Technical Report No. 164

LEAF AREA DYNAMICS ON THE PAWNEE GRASSLAND, 1970-1971

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ABSTRACT

This report contains data on the leaf area dynamics of the Pawnee National Grassland in northern Colorado. Specific objectives were (i) to measure seasonal changes in leaf area during 1970 and 1971, (ii) to estimate the influence of irrigation, irrigation plus nitrogen fertilization, and grazing on leaf area, and (iii) to calculate average daily aboveground productivity per unit of leaf area during the peak of the growing season. The point quadrat method was used for leaf area measurement. Peak leaf area was reached in mid-June of both years with a maximum Leaf Area Index (LAI) of 0.55 in 1970. Both years were drier than average, but seasonal distribution of rainfall was different with a corresponding seasonal difference in LAI. Irrigation alone increased LAI by about two-thirds, and irrigation plus fertilization increased LAI by approximately tenfold. The different grazing treatments had very similar leaf area values. Aboveground productivity per unit leaf area averaged about 5 g/day/m^2 of leaf area in May and about 4 g in June and July 1970. An appendix includes supplementary information on (i) the relationship of green leaf area and shoot dry weight for *Bouteloua gracilis* (see Technical Report 72 (Knight, 1971) for the same relationship in other species) and (ii) the percent interception of direct sunlight by green leaves at different times of the day. As reported in Technical Report 72, the minimum interception is during midday.

INTRODUCTION

Leaf area is another basis for vegetation analysis and is especially useful where vegetation function or vegetation comparison is of interest. Numerous studies have demonstrated how leaf area is an important variable contributing to primary productivity (e.g., Brougham, 1956; Donald and Black, 1958; Watson, 1958; Saeki, 1960; DeWitt, 1965; Pearce, Brown, and Blaser, 1965; Duncan et al., 1967; and Loomis, Williams, and Duncan, 1967). Other ecosystem processes are also influenced by leaf area, e.g., evapotranspiration and rainfall interception. This report presents new information on (i) seasonal changes in the leaf area of an arid, shortgrass prairie, (ii) the influence of irrigation, irrigation plus nitrogen fertilization, and grazing on leaf area, and (iii) aboveground productivity per unit of leaf area. The study is part of the Grassland Biome of the U.S. International Biological Program and was conducted on the Pawnee National Grassland in north central Colorado (25 miles south of Cheyenne, Wyoming) during 1970 and 1971.

THE STUDY AREA

The Pawnee National Grassland is an arid, shortgrass prairie dominated by *Bouteloua gracilis* (H.B.K.) Lag., *Buchloe dactyloides* (Nutt.) Engelm., *Aristida longiseta* Steud., *Carex heliophila* MacKenz., and *Opuntia polyacantha* Haw. (Klipple and Costello, 1960; Hyder et al., 1966). The annual precipitation averages about 30 cm, but varies between 10 and 50 cm with about 75% occurring between May and September. The frost-free period averages 135 days, and during this time the mean maximum temperature is about 25°C (29.5°C in July).

Data for describing the seasonality of leaf area and evaluating the influence of grazing were obtained from three 0.5-ha plots, one in a 30-year exclosure and one each in a heavily and lightly grazed management unit. The management units appeared to be grazed quite uniformly and were at least ¼ mile from the nearest watering tank. The heavily grazed unit had been summer grazed (May 1 to October 31) at the rate of 0.7 ha/yearling month for the last 30 years and the lightly grazed unit at the rate of 1.4 ha/yearling month (Bement, personal communication). All plots were located on uniform 5 to 10% slopes and the same Ascalon soil series, a sandy loam. The heavily grazed plot was within 30.5 m of the exclosure, and the lightly grazed plot was less than 1 km distant.

Leaf area data were also obtained from an ungrazed experimental area subject to irrigation and nitrogen fertilization. Irrigation was done with a sprinkler system beginning May 1 and ending August 15, 1971, the objective being to maintain soil water potential below 0.80 bars at a depth of 10 cm. The average total application was 479 mm on the plots that were also fertilized and 397 mm on the plots subject to irrigation only. Nitrogen was applied at the rate of 150 kg N/ha (450 kg/ha of ammonium nitrate) on June 1, 1970. The experimental plots were located on a more coarse-textured soil to the west of the Pawnee headquarters, about 3 km from the grazed plots, but had approximately the same species composition. Each treatment was replicated twice with two control plots.

METHODS

Leaf area was measured as leaf area index (LAI), which is leaf area per unit ground surface area. LAI was divided into four components to facilitate measurement: general ground cover LAI, shrub LAI, bunchgrass LAI, and cactus LAI.

Grass and Forb Ground Cover

Over 95% of the LAI on the Pawnee grassland is in grass and forb ground cover, primarily *Bouteloua gracilis*, 3 to 6 cm tall; bunchgrasses, shrubs, and cactus contribute very little to the total LAI. The non-destructive point quadrat technique of Warren-Wilson (1963) was selected for this largest component. This method requires the determination of the average number of contacts per pin at various angles from the horizontal with the averages then being multiplied by theoretically obtained coefficients to obtain LAI. The more pin angles used, the more accurate the estimate; but Warren-Wilson suggests that three should be very adequate if total LAI is the main objective.

Three pin angles were used in 1970 to measure LAI on the Pawnee grassland: 8°, 32.5°, and 65°. A motorized point frame was constructed for each of the three angles (Fig. 1); the motorized pins speeded the field work considerably. A total of 350 pins were observed at the 8° angle and about 750 pins at the 32.5° and 65° angles. About 18 man-hours were adequate for one LAI determination.

Pin contact data for individual species were recorded as well as whether the material contacted (leaf or sheath) was green or brown (living or dead). If a leaf was mostly green but the portion contacted was brown, a brown contact was recorded. All material recorded for the LAI calculations was standing live or standing dead, and the data were not separated by height

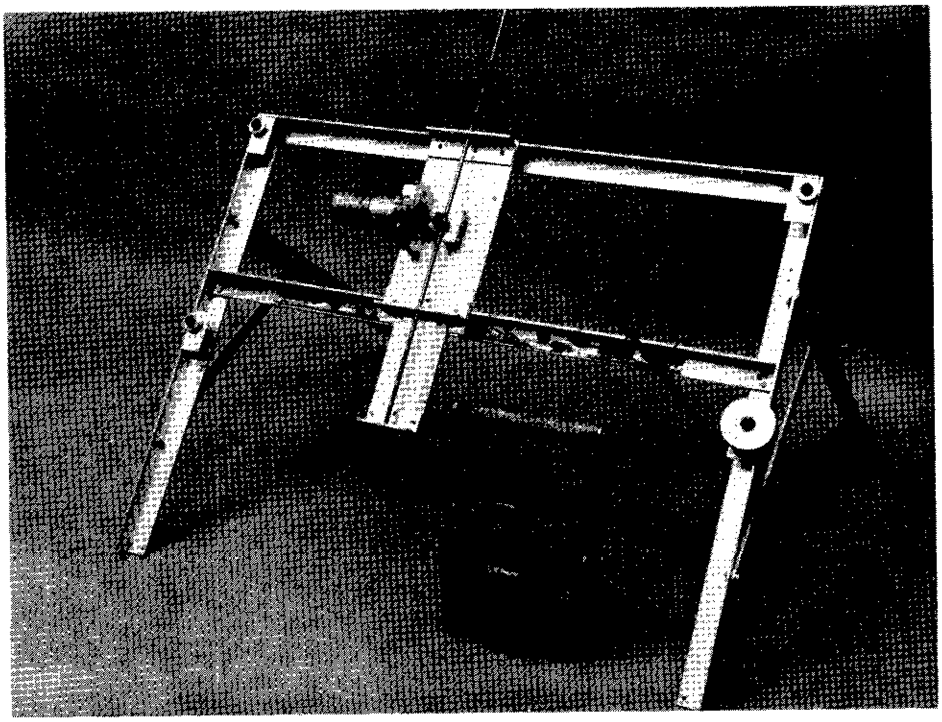

Fig. 1. The motorized point frame used to measure LAI of the general grass and forb ground cover.

strata. The pins were kept very sharp so that they literally pricked the leaves when touched, and the points tapered sufficiently so that rarely did the shank interfere. Wind shields were used on windy days, though wind was rarely a problem in the low vegetation.

Sample adequacy was evaluated by determining the mean number of contacts per frame for living *Bouteloua gracilis*, then calculating the standard error of that mean, N being equal to the number of frames. A sample was considered adequate when the standard error of the mean for each angle was less than 10% of the mean for that respective angle. If a sample was adequate for *Bouteloua*, it was assumed adequate for total green contacts of all species combined.

After determining sample adequacy the LAI was calculated by the equation suggested by Warren-Wilson (1963):

$$LAI = .089f_{8°} + .462f_{32.5°} + .453f_{65°} \qquad (1)$$

where f_n is the average number of contacts per pin for each of the three angles. Separate calculations were made for total green LAI, *Bouteloua* green LAI, and *Bouteloua* brown LAI. The method was compared with direct leaf area measurements, and the results were within 0.05 units. Species other than *Bouteloua gracilis* were not contacted frequently enough for an accurate LAI determination.

After sampling for one summer with three pin angles a coefficient was calculated so that green LAI could be estimated by using just one angle, 32.5°, thereby reducing the field time required. The coefficient was calculated by dividing the LAI obtained with equation (1) by the average number of contacts per pin at the 32.5° angle. This was done for 10 sets of data with the average coefficient being 0.87. This coefficient was checked three times using three angles with a maximum resulting LAI error of only 0.05. The equation used for green LAI during the second summer was then:

$$\text{Green LAI} = 0.87 f_{32.5°} \qquad (2)$$

I consider 0.87 to be a more accurate coefficient for the Pawnee grassland green general ground cover using the 32.5° pin angle alone than Warren-Wilson's coefficient, 1.1.

LAI was measured every 3 to 4 weeks during the growing season on the exclosure and each of the grazed plots and at peak biomass on the irrigated and fertilized plots..

LAI Determination for Bunchgrasses, Fringed Sage, and Cactus

The point-quadrat technique was not utilized for *Aristida longiseta* Steud. and *Artemisia frigida* Willd. because of the difficulty of observing the point as it moved through these more densely foliated plants or on *Opuntia polyacantha* Haw. because of its unique growth form. The method used instead was to carefully measure the leaf area on different sized plants, then to develop a regression line of plant leaf area to plant dry weight. Biomass data (g/m^2) were available for each of the three species, and these data could be converted to leaf area per square meter (LAI) using the regression lines. These three species contribute less than 5% to the total LAI.

The Larger Shrubs

The LAI of the two shrub species, *Chrysothamnus nauseosus* (Pall.) Britt. and *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, was also measured. The average height and diameter for each species was determined, and the amount of leaf area was then measured on two average sized plants of both species. It was then possible to estimate LAI by multiplying the average leaf area per plant by the plant density. These shrubs contributed no more than 2% to the total LAI.

RESULTS AND DISCUSSION

The maximum total green LAI attained in the exclosure during 1970 and 1971 was 0.50, which was reached about mid-June 1970. Most leaf area increment occurs between April 20 and June 15 with a steady decline after this period (Fig. 2). The decline of the total green LAI after June 15 is mirrored by a similar decline of chlorophyll quantity found by Rauzi and Dobrenz (1970) in similar vegetation 25 miles north of the Pawnee National Grassland.

The LAI difference between 1970 and 1971 seems to reflect different precipitation patterns. The spring of 1971 received approximately 190% more precipitation, and LAI increment was more rapid than during the same period of 1970; but June and July were 80 and 77% drier, respectively, and the maximum LAI was about 25% less than in 1970. The LAI increase from .04 to 0.10 in September and October 1971 occurred following rain and snow totaling about 59 mm in September.

The grazed study areas also reached peak LAI about mid-June, even though grazing began in May. Apparently, the livestock grazing pressure had little or no effect on leaf area increment since the maximum LAI values were within .07 of the exclosure value both years, or alternatively, the grazed areas had greater potential for leaf area production. In fact, the

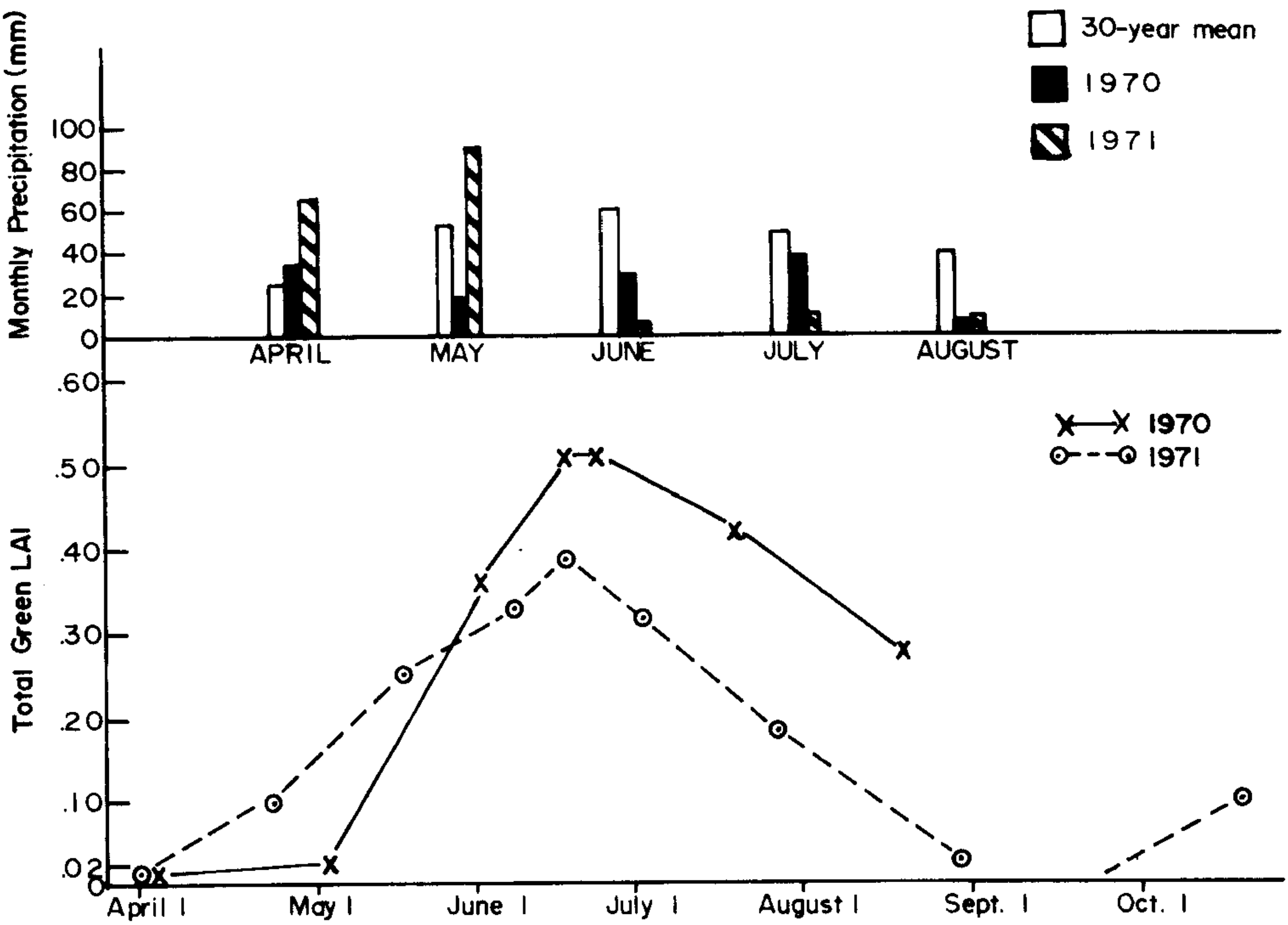

Fig. 2. The 1970-71 seasonal patterns of precipitation and total green LAI in a 30-year exclosure on the Pawnee shortgrass prairie.

heavily grazed area attained a green LAI 10% higher than the exclosure in 1970 and 2.5% higher in 1971. This is not easily explained, although a possible explanation could be related to the greater abundance of *Bouteloua gracilis* in the heavily grazed area--a species that is tolerant of grazing pressure. *Bouteloua gracilis* comprised 86% of the total green LAI in the heavily grazed plot, 77% in the lightly grazed plot, and only 60% in the exclosure. Also, the cactus LAI was higher in the heavily grazed unit than in the exclosure, and grazing pressure probably did not modify this LAI component during the season.

Green leaf area attrition after the June peak was remarkably similar under the different grazing treatments, although the attrition rates were slightly higher in the grazed units than in the exclosure (Fig. 3). The data from the exclosure for *Bouteloua gracilis* green LAI showed no leaf area attrition between mid-June and mid-July 1970, but showed considerable loss in the same period of 1971. The 1971 summer drought probably caused this more rapid leaf area loss.

Although grazing increased the rate of LAI decline as expected, the slight difference between the grazing treatments is intriguing. A possible explanation may be the difference in species composition between the two areas, the heavily grazed unit having more biomass in species which grow better under grazing pressure, e.g., *Bouteloua gracilis*. Another contributing factor could be the slower soil water depletion found by Galbraith (1971) in the heavily grazed area, which could allow growth to occur later into the summer.

The leaf area measurements taken on the plots subjected to either irrigation or irrigation plus nitrogen fertilization indicate that water is

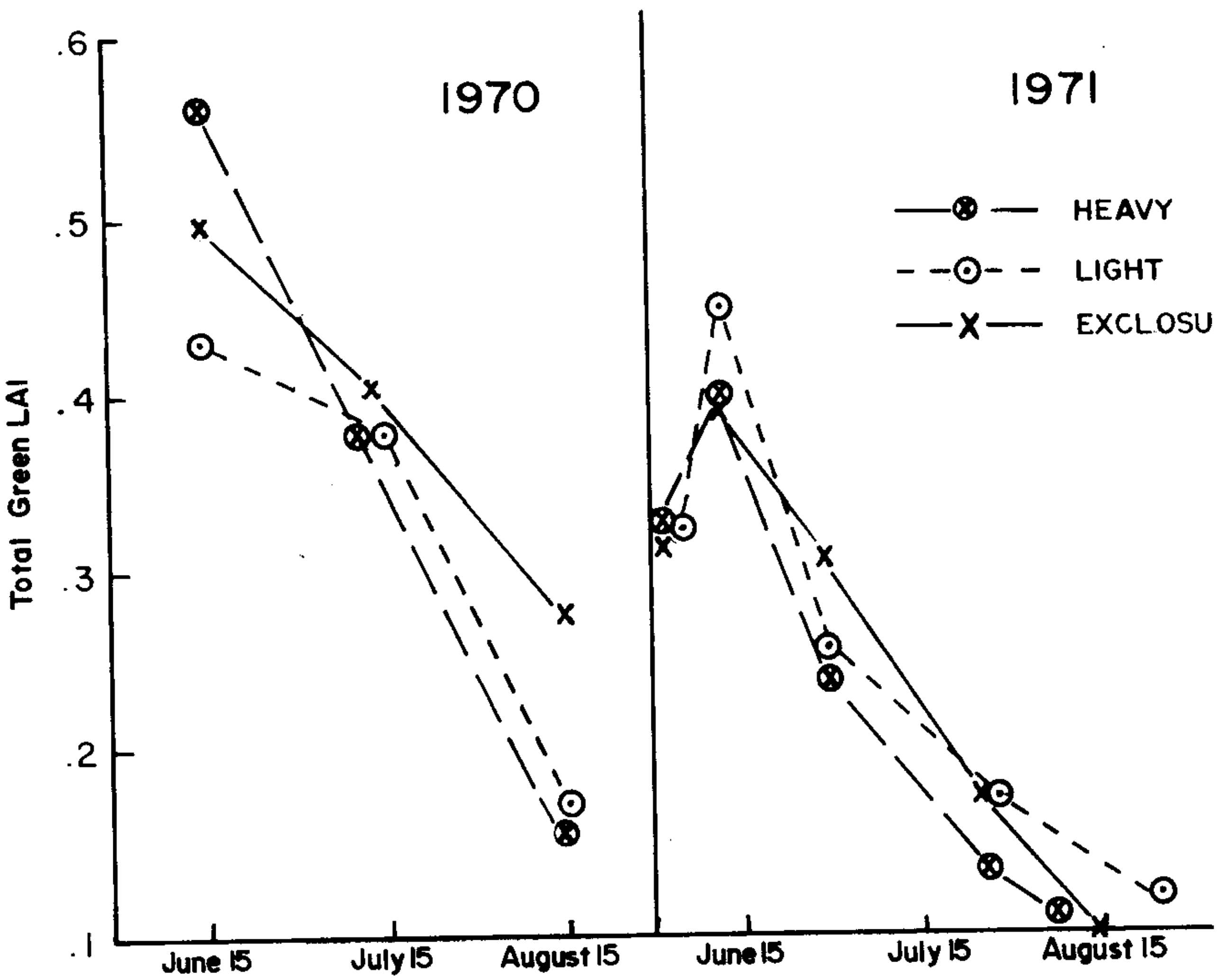

Fig. 3. LAI attrition in 1970-71 on sites subjected to zero, light, and heavy livestock grazing.

the primary limiting factor (at least in June and July), but nitrogen is also required to produce an LAI much greater than 0.5 on the experimental area of the Pawnee National Grassland. The average maximum LAI during 1971 was 0.3 on the control plots, 0.5 on the irrigated-only plots, and 3.0 on the irrigated-plus-fertilized plots. Irrigation alone increased the maximum LAI by about two-thirds, but when combined with nitrogen fertilization, LAI was increased by about 10 times over the control. The growing season was clearly lengthened by both treatments.

Two plots were also subject to the nitrogen treatment alone. Unfortunately, our measurements were not timed properly to determine LAI at maximum biomass, but observations suggest that LAI production may be more rapid on the fertilized plot in the spring when moisture is not limiting. During late June and July 1971, however, no difference in green LAI could be detected between the control and the fertilized plot, suggesting a higher rate of leaf area attrition on the fertilized plot. It is possible, of course, that grassland subject to nitrogen fertilization could have a higher LAI during years with more rainfall than occurred in 1971.

LEAF AREA AND PRODUCTIVITY

LAI measurements from native vegetation are scarce, but those recorded in the literature are higher than the maximum LAI observed (0.55) on the Pawnee upland in 1970-1971. The Pawnee shortgrass prairie is semiarid, however, and the low LAI could be expected. Furthermore, precipitation during 1970 and 1971 was about 20% below the 30-year mean with the deficit occurring mostly between May and August (Striffler, personal communication).

An LAI less than 1.0 suggests that light probably is not a critical limiting factor for production, but this conclusion is not warranted if some leaves are clumped and consequently shaded. Shadows on leaves were observed, but it is not known that this shade substantially reduces the rate of photosynthesis on the Pawnee National Grassland.

The relationship between leaf area and productivity is complex partially because leaf area is both a controlling factor and a result of productivity and also because productivity is controlled by other factors such as leaf moisture status. Leaf area is probably most critical during the early part of the growing season when LAI is low and moisture is available. While predicting productivity from LAI alone may not be dependable, predictions are possible when LAI is combined with other data. Black (1963), for example, produced a graphical model for irrigated clover in Australia from which aboveground productivity could be predicted using LAI and solar radiation. In mid-June on the Pawnee the LAI is about 0.5 and solar radiation about 630 cal/cm^2/day (Nunn, personal communication). Black's model would predict 3.5 g/m^2/day for Pawnee, which is about 1.5 g higher than the maximum rate observed in 1970-1971. The better moisture regime of the clover could account for the difference.

Productivity also can be expressed on a per unit leaf area basis which is useful for comparative purposes. Data for *Bouteloua gracilis* aboveground biomass on the Pawnee exclosure were available for 2-week periods (Uresk and Sims, personal communication) and were used to estimate average daily aboveground net productivity per unit of leaf area (Table 1). Root productivity was not included because growing roots could not be separated from older

Table 1. Estimation of aboveground net productivity (dry wt) per unit of leaf area for *Bouteloua gracilis* during three time periods, 1970.

Time Period	Average Daily Biomass Increment ($g/m^2/day$)	LAI at Middle of Time Period	Leaf Area ($g/day/m^2$)
May 5-19	0.83	0.15	5.5
June 1-16	1.25	0.30	4.2
June 29-July 15	1.30	0.30	4.3

roots. During May, June, and July 1970, the average rate for *Bouteloua gracilis* ranged from 4 to 5.5 g/day/m^2 of leaf area. The higher value occurred in May, which seems unusual for a warm season grass, but this anomaly could be attributed to carbohydrate translocation from the roots or crown early in the growing season. Also, moisture was more available in May. The June and July estimates (4.2 and 4.3 g/day/m^2 of leaf area) are probably more representative when moisture is limiting. The estimates are, of course, subject to the inherent errors of the harvest method used for biomass measurement which lead to underestimation, but similar results were obtained with other sets of data. For example, during May and early June 1970 on the same exclosure, aboveground net productivity of all species combined averaged 4.5 g/day/m^2 of leaf area. Comparable results for the grazed areas during the same time period were 5.4 (light) and 4.5 (heavy). The rates decline as the growing season progresses and moisture stress increases. The similarity of the values for all species combined to those for *Bouteloua gracilis* alone is not surprising since *Bouteloua gracilis* comprises such a large proportion of the total biomass.

The productivity estimates presented in this paper are less than photosynthetic rates which are based on CO_2 uptake per unit leaf area and encompass both root and shoot productivity. Downton (1971) reports that C_4 species, of which *Bouteloua gracilis* is one, assimilate from 60 to 100 mg CO_2/dm^2 leaf area/hr when grown under optimum conditions, while C_3 species fix between 10 to 35 mg CO_2/dm^2/hr. These photosynthetic rates can be converted to approximate aboveground productivity by assuming a dry-weight gain to CO_2 uptake ratio of .70, a shoot dry-weight gain to total plant dry-weight gain ratio of .80 (a minimum estimate based on data collected by

Monk (1966) for annual plants), and a 10-hr photosynthetic period per day. The range for C_4 plant aboveground net productivity per day then becomes 340 to 720 mg/dm^2 leaf area using the photosynthetic rates reported by Downton (1971). The productivity values in Table 1 for *Bouteloua gracilis* are readily converted to a daily average of 450 mg/dm^2 leaf area, which is within the observed range for C_4 plants and higher than the rates expected for most crop plants which are in the C_3 category.

In summary, the results of this study demonstrate the magnitude of leaf area change during the growing season and disclose some responses of shortgrass prairie leaf area to seasonal precipitation, grazing, irrigation, and nitrogen fertilization. Predicting average daily productivity from leaf area data seems to have potential, but further research is needed to clarify the effect of seasonal environmental changes, plant age, and management influences on productivity per unit leaf area.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Black, J. N. 1963. The interrelationship of solar radiation and leaf area index in determining the rate of dry matter production of swards of subterranean clover (*Trifolium subterraneum* L.). Australian J. Agr. Res. 14:20-38.

Brougham, R. W. 1956. Effect of intensity of defoliation on regrowth of pasture. Australian J. Agr. Res. 7:377-387.

DeWitt, C. 1965. Photosynthesis of leaf canopies. Mededeling 274, Instituut voor Biologisch en Scheikundig Onderzoek van Landbouwgewassen, Wageningen. Neth. Agr. Res. Rep. 663.

Donald, C. M., and J. N. Black. 1958. The significance of leaf area in pasture growth. Herb. Abstr. 28:1-16.

Downton, W. J. S. 1971. Adaptive and evolutionary aspects of C_4 photosynthesis, p. 3-17. *In* M. D. Hatch, C. B. Osmond, and R. O. Slatyer [ed.] Photosynthesis and photorespiration. Wiley-Interscience, New York.

Duncan, W. G., R. S. Loomis, W. A. Williams, and R. Hanau. 1967. A model for simulating photosynthesis in plant communities. Hilgardia 38:181-205.

Galbraith, A. F. 1971. Soil water study of a shortgrass prairie ecosystem. Ph.D. Diss. Colorado State Univ., Fort Collins.

Hyder, D. N., R. E. Bement, E. E. Remmenga, and C. Terwilliger, Jr. 1966. Vegetation-soils and vegetation-grazing relations from frequency data. J. Range Manage. 19:11-17.

Klipple, G. E., and D. F. Costello. 1960. Vegetation and cattle responses to different intensities of grazing on short-grass ranges on the Central Great Plains. U.S. Dep. Agr. Tech. Bull. 1216. 82 p.

Knight, D. H. 1971. Some measurements of vegetation structure on the Pawnee Grassland, 1970. U.S. IBP Grassland Biome Tech. Rep. No. 72. Colorado State Univ., Fort Collins. 43 p.

Loomis, R. S., W. A. Williams, and W. G. Duncan. 1967. Community architecture and the productivity of terrestrial plant communities, p. 291-308. *In* A. G. San Pietro, F. A. Greer, and T. J. Army [ed.] Harvesting the sun. Academic Press Inc., New York.

Monk, C. 1966. Ecological importance of root/shoot ratios. Torrey Bot. Club Bull. 93:402-406.

Pearce, R. B., R. H. Brown, and R. E. Blaser. 1965. Relationships between leaf area index, light interception and net photosynthesis in orchardgrass. Crop Sci. 6:15-18.

Rauzi, F., and A. K. Dobrenz. 1970. Seasonal variation of chlorophyll in western wheatgrass and blue grama. J. Range Manage. 23:372-373.

Saeki, T. 1960. Interrelationships between leaf amount, light distribution and total photosynthesis in a plant community. Bot. Mag., Tokyo 73:55-63.

Warren-Wilson, J. 1963. Estimation of foliage denseness and foliage angle by inclined point quadrats. Australian J. Bot. 11:95-105.

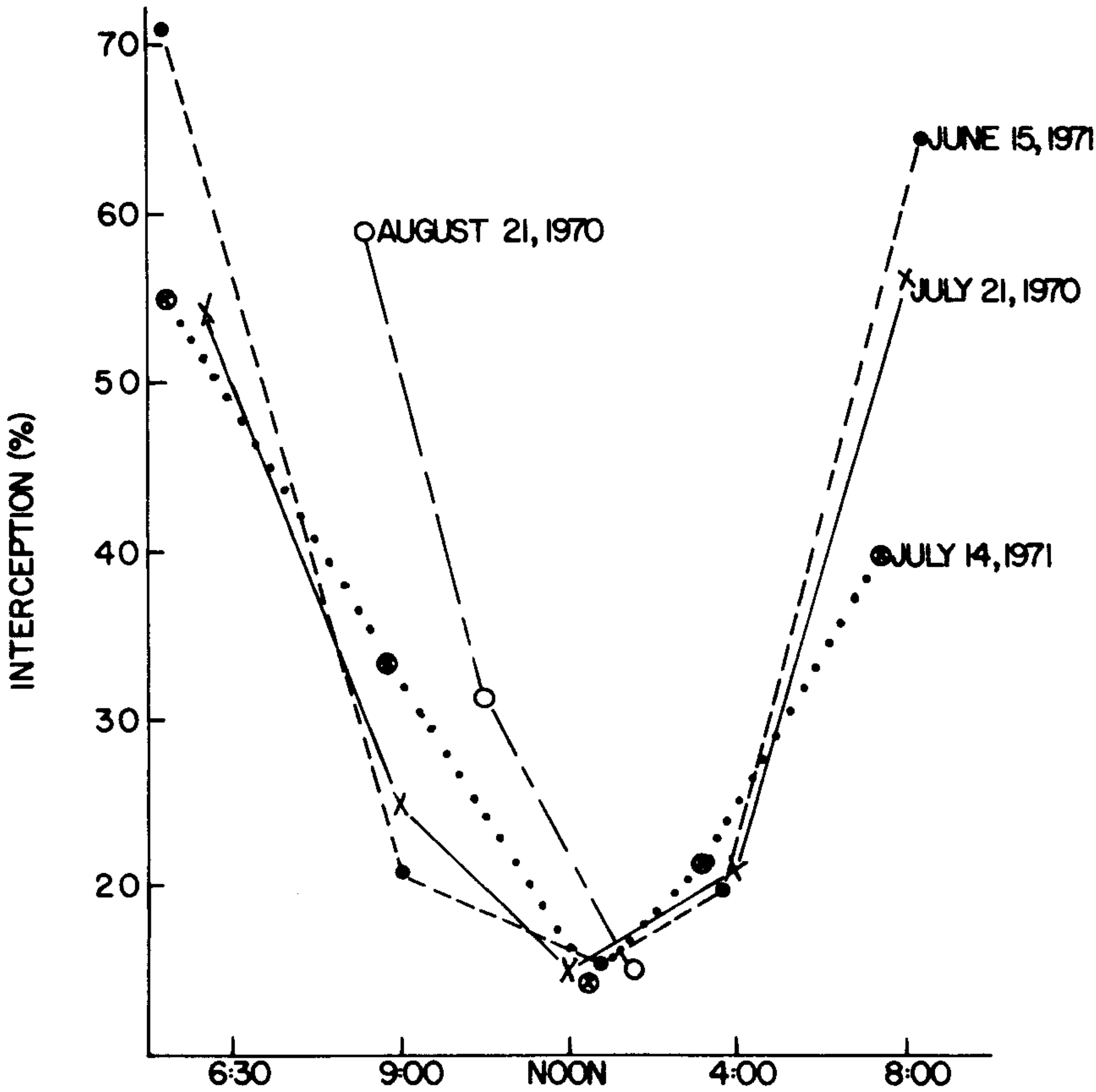
Watson, D. J. 1958. The dependence of net assimilation rate on leaf area index. Ann. Bot., London (N.S.) 22:37-54.

APPENDIX

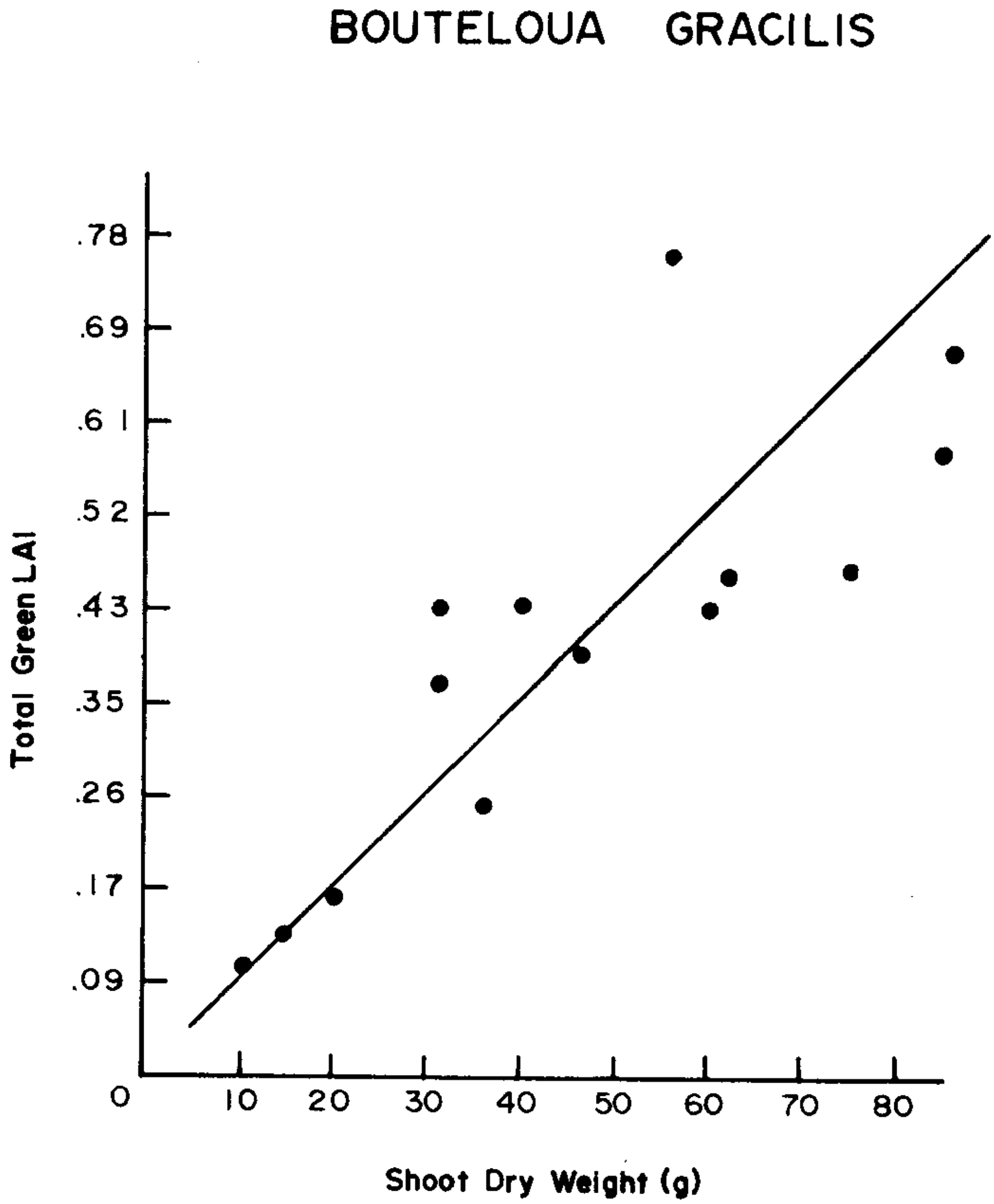
Two graphs are presented in this Appendix which may be of value to other phases of the IBP Grassland Biome program. Appendix Fig. 1 shows the percent of direct sunlight that would be intercepted by green leaves at different times of the day. The methods for collecting the data on this graph are described in Technical Report 72 (Knight, 1971).

Appendix Fig. 2 shows the relationship between green leaf area and live shoot weight of *Bouteloua gracilis*. Small quadrats were measured with the point quadrat method to determine leaf area, after which the plots were clipped and the dry weight of live material determined. Similar graphs for other species are included in Technical Report 72.

Finally, Appendix Table 1 includes the LAI data gathered during 1971. These data have been summarized for the most part in Fig. 2 and 3. Comparable data for 1970 are in Technical Report 72.



Appendix Fig. 1. The percent interception of direct sunlight that could be expected on the Pawnee National Grassland at different times of the day.



Appendix Fig. 2. A graph depicting the relationship between green LAI and shoot dry weight for *Bouteloua gracilis*.

Appendix Table 1. Green LAI data for 1971.[a/]

Date and Plot	LAI *Bouteloua gracilis*	Total Green LAI
April 24		
Exclosure	.07	.10
Heavy	.12	.13
May 1		
Moderate	.12	.17
Light	.13	.15
May 15		
Heavy	.21	.23
Light	.18	.25
June 4		
Exclosure	.24	.32
Heavy	.30	.32
Light	.30	.33
Moderate	.26	.34
June 14		
Exclosure	.22	.38
Heavy	.39	.40
Light	.38	.45
Moderate	.41	.51
June 28		
Exclosure	.20	.30
Heavy	.22	.23
Light	.21	.26
Moderate	.21	.27
July 22		
Exclosure	.14	.18
Heavy	.13	.13
July 26		
Light	.11	.18
Moderate	.11	.14
August 23		
Exclosure	.06	.07
Heavy	.05	.06
Light	.09	.14
Moderate	.07	.08
October 16		
Exclosure	.09	.10
Heavy	.09	.09

[a/] Other LAI measurements were made for Dr. Joe Trlica and Dr. Lee Miller, both of Colorado State University. Both investigators now have the data.