.35% on August 3. Percent weed cover was significantly higher on August 3 near plants that had been irrigated (Table 6). The difference was due primarily to the early irrigation.

Despite all our efforts to select plants within each block that were highly uniform, the harvest data revealed a tremendous amount of variation among the plants within blocks. This variation is apparently due to: 1) differences in the beginning size of plants which escaped detection because of our overemphasis on culm count and maximum height, especially the former; 2) differences among plants in the

"Statistically significant at the 5% level of probability

amount of stored food at the beginning of the season; 3) differences in sites, especially in temperature and moisture. where the individual plants were growing; and 4) genetic differences among the plants.

For a period of 16 years, records were kept of temperature, precipitation and degree of cloudiness as well as of plant development for several species of grasses at Dubois, Idaho, near Rexburg (Blaisdell 1958). Development of cool-season bunchgrasses was rather highly correlated with precipitation during the latter part of the growing season. As in the present study, maturation was delayed by additional moisture.

INFLUENCE OF TEMPERATURE ON PRODUCTIVITY

In 1971, soil temperature at 20-cm depth on the north side of and adjacent to each plant was recorded for every plant at the time its linear measurements were taken. All of the plants observed in 1973 were also checked for temperature. From these data, it became apparent that the individual sites varied somewhat in soil temperature on any given day and we concluded that the plants at the warmer sites not only began growth earlier in the spring, as expected, but also achieved greater maximum height than did the plants at the cooler sites. Our 1973 data suggested that growth in the spring commenced at all sites when soil temperatures at the 20-cm depth reached about 4 C and remained there for some time, probably at least three or four days. Extrapolation of the 1971 data was consistent with this observation; however, the sites that were warmest in April were not necessarily the warmest in May or June, although there was some tendency this way. Correlation between the soil temperature during the early phase of stage 2, up to the middle of May in the Rexburg area, and the

maximum plant height was positive and relatively high (Fig. 2). At Ricks College, maximum plant height increased an average of 5 cm for each degree increase in soil temperature, up to 10 C on May 20. At Menan Buttes, the average increase per degree Celsius was 3 cm. On the other hand, correlation between soil temperature during late stage 2 seemed to be negative. At Curlew Valley, soil temperatures were first taken and plant measurements recorded on May 24 and 25, 1971, and at this time the plants were almost into the anthcsis stage; here each increase on one degree, from 12 to 18 C, resulted in 3-cm decrease in maximum height later attained and also in 3-cm decrease in maximum seed-head height at the South Sage site, and 4.5 cm and 2 cm, respectively, at the North Sage site. The data from the Curlew Valley sites arc of some special significance because we had, by this time, become more consistent in our methods of measuring soil temperature.

Blaisdell (IBS8) reported a high correlation between stage 1 temperatures and date of anthesis; unfortunately, we do not have stage 1 temperatures for 1971. We found no correlation between stage 2a temperatures and date of anthesis. Higher soil temperatures during phenological stage 2b, however, resulted in a three-day delay in anthesis al the Sand Dunes for every increase in temperature of one degree Celsius above 10 C. Apparently the positive effect of high temperature during the very early growth period becomes a negative effect later on.

RELATIONSHIP BETWEEN COVER AND PRODUCTIVITY

We used the quadrat-transect method in 1971 to estimate density and cover of vegetation at four of the localities involved in this study. Quadrats were established with the aid of a wooden frame 40 cm wide by 250 cm long with red markings along the long sides 25 cm apart to assist us in estimating percent cove;:. At least 20 plots were established in each transect. Average density was multiplied by average plant biomass, as determined from harvest data, to give estimated hiornass per hectare (Table 7). Correlation between cover and biomass is shown in Figure 3.

On grounds of logic, we would be quite confident of a correlation between cover and biomass, but we would expect variations in site -- moisture, soil characteristics, temperature, insects, etc. -- to affect biomass also. The limited data we have indicate that for O. *humenoides*, each increase in cover of 0.1 % results in an increase in biomass of 4 kg/ha.

O. hymenoides was not a dominant species at any location in this study. Of 22 species observed at the Menan Buttes, it was fourth in percent cover and also in percent frequency. At the west Sand Dunes site, it was 13th out of 28 in percent cover, at Curlew Valley north it was 27th in percent cover out of 41 species observed, and at Curlew Valley south it was 5th in percent cover out of 12 species, Number of species in this case refers only to those species encountered in the transects for which species differences were noted; in some cases, similar species were lumped and counted as one species, and in all of the transects there were likely other species present that were not encountered. Macroscopic species, including lichens and mosses, were counted and recorded in as complete a manner as possible.

ESTIMATING PRODUCTIVITY FROM LINEAR MEASUREMENTS

Several advantages result from being able to estimate the dry weight of plants from linear measurements of living plants. These advantages include: 1) being able to make successive measurements on the same plant, thus acquiring a picture of weight change patterns on each individual plant over a period of time; 2) the time saved -- it is very time consuming to dig, dry and weigh plants; 3) the grouping of plants into blocks or replications prior to manipulating the environment in order to gain better control of experimental error; and 4) elimination of some erosion problems that often result when large numbers of plants are dug and the ground left bare -- this is especially significant on stabilized sand dunes where "blow-outs" readily occur when small areas are left without cover.

Figure 2. Effect of soil temperature at 20-cm depth in mid-May on total plant height reached later in the season. At this time of year, the plants at Ricks College were in the early logarithmic phase of growth, the plants at the Menan Buttes in late logarithmic phase, and the plants at Curlew Valley in the decelerating phase of growth (see Table I). Clear symbols indicate average of four or more plants.

Table 7. Status of Oryzopsis hymenoides* in four communities, 1971

Figure 3. Relationship between percent cover and biomass in Oryzopsis hymenoides and Stipa comata at four sites. The upper graph shows O. hymenoides; the lower graph shows both species. Where it occurs, S. comata has much higher coverage than does O. hymenoides. $(B = \text{biomass in kg/ha}$; $C = \text{percent cover.}$

Estimates of weight from linear data should ideally do two things: 1) give values that accurately distinguish between two plants on the same date; formulas which do not give the exact weights but give values that are biased in the same direction arc still of value; 2) give values that accurately distinguish between weights of the same plant on two different dates; any bias present must be consistently in the same direction as far as the particular plant is concerned. Regarding the measurements made in this study, maximum leaf length was of greatest value in meeting the second of these two criteria, but average leaf length and culm count were of greatest value in meeting the first. We were able to make fairly good comparisons of different plants for root and crown weight, but we were not able to make really satisfactory comparisons between dates from these estimates. On the other hand, while both kinds of comparisons were more accurate for both foliage and seed weights than for root or crown weights, the date-by-date comparisons were especially satisfactory for foliage and seed weights.

Over 150 O. hymenoides plants were harvested in the Rexburg area in 1971 and an additional 22 were harvested in 1972; comparisons made between the weights of the harvested plants and their linear dimensions led to the development of several formulas. Estimation of foliage dry weight and fruit-seed dry weight was most accurately accomplished; the following formulas were derived:

$$
Y_{f} = 8.0 \times 10^{-5} A^{2}C + 2.0 \times 10^{-5} ACM -
$$

.015 C + .25 D + .04 (SN)^{1/2} - .4 (1)

$$
Y_f = 5.14 \times 10^{-5} \text{ ACM} + .18 \text{ D} + .054 \text{ (SN)}^{1/2} - .61 \text{ (2)}
$$

$$
Y_f = 8.15 \times 10^{-5} \text{ ACL} + .18 \text{ D} + .054 \text{ (SN)}^{\frac{1}{2}} - .61 \quad (3)
$$

$$
Y_f = 4.0 \times 10^{-5} \text{ ACL} + 3.4 \times 10^{-5} \text{ L}^2\text{C} + 1.6 \times 10^{-5} \text{ CLP} + .18 \text{ D} + .054 \text{ (SN)}^{1/2} - .61 \tag{4}
$$

$$
Y_{f} = K_{1} ACL + K_{2} D + K_{3} (SN)^{1/2} + K_{4}
$$
 (5)

$$
Y_r = .02 C + .08 D + .14 A + .34 S - .31 N - 1.91 (6)
$$

$$
Y_C = 42.4 D - 2.2 D^2 + 2.7 A - .17 C - 200 \tag{7}
$$

$$
Y_S = .00495 SN + .0029 A - .0026 H - .0158
$$
 (8)

where

ge number of leaves per culm

 $K_1, K_2,$ K_3, K_4

constants derived separately for each species of cool-season bunchgrass for use in formula 5

The formulas were derived primarily from 1972 data; some details of the derivation will be presented in the Discussion. Formulas 1 and 2 and 6 through 8 were used in estimating 1971 weights from the linear data collected in 1971 (see Figs. 4 and 5). Formulas l and 8 gave the best fits. Formula 3 was the best for predicting 1972 weights and is the formula we recommend for future studies; it could not, however, be used on the 1971 data because not all of the needed information was punched on the 1971 data cards. In future studies, formula 4 should be checked against formula 3 because it ought to reveal the week-by-week changes better than any of the other formulas. Our data were not sufficiently complete in the early part of the season --March and April in Curlew Valley, for example -- to test this formula adequately.

Figure 4. Scatter diagram plotting actual dry weight against estimated dry weight of foliage. Much better correlations were obtained later in the season as measuring of the parameters needed to estimate dry weight became more consistent.

s C I) p

Figure 5. Scatter diagram showing increase in leaf length as measured by single maximum length leaves per plant or averaging all leaves on each of five clones. The dips in the average leaf lengths are associated with the emergence of new leaves in the early part of the season.

Formula 5 is a generalized. formula applicable to all species of cool-season grasses; only the constants would have to be calculated separately for each species. Differences in $K₁$ would be due to differences among species in basal diameter of the culms, leaf width and relative length of leaves from collar to tip. Differences among species in the density of culms within the crown and in tendency to produce crowns with dead centers, as in *Oryzopsis,* are reflected in $K₂$ values. Differences among species in seed stalk diameter, number of seeds per head and the length of seed stalks would be reflected in differences in K_3 values. K_4 corrects for nonlinearity of the curve in very young plants. Although these four constants would be calculated separately for each species of bunchgrass from actual harvest data, it is possible that K_1 could be estimated fairly accurately from culm diameter divided by leaf length and $K₂$ from crown diameter divided by number of culms. The K1 to K4 constants for 0. *hymenoides* and *S. comata* are shown in Table 8.

At the end of the 1971 season, partial analysis of the data indicated that some changes in method of making and recording the linear data could improve the program. The following improvements were therefore made before gathering the 1972 data: 1) four galvanized spikes were placed around each plant prior to the first measurement so that the heads of the spikes were flush with the top of the crown where the new green foliage originates; all subsequent measurements of leaf length, seed stalk height, etc., were made from the tops of the spikes; 2) a light-weight, steel measuring device (calipers) for obtaining crown diameter data was prepared (Fig, 6); this device has two parallel sides which can be adjusted to any width desired from O to 50 cm by sliding one arm of the device along an iron rod welded at right angles to the other arm - steel bearings on both sides of the movable arm ensure easy sliding and perfect parallelism of the arms; 3) the' individual leaf measurements of each culm were punched onto additional data cards. In 1971, average leaf length and average number of leaves per culm were punched on the cards, the averages themselves being calculated daily using hand calculators. By punching the raw data directly onto additional cards, these two values and also average longest leaf could be calculated by computer; of greater importance, they could be stored for further use.

To test the extent to which these modifications improved the accuracy of the data, many of the plants in 1972 were measured twice, sometimes by the same person, sometimes by different people, Measurements of maximum leaf length differed, on the average, 4.04 cm or 10.0 % when the spikes were not used; with the aid of the spikes, the measurements differed by only 2.8 mm or 1.07 % , The average difference between two measurements of the same crown diameter decreased from 15.2% to 12.7% when the calipers were used.

Table 8. Constants to put into the generalized formula

$$
Y_f = K_1 ACL + K_2 D + K_3 (SN)^{1/2} + K_4
$$

in order to estimate the foliage dry weight (Y_f) of cool-season bunchgrasses from measurements of average leaf length (A) , average longest leaf on a culm (L) , culms per plant (C) , average crown diameter (D) , number of seed stalks (N), and number of seeds per seed stalk (S)

Figure 6. The calipers used in measuring crown diameter improved consistency in measuring and increased the speed of measuring.

One of the advantages of estimating productivity from linear measurements rather than harvesting and weighing the plants is, as indicated before, that time may be saved. Records were kept of the amount of time involved in making measurements and in digging and weighing plants. We found that two people working together could make all of the measurements except the culm count in 3 to 5 min; a third person could count the culms in about the same length of time. Hence, about 12 man-minutes are needed to record all of the linear data for one plant. In 1972, working with different people who were both younger and less experienced, about 18 man-minutes were needed. It took another minute, on the average, to keypunch the data and 30 seconds to verify. About $4\frac{1}{2}$ plants per man hour could be completely processed, in other words. To harvest a plant, on the other hand, required over $2\frac{1}{2}$ hr using the experienced help (1971) and over $3\frac{1}{2}$ hr with the inexperienced help (1972). The breakdown was as follows: two people can harvest and bag one plant in about 20 to 30 min in the light soil in which these plants were growing; another 45 min to 1 hr is taken to prepare the plant for drying and to weigh it following drying, with two people working together; one person can keypunch and verify the data in another 1 to $1\frac{1}{2}$ minutes. Consequently, 10 to 12 times as many plants can be processed in a given period of time if accurate estimates of plant dry weight can be obtained by using formulas and linear data instead of harvesting the plants: in addition, the plants are still alive and can be measured again.

RADIAL ASYMMETRY IN ORYZOPSIS HYMENOIDES CROWNS IN RELATION TO COMPASS DIRECTION

Three measurements of crown diameter were made on each plant: a north-south or 0° measurement; a 120° measurement; and a 240° measurement. In making and recording the measurements, we methodically gave the north-south measurement first and then generally continued our readings in a clockwise manner. Because of the mechanical way in which this was done, it occurred to us that it would be possible to make comparisons of crown diameters among the three compass directions as the data eards were run through the computer. During the summer of 1971, a total of 2964 crown diameters were measured, 988 in each of the three directions. The differences among the three directions were very highly significant ($F = 27.0$, $P = 2.78$ x 10⁻¹²). The crowns tended to elongate in the north-south direction; average diameters were: north-south 0° 7.924 cm; ESE-WNW 120° 7.340 cm; WSW-ENE 240° 7.430 cm.

Inasmuch as the data on the influence of temperature on plant growth (Fig. 2) suggest a relatively high positive correlation between early spring soil temperature and growth, we assume that the additional warmth at the south edge of each clump of grass in the early spring causes more rapid growth toward the south (and southwest) than in other directions. Over a period of years this results in a measurable asymmetry of the clumps of grass. The probability of the differences in our measurements being due to chance alone is so low as to be considered, for practical purposes, an impossibility.

ROOT MASS ACCUMULATION OVER A PERIOD OF YEARS

In shrubs, it is easy to see that much of the production accumulates over the years in the form of xylem and other tissues in the stems. By counting growth rings, it is possible to correlate biomass and age and hence calculate average annual rate of accumulation (e.g., see Hewett et al. 1963). The situation is much more complex for root accumulation than for topgrowth accumulation, of course. In grasses, the topgrowth does not accumulate, but there is obviously an accumulation in roots and crowns of organic matter. The extent of this accumulation has not been studied for grasses growing in natural ecosystems. To get at this problem, we need first to have some way of estimating the age of the plants or their average annual rate of growth.

In 1971, culm counts were made every 10 days on all 381 plants; counts ranged from 3 to 140 culms per plant in 0. *hymenoides* and from 27 to 220 culms per plant in *S.* comata. There was no evidence of an increase in number of culms on any plant during the 1971 growing season. We surmised, therefore, that increase in culms must occur as new growth begins in the spring. Fifty-three *0. hymenoides* plants were checked to see how culm count varies from year to year; 40 in 1972 and 13 in 1973. Unfortunately, during 1972 there was some vandalism at all of the sites except Plano. This consisted of pulling the identification stakes and moving some around and this, together with weathering of the wooden slakes and snow hiding some of them when we began our 1973 counts, resulted in difficulty in locating the exact plants we wanted to observe. We could locate with complete certainty only three of the 40 plants we had measured in 1972; therefore, ten of the plants counted in 1973 are different plants. Nine of these 10 had exactly the same number of culms as in 1971 and the tenth had only increased one culm (from 24 to 25). This would suggest that increase in number of culms per plant, and hence growth in crown diameter. must be a very slow process or else something which is limited primarily to very favorable years. The comparisons between 1971 and 1972, on the other hand, suggest considerable growth of some plants. Some of the 40 plants decreased in number, some remained the same, and some increased. Much of the decrease was associated with gopher activity. The average for all 40 plants was 37.5 culms in 1971 and 52.1 in 1972. Ignoring three plants destroyed or severely damaged by gophers and three plants which could not be identified with certainty, the remaining 34 plants had an average of 39.0 culms in 1971 and 49.7 culms in 1972 for an increase of 10.7 culms per plant or a 27 .4 % increase in number of culms per plant. On the Hicks College site, the plants which were irrigated in 1971 increased markedly more than did the nonirrigated plants, but the relationship did not hold at the other sites. Since there was no grazing by livestock at the Hicks site and there was heavy grazing at the other sites, we have speculated that the irrigated plants may have been more palatable and hence more heavily grazed so that the potential increase in number of culms due to irrigation was prevented from materializing. The eight plants observed in 1972 at the Hicks College site can be grouped in three classes on the basis of irrigation and increase in number of culms; those that received 8 cm of water at one time, either in June or July, increased an average of 40 culms per plant or 65%, those which received 4 cm of water at either or both applications increased an average of 8 culms per plant or 27%, and those which received no water in addition to natural precipitation increased an average of 3 culms per plant or 10.3 % . The differences among the three groups were not statistically significant (Table 9).

The average increase in number of culms from 1971 to 1972 was relatively uniform from site to site although it varied considerably from plant to plant. As the plants became larger, the percent increase in culms was greater; however, the largest plant in the subsample of 34 had only 69 culms. A relatively small number of 0. *hymenoides* plants in this study had over 100 culms, 5.3% of the total, suggesting that the rate of increase in culm count levels off as the plants become older. Taking these observations into account, we developed a model which we hope can eventually be useful in estimating the age of bunchgrasses from measurements of crown diameter and culm count. At this time, the model attempts to account for increase in number of culms per year as follows: 1) plants increase, on the average, 5 culms per year for the first 5 or 6 years; 2) the number of culms then increases 20% per year for the next 4 or 5 years; 3) from that point on, the increase in number of culms per year is at a decelerating rate according to the formula:

$$
i = (55,000/C^2)
$$

where i is the annual increase in number of culms and C is the number of culms just prior to increase.

A long-range study is needed to ascertain how accurate this model is and to what extent it can be applied to other cool-season bunchgrasses. Rates of increase in number of culms per plant probably vary considerably from site to site and from year to year. Probably the value of this model can be markedly enhanced by incorporating precipitation data into it; the dendrochronology of associated shrubs could be used for this purpose in making estimates of the age of grass plants once the patterns of size increase have been worked out. For the present study, we needed some method of obtaining at least a very rough estimate of the age of the plants.

In Figure 7, root mass is plotted against estimated plant age. Two estimates of plant age were used for each plant; one based on number of culms and calculated using the above model and one based on crown diameter assuming approximately 1-cm increase in diameter per year. When the two estimates differed, age was considered to be that based on the average of the two or that based on crown diameter alone, whichever was more. If the age estimates are correct -- and they could be very far off -- accumulation of root mass is at an average annual rate of .69 g per plant (Fig. 7). A correction is needed for presumed nonlinearity in very young plants; incorporating this, the formula is

$$
R = .69 A - 1.2 \tag{9}
$$

where

$$
R = total root biomass
$$

$$
A = the age of the plant
$$

Thus, root biomass at any given time will equal, on the average, 0.69 times the age of the plant minus 1.2 g, Since *A* in this formula is derived from linear measurements of crown diameter and number of culms per plant, formula 9 is obviously related to formula 6.

Table 9. Influence of irrigation on increase in number of culms from the summer of 1971 to the spring of 1972, Ricks College site

Total Irrication			Specific Avg. No. Avg. No. Per Cent Trestpent Culms, 1971 Culms, 1972 Increase		Combined Averages
0 _{ct}	$0 - 0$	29	32	10.3	10.3
4 _{cc}	$2 - 2$	33	37	12.1	
4 cc	$A = 0$	23	26.5	15.2	25.5
$4 - c$	$0 - 4$	57	55.	45.5	
e_{cr}	$4 - 4$	ぬ	43	45.3	
8c	$8 - 0$	ϵ 4	99	54.6	60.9
8 ல	$0 - 8$	59	104	76.3	

All differences non-zignificant, stetistically

Figure 7. Relationship between the estimated age of *Oryzopsis hymenoides* plants and the biomass of the roots. The age was estimated from either formula 9 or from crown diameter alone; when the two estimates differed, the two were averaged for small plants or crown diameter alone *was* used for large plants in which it was argued that the large amount of dead material in the center of the clump indicated plants older than the formula suggested. $(R =$ root biomass in grams; $A =$ estimated age in years.)

In addition to the 280 0. *hymenoides* plants studied in the Rexburg area, 52 S. *comata* plants were observed. The *Stipa* plants reached maximum size very early, the maximum leaf length being reached in most cases by June 23 in 1971. There was no statistical difference in harvest dry weight of plants on May 21 and August 4. The combined foliage and root weight of the average plant was 12.94 g, 68 % of which was roots and 32 % foliage. Crowns were large, averaging 20.0 g per plant: thus, roots and crowns together made up 88% of the bulk of the average plant, and in some plants the roots and crowns approached 95 % of the total bulk,

Irrigation appeared to increase the amount of foliage produced and to delay the time of reaching maximum leaf length. At the Ricks College site, irrigation appeared to delay date of anthesis. Topgrowth of the irrigated plants at the four Rexburg area sites averaged 4.36 g and that of the nonirrigated plants 3.41 g; thus, each centimeter of water applied in early June appears to have increased topgrowth by 0.29 g per plant, or 6.8% . The 2-cm application, however, was apparently not at all effective. At the Ricks College site. plants which were not irrigated reached maximum leaf length on about June 26; those receiving 2 cm of irrigation on June 1 reached maximum leaf length on about June 30; and those receiving *4* cm of irrigation reached maximum leaf length on about July 3. In other words, each centimeter of irrigation applied in June delayed maximum vegetative growth about two days. The July irrigation seems to have stimulated a second spurt of growth immediately after irrigation; this was most pronounced at the Menan Buttes site. The June irrigation also seemed to retard flowering at the Hicks College site though not measurably so at any of the other sites. The date anthesis began was June 15 on all but three of the plants; two of the four plants receiving 4 cm of irrigation at the Ricks College site had anthesis delayed, one of them about 10 days and the other about 30 days. Another plant receiving no irrigation initiated anthesis about five days later than the average.

DISCUSSION

Obviously, if we could measure leaf width, leaf length, leaf thickness, culm diameter and culm length accurately, and if we knew the number of culms per plant, the geometric shape of the leaves and culms and the specific gravity of the dried tissues, we could estimate the foliage weight of each plant quite accurately without harvesting it. Likewise, if we knew root length, number of roots and rootlets per plant, root diameter, root geometry and the specific gravity of dried root tissues, we could accurately estimate root weight. Measurements of leaf length, number of culms, leaves per culm, etc., are easily made, of course, and geometric patterns can be analyzed and classified quite readily for leaves and culms; on the other hand, root measurements are not easily made. Much of our effort in this project went toward measuring a number of plant dimensions, both easy and difficult measurements, and attempting to isolate correlations that would enable us to estimate those parameters difficult to measure directly.

In 1971 we harvested, dried and weighed well over 100 plants which had been carefully measured prior to harvest and, with the aid of the computer, made comparisons between the harvest weights and the several measurements. Correlations were very high between the harvested plants and the linear measurements. When actual harvest weights were plotted on a scatter-diagram graph against the estimated weights calculated from formulas derived from the regression coefficients, however, it was apparent that the deviations were too high to be very useful; probably some very low and some very high weights were estimated correctly and resulted in the high correlations. Therefore, we harvested an additional 22 plants in 1972 which were very carefully analyzed, culm by culm and root by root. From these analyses we developed some basic formulas which we then combined into about 80 different formulas which we then tested against the harvest data. Those which were best in estimating 1972 harvest data were then tested against the 1971 harvest data; formulas 1 through 8 resulted from these tests.

Working with individual culms and roots of the 1972 plants, a dissecting microscope was used to measure leaf width and root diameter. Good formulas for estimating the dry weight of single culms were derived by multiplying culm diameter by either length of the longest leaf or the average length of all the leaves on the culm and modifying this by various factors:

$$
W = 2.97 \text{ DA} + .03 \text{ L} + 1.56 \tag{10}
$$

$$
W = 2.94 DA + .06 T + .65
$$
 (11)

$$
W = 3.35 \text{ DA} - 1.27 \text{ A} + 16.97 \tag{12}
$$
\n
$$
W = 3.79 \text{ DA} - 0.61 \text{ T} + 74 \text{ J} + 1.07 \text{ T}
$$

$$
W = 3.72 \text{ DA} - .06 \text{ L1} + .74 \text{ L} + 1.65 \text{ I}
$$

- 28.99 (13)

$$
W = .004 \text{ DLT} + 86.66 \text{ D} + 2.87 \text{ L} - .97 \text{ T} - 52.36 \qquad (14)
$$

where

- $\mathbf D$ basal culm diameter in millimeters
- A average length of all leaves on a given culm in centimeters
- L length of longest leaf on the culm in centimeters
- T total length of all leaves on the culm in centimeters

In the above sequence, each formula gives a slightly higher correlation and as low or slightly lower standard error of estimate than the preceding one; however, logic suggests that formula 11 is still a better formula than formula 12, in which the estimate of dry weight is determined in part by subtracting the average leaf length from diameter times leaf length and, in part, on using a rather large intercept value. The shorter culms tend to have fewer leaves per culm; hence the average leaf length is greater than it should be for short culms in order to give an accurate estimate of weight and this bias must be corrected by a large intercept value.

\1/hen the culm diameter is squared, as it should be if the culms are solid rather than hollow, the formulas are further improved:

$$
W = .95 \text{ AD}^2 + 1.31 \text{ A} + 11.05 \qquad (15)
$$

\n
$$
W = .89 \text{ D}^2 \text{A} + .68 \text{ T} + 11.31 \qquad (16)
$$

\n
$$
W = .83 \text{ D}^2 \text{A} + 2.06 \text{ L} - 4.18 \qquad (17)
$$

$$
W = .96 \text{ D}^2 \text{A} - .05 \text{ LT} + 2.96 \text{ L} + \tag{2.9}
$$

$$
W = 1.54 T - 33.29
$$
 (18)

$$
W = 1.34 D2A - .02 DLT + 1.38 L +
$$

$$
1.32 T - 22.73
$$
 (19)

Coefficients of determination (R^2) increase from .943 in formula 10 to .971 in formula 19 and standard errors of estimate decrease from 32.6 in formula 10 to 24.8 in formula 19. Many other formulas were tested, but correlations were slightly lower and standard errors of estimate slightly greater in most of them.

Inasmuch as leaf length and culm diameter were obviously highly correlated, we tried estimating dry weight of culms from culm diameter directly. The best formulas we came up with were

$$
W = 24.6 D2 + 2.5 L - 21.4
$$

\n
$$
W = 27.7 D2 + 2.4 A - 17.6
$$
 (20)
\n(21)

 R^2 = .977 for both formulas and the standard errors of estimate were 21.0 and 20.8, respectively. This suggested that, in the formulas for estimating whole plant weights, leaf length could be substituted for culm diameter. Other correlations that were apparent when individual culms and roots were examined were between root number and number of culms, root length and leaf length, root length and number of seeds per head, and seed weight and leaf length. There were negative correlations observed between root size and number of seed heads per plant and between seed weight and height of seed stalks. We speculated that the reason root length was positively correlated with number of seeds per head is because seeds per head gives a measure of the phenological stage of development of the plant.

From these formulas, others were derived for estimating whole plant weights in the field. We have confidence in the estimates of foliage dry weight and seed weight obtained from these, especially formulas 3, 4 and 8. Because accurate measurements of leaf length are so easily obtained and leaf length is so important in determining foliage dry weight, changes in weight from week to week are accurately estimated from the linear measurements using these formulas. We are less confident in the estimates of root weight, especially in regard to weekly changes in weight and in observing the influence of temperature and moisture on root weight. On the other hand, our data indicate that, on any given date, the relative weights of root biomass are quite accurately indicated by the estimates using these formulas and thus they can be used to select plants which are uniform as to root biomass prior to imposing various treatments on them. In this study, there was great variation

among plants of the same replication in root harvest weight even though irrigation treatments were identical and despite the fact that we tried to choose plants at the beginning of the study that were as nearly identical as possible for the different harvest dates of the same irrigation treatment. If we had had formula 6 to use in making our selections and assignments to treatment and replication, we would have done much better.

As we gathered data in 1971, and later as we analyzed it, two questions arose: 1) how accurately were we measuring the exact leaf length, crown diameter, number of culms per plant, leaves per culm, etc.; and 2) how faithfully could we reproduce our measurements, especially when two people were making the same kind of measurement? It soon became apparent that we were having real difficulty in measuring leaf length accurately; crown diameter measure~ ments and, to begin with, culm counts also gave trouble. To correct these problems we introduced the improvements already described: the galvanized nails for measuring leaf length and the calipers for measuring crown diameter. After the first two or three measurements were taken, we began carrying three long, slender objects with us to help in counting culms. These were inserted between leaves on each plant in three directions so that they divided the plant into seven sections. Working with the smaller number of culms in each section, it was easier to keep track of the count and the average difference between immediately successive counts of the same plant decreased from 38.0 to 5.6%.

Soil moisture measurements were taken at the time of harvest of plants in 1971. In May, the percent moisture adjacent to S. *comata* plants was 10.1 % ; in August, the percent moisture adjacent to plants which had not been irrigated was 2.5%, hut it was 4.0% adjacent to plants which had been irrigated. In August, the percent moisture adjacent to *O. hymenoides* plants which had not been irrigated was 2.33 % and adjacent to plants which had been irrigated it was 2.51%. The differences were not statistically significant. There was a very low, but statistically insignificant, negative correlation between the amount of irrigation water applied and the soil moisture in August $(r = -23; r^2 = .05)$,

ACKNOWLEDGMENTS

The following Ricks College students worked on the project either full time or extensively as part-time helpers: Neal Hayes, David Merkley, Carol Craik, Suzanne Benson and Solveig Pearson. All were very conscientious and the project would have been impossible without them. Other students helped for a day or so, without pay in most cases.

These include: Todd Tueller, Wayne Whaley, Rhonda Sutherland, Beth Cazier and several others, Their help pulled us through critical times, especially at the beginning and end of the school years when the laboratory facilities we were using were in great demand. Gordon Hoagland wrote the FORTRAN programs for the analyses of the 1972 data, and Lynn Davenport made the Ricks College computer available for the analyses; we are very grateful to them for their help and cooperation. Randy Shinn not only made sleeping facilities available for us during our visits to Curlew Valley, but he also provided us with transportation and gave us ideas that we found stimulating and helpful. Sam Brewster, Jr., of the Ricks biology faculty offered helpful criticisms and suggestions and spent time in the field with us helping with some of the counts and harvests. The personnel at the computer center in Logan were always very helpful as well as patient; we thank Chuck Romesberg, Verne King, Ethel Matthews, Alma Olsen and Vicki Shinn for their help.

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