



Effect of supplemental water on morphology, density, survival and population dynamics of *Agropyron smithii* and *Bouteloua gracilis*
by Kurt William Swingle

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Biological Sciences
Montana State University
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Abstract:

Supplemental water was applied to native grassland over four summers and the growth responses of two clonal grass species were measured. Irrigation was applied at four levels: 1.) Natural rainfall only (control), 2.& 3.) Natural rainfall plus water supplements equaling a total weekly minimum of 6 mm and 12 mm water and, 4.) heavy irrigation (a minimum total of 25 mm each week). These irrigation regimens were implemented on two fields in Eastern Montana, one dominated by *Bouteloua gracilis* the other by *Agropyron smithii*. Culm densities (culms/m²), measured for *Agropyron smithii*, increased with irrigation and declined slowly in the six years after irrigation was discontinued. Within year survival was recorded for early spring cohorts of *Agropyron smithii* (20 culms) and *Bouteloua gracilis* (30 culms). *Agropyron smithii* culm survival was slightly enhanced by all levels of irrigation but *Bouteloua gracilis* survival was not affected by irrigation. Morphologic characters (culm height, number of nodes on culms, seasonal length maxima, and total length of green tissue supported by culms) were also measured.

All of these showed plastic responses to supplemental water; however, only heavy irrigation consistently produced responses which were significant. Rates of leaf senescence and emergence (seasonal means among the irrigation treatments) were calculated. No statistical difference among treatments could be found for these seasonal means. A weak correlation to both plant water potential and season was found in the leaf emergence rates. Senescence rates were not correlated with season or water potential.

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26 November 1986
Date

J. WEAVER
Chairperson, Graduate Committee

Approved for the Major Department

5 December, 1986
Date

Peter F. Brussard
Head, Major Department

Approved for the College of Graduate Studies

8 December 1986
Date

Henry L. Parsons
Graduate Dean

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ABSTRACT

Supplemental water was applied to native grassland over four summers and the growth responses of two clonal grass species were measured. Irrigation was applied at four levels: 1.) Natural rainfall only (control), 2. & 3.) Natural rainfall plus water supplements equaling a total weekly minimum of 6 mm and 12 mm water and, 4.) heavy irrigation (a minimum total of 25 mm each week). These irrigation regimens were implemented on two fields in Eastern Montana, one dominated by Bouteloua gracilis the other by Agropyron smithii. Culm densities (culms/m²), measured for Agropyron smithii, increased with irrigation and declined slowly in the six years after irrigation was discontinued. Within year survival was recorded for early spring cohorts of Agropyron smithii (20 culms) and Bouteloua gracilis (30 culms). Agropyron smithii culm survival was slightly enhanced by all levels of irrigation but Bouteloua gracilis survival was not affected by irrigation. Morphologic characters (culm height, number of nodes on culms, seasonal length maxima, and total length of green tissue supported by culms) were also measured. All of these showed plastic responses to supplemental water; however, only heavy irrigation consistently produced responses which were significant. Rates of leaf senescence and emergence (seasonal means among the irrigation treatments) were calculated. No statistical difference among treatments could be found for these seasonal means. A weak correlation to both plant water potential and season was found in the leaf emergence rates. Senescence rates were not correlated with season or water potential.

GENERAL INTRODUCTION

In the semi-arid northern Great Plains, shortage of water most limits formation of plant biomass (Whittaker 1975 p. 202). The objective of the project described in this thesis was to measure the effects of irrigation on five plastic morphological characteristics and on the population dynamics of two important range grasses, Agropyron smithii and Bouteloua gracilis.

To measure the effects of increased water, comparisons were made among plants grown under four different levels of irrigation. The morphological and population responses and methods for their measurement are discussed separately in the four main sections of this thesis. The study site and the irrigation treatments used are described first.

The Study Site

The study was conducted under conditions thought to be representative of the Northern Great Plains at the Fort Keogh U.S.D.A. Livestock and Range Research Station, Miles City, Montana. The study plots were located on two level, ungrazed fields. The vegetation on one was a relatively pure stand of Agropyron smithii while the second was dominated by Bouteloua gracilis. The sites were chosen for their topographic homogeneity, monospecific composition, and

availability of the water with which treatments were made. The soil of the Agropyron site was identified by USDA/SCS personnel as a Kobar Silty Clay loam and the Bouteloua field was classified as having a Havre loam (M. Nichols, personal communication). A more detailed description of the study sites appears in Weaver et al. (1981).

Climatic conditions of the area are summarized in Table 1.

Table 1. Average temperature and precipitation (1941-1970) for Miles City FAA (NOAA 1972).

	May	June	July	August	Annual
Temp.(C)	13.5	18.3	23.6	22.5	7.4
Ppt.(cm)	5.2	8.4	3.9	3.0	35.4

Irrigation Regimen

Four irrigation treatments were applied on two sites for four years. Two levels of irrigation (6 mm and 12mm) were chosen to simulate results of two levels of weather modification success. Plant responses under these treatments were compared with plant responses under unwatered (control), and heavily watered (wet) conditions. The object of the two simulated levels was to eliminate all rain-free periods (droughts) of over a week's duration. The quantities of water deliverable under weather modification were not known and are still under investigation (Barge et al. 1986). This being the case, two levels of weekly supplemental

increase were arbitrarily selected: 6 mm and 12 mm of water. If natural precipitation was inadequate to meet these levels, irrigation was applied until the weekly total met these minima.

The water treatments were applied with sprinkler irrigation on four plots at each site. The "control" plot received only natural precipitation. Measured amounts of water were supplied to two other plots such that during each week each plot would receive a minimum of 6 mm or 12 mm of water. The fourth, "wet", plot was irrigated until soil moisture blocks (Taylor et al. 1961) placed at depths of 25 and 75 cm showed a water potential of -0.2 MPa or less. In the absence of natural precipitation, the amount of irrigation required to maintain the high water potentials of the wet treatment was approximately 25 mm/week.

The size of each study plot was 14 x 14 meters. Water sprinklers were placed 50 cm above the ground and configured to provide uniform distribution of water over an area 19 x 19 m including the plot. Irrigation was performed only between the hours of 3:00 A.M. and 9:00 A.M. to minimize evaporation. Also, to prevent drifting water, irrigation was restricted to periods when winds were less than 13 cm/sec. A detailed description of the treatment procedures has been written by Weaver et al. (1981).

Field data were collected principally by John Newbauer (1977-1979), and in 1980-1981 by Carol Johnson, Brent Haglund, and Tad Weaver.

Effectiveness of Irrigation Treatments

The degree to which watering treatments were effective in relieving water stress was documented by measuring plant and soil water potentials. Whole plant water potentials of Agropyron smithii and Bouteloua gracilis were measured throughout the field season with a Scholander pressure bomb and with the methods described by Ritchie and Hinkley (1975). Measurements were made at or before dawn on randomly selected plants.

Results of these pressure bomb measurements are summarized in Figures 1 and 2. When plant water potentials are lower than -2.0 MPa, plant physiological growth processes largely stop functioning (Hsiao 1973). Accordingly, in these figures, those measurements which are less than -2.3 MPa are classed as infinitely low. The reason water potential values from different treatments overlap, as shown in Figures 1 and 2, is that experimental design allowed equal amounts of water to fall on all treatments when natural rainfall exceeded the treatment minima.

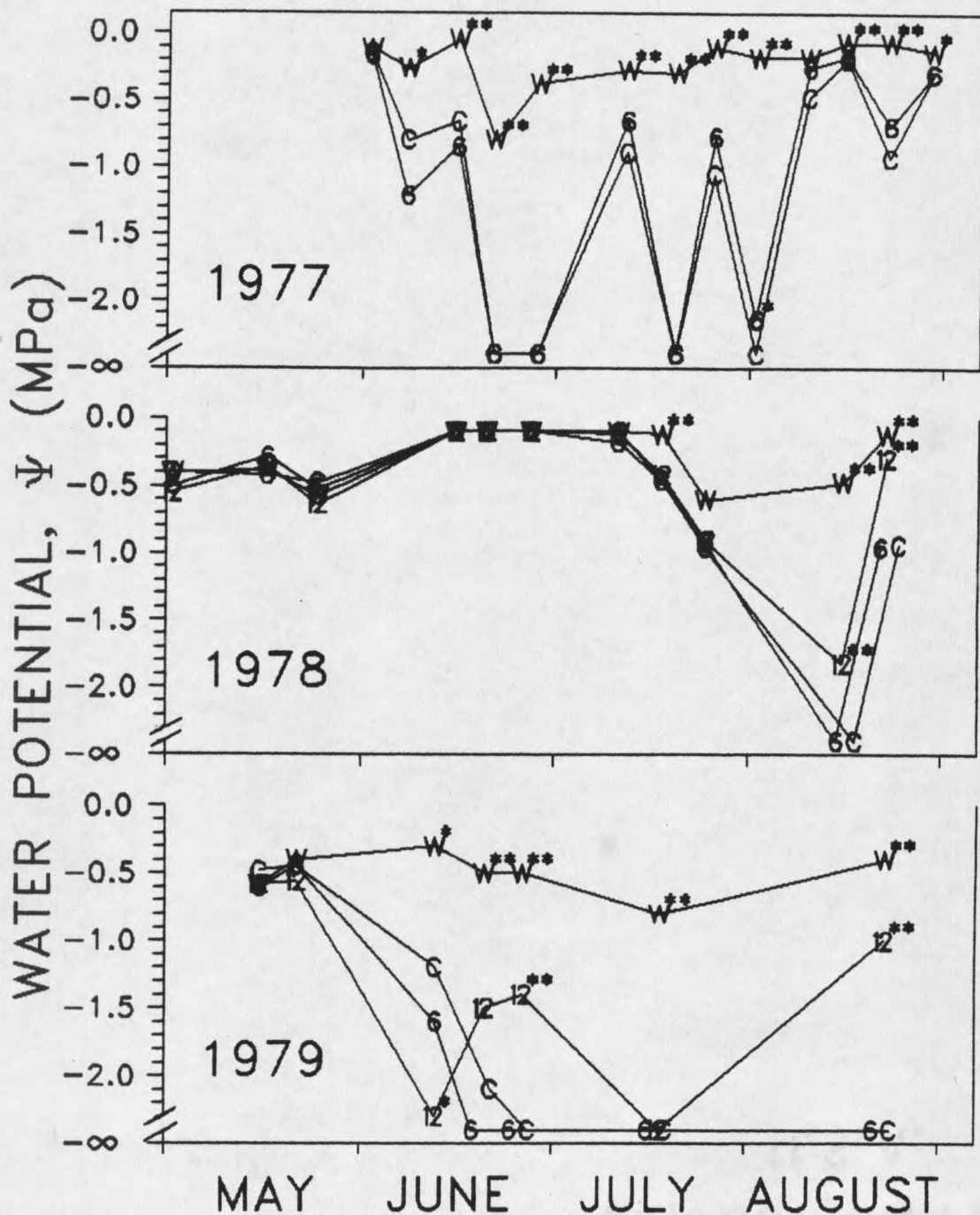


Figure 1. *Agropyron smithii* water potentials 1977 - 1979. The four irrigation treatments are: control (C), 6 mm (6), 12 mm (12), and wet (W). Points are means of five Scholander pressure bomb measurements. Significance of differences from the control on a given date are indicated by single ($p < .05$) and double ($p < .01$) asterisks.

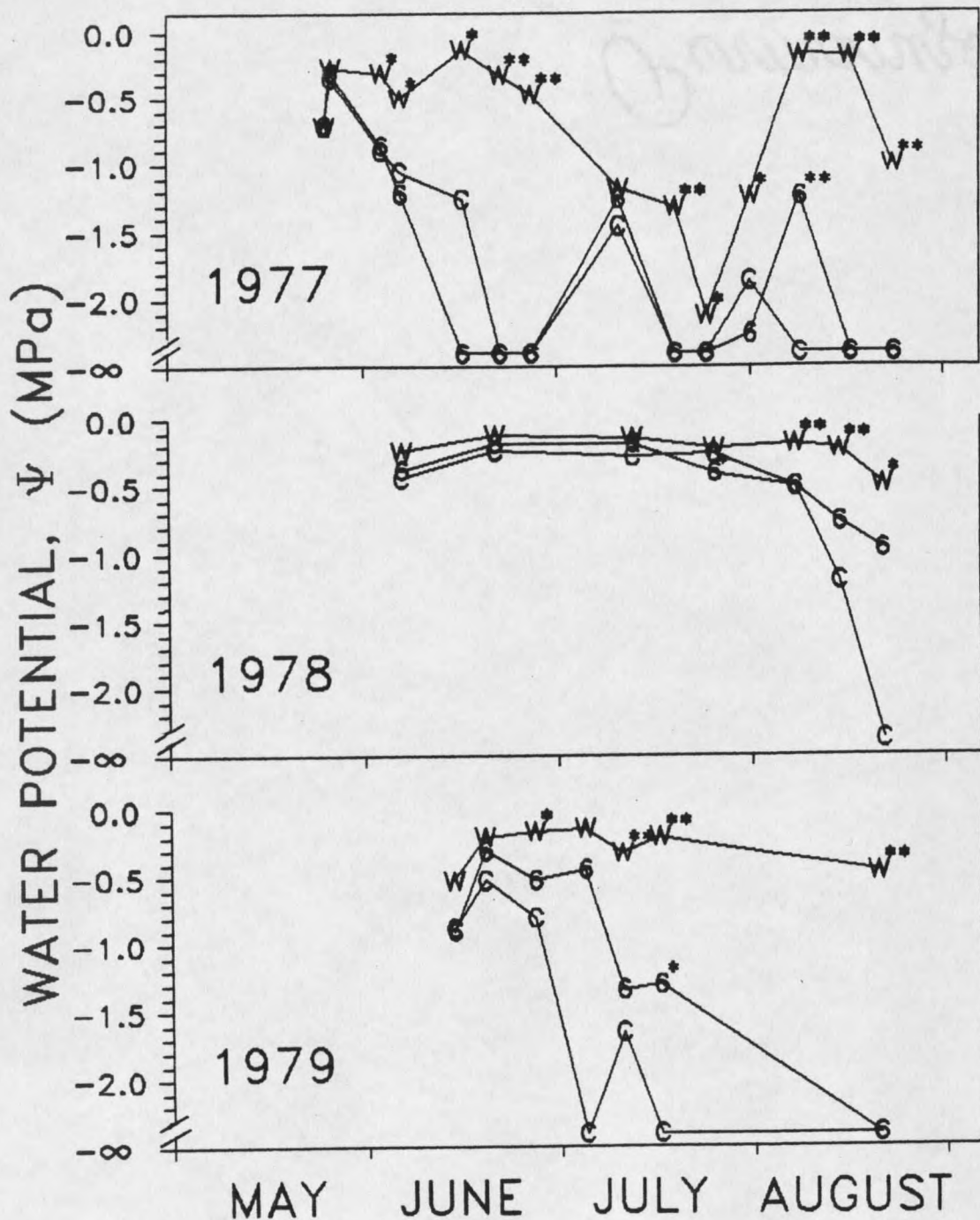


Figure 2. *Bouteloua gracilis* water potentials 1977 - 1979. The three irrigation treatments are: control (C), 6 mm (6), and wet (W). Points are means of five Scholander pressure bomb measurements. Significance of differences from the control on a given date are indicated by single ($p < .05$) and double ($p < .01$) asterisks.

Throughout this thesis it should be remembered that the treatment levels were not constant. In the dry summer of 1979, irrigation treatments resulted in very great differences in water potential among the treatment plots. During periods of plentiful rainfall (Table 2), no supplemental water was needed to meet the water minima and all four treatments received the same amount of (natural) precipitation. In this situation the control plants received as much water as the wet treatment plants. This happened frequently in May and July of 1978, when natural rainfall was much higher than normal.

Table 2. Natural precipitation (cm) at Miles City, MT: 1977-1985¹.

Year	Sept.- April	May	June	July	Aug.	Summer ²	Annual ³
Normal ⁴	14.7	5.2	8.4	3.9	3.0	20.7	35.4
1977	10.8	6.2	3.5	4.9	5.7	20.3	31.1
1978	20.5	17.3	3.5	6.4	2.1	29.3	49.8
1979	24.7	3.5	2.0	7.1	1.7	14.2	38.9
1980	5.6	0.7	7.7	1.3	5.2	15.0	26.6
1981	9.0	7.3	6.5	0.9	2.8	17.6	37.0
1982	14.1	6.6	13.0	1.8	1.5	22.9	37.0
1983	15.9	3.5	4.0	4.8	0.8	13.1	29.0
1984	10.7	2.3	9.0	0.5	2.3	14.1	24.8
1985	8.9	2.9	2.4	7.9	4.7	17.9	26.8

¹ Precipitation data from NOAA Climatological Data, Montana, Miles City FAA (1976 - 1985).

² Summer precipitation was calculated as the sum of May, June, July, and August rainfall.

³ Yearly precipitation was calculated by summing monthly precipitation from September of the previous year though August of the present year.

⁴ Seasonal Normals are averages covering the years 1941 to 1971.

Questions Addressed

The different degrees of release from water stress resulting from the four irrigation regimens was expected to produce a variety of plastic modifications in both community and individual plant structure. Four questions regarding plastic responses were considered in detail: 1.) Would water supplements change culm density? 2.) Would water supplements cause an increase in culm survival? 3.) Would increased water cause morphological changes in these grasses? 4.) Would water supplements change leaf population dynamics? These topics are addressed individually in Sections I through IV.

In general, the plant response to an increase in a formerly limiting resource (in this case water) is expected to be more abundant, longer lived, and larger individuals (Simpson 1981 p. 116, Kramer 1969 pp. 356-360). However as a consequence of such changes, density dependent factors such as competition for light or mineral nutrients, may become increasingly important, and this in turn may affect density, survival, and size in the opposite direction. For this reason, both the magnitude and the direction of plastic response were of interest in this study.

PART I

The Effect of Supplemental Water on Culm Density
in a Stand of Agropyron smithii

INTRODUCTION

The density of a stand of plants may be regulated by a variety of factors such as predators, pathogens, and competition for scarce resources (Antonivics and Levin 1980). While the physiological effects of water stress (Hsiao 1973, Simpson 1981) and plant density dynamics have been discussed (Harper 1977 pp. 151-381), no field experiments have determined the effects of water availability on plant density. This section describes increases in culm density of a clonal plant, Agropyron smithii, as a growth response to irrigation, and the subsequent decrease in density after irrigation was discontinued.

METHODS

To determine Agropyron smithii culm-density response to increased water, portions of a pure stand of the grass were treated with four levels of irrigation. Culms were counted in permanent quadrats located within the study plots, to give a record of density fluctuation experienced by the Agropyron population during irrigation years (1977-1980) and post-irrigation years (1981 - 1986).

Ten permanently marked 10 x 30 cm quadrats were placed at 1 m intervals along the central section of an untrampled 2 x 14 m strip in the center of each study plot. These quadrats were used throughout the project. Sampling was done at approximately weekly intervals. The culms of Agropyron smithii present in these quadrats were grouped according to size classes. The two classes consisted of those plants with one to two leaves, and those with three or more leaves.

The sampling regimen was maintained from May to late August of 1977 and 1978. Irrigation treatments were discontinued at the end of 1980. Isolated density measurements were made on 16 May and 28 August in 1979; 21 August in 1980; 28 June, 20 July, and 27 August in 1981; 25 July in 1982; 15 June in 1983; and 24 June in 1986.

Statistical analysis of the results were made using Student's t multiple comparisons of means in 10 quadrats against the control treatment mean. Bartlett's test for homogeneity of variances showed unequal variances among the treatments. Efforts at transformation of the data proved unsatisfactory, so the analysis was made with a method for comparison of means with unequal variances and unequal sample sizes, as described by G. W. Snedecor and W. G. Cochran (Statistical Methods 1980 Chapter 12).

RESULTS

Initial Field Conditions

Before irrigation treatments were started, measurements were made in the test plots to determine the initial degree of uniformity at the site. On 24 May 1977, the date of the first measurements, culm densities for >2 leaf culms (which shall be termed "large culms") were 22.2/quadrat ± 1.9 S.E. for the control plot, 25.5/quadrat ± 2.1 S.E. for the 6 mm plot, and 26.3/quadrat ± 2.8 S.E. for the wet plot. Student's t-test did not show heterogeneity in culm density between sites at the 0.05% confidence level. Multiplication of plot data by 33.33 converts plot data to a 1 m^2 area. This yields an initial density of 740 large culms/ m^2 in the control plot. Culms with ≤ 2 leaves (which shall be termed "small culms") had an initial density of 2.4/quadrat in the control plot, 1.4 in the 6 mm plot and 0.8 in the wet plot.

Intraseasonal Dynamics

Intraseasonal density-dynamics are illustrated in detail with 1977 - 1978 data, since plant numbers were recorded at regular intervals only in these two years.

Control Plot. Within a given season, water conditions varied considerably, and this affected culm numbers. Water was usually most abundant in the spring, and became less so through the summer (Figure 1). The control plot experienced intraseasonal fluctuations in culm density, which paralleled changes in water availability.

During the first part of the 1977 season, control culm numbers changed little (Figure 3). After 12 July, however, density of the large culms decreased steadily to an end-of-season value of 12.9 culms/quadrat or roughly half the early season value. Relatively rare small culms also showed little early season variation. After 10 August the density of small culms increased to a value of 11.8 culms/quadrat.

In 1978 (Figure 4), numbers of large culms in the control plot increased through the early season. By late June the density had reached 25.3 culms/quadrat or 843 culms/m². After that time, large culm density decreased but only moderately. Small culms in 1978 decreased steadily from a high of 9.8 culms/quadrat early in the season; and reached a density of 0.3 culms/quadrat on 1 July. Small culms remained at these relatively low densities for the remainder of 1978.

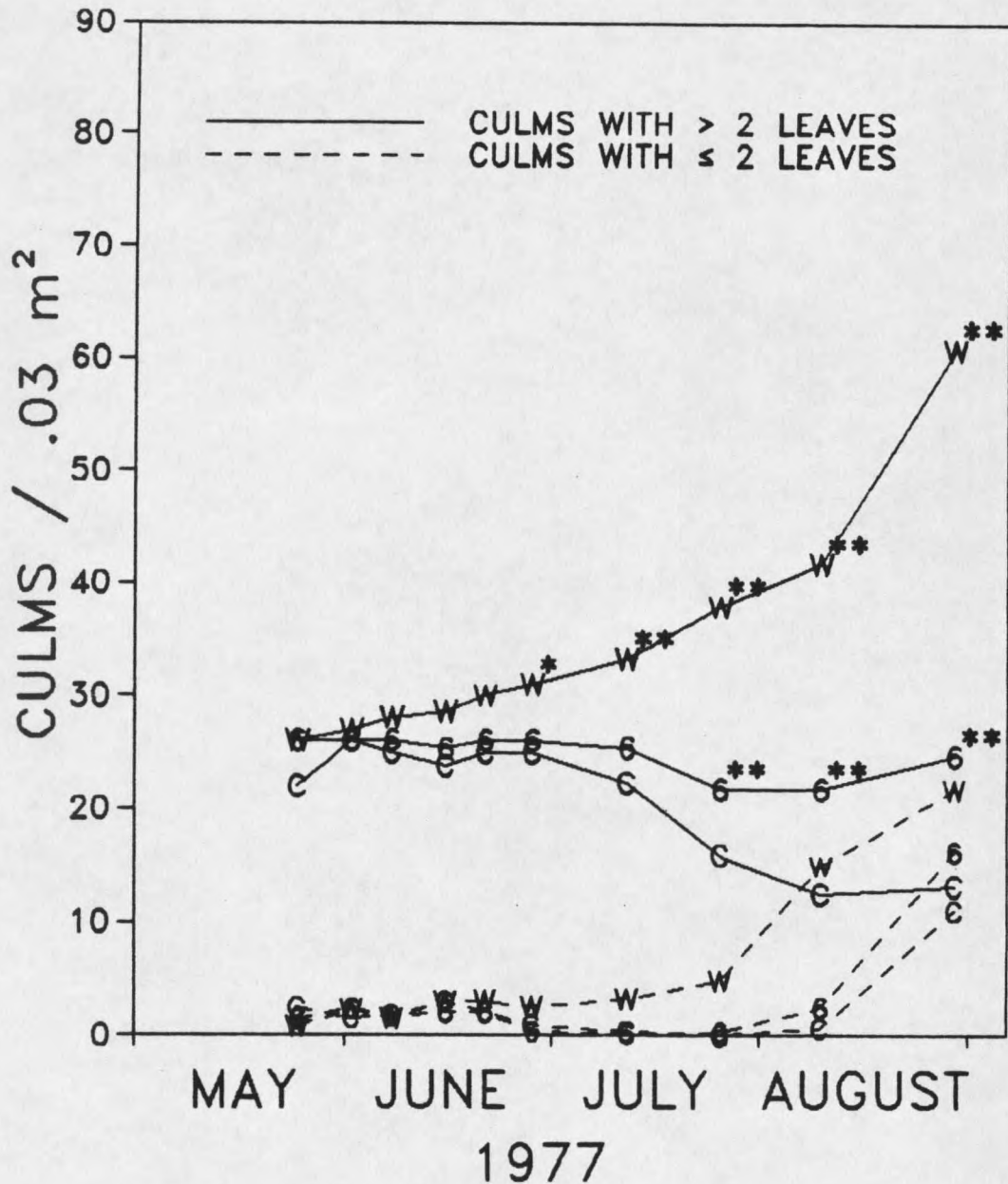


Figure 3. *Agropyron smithii* culm density 1977. The four irrigation treatments are: control (C), 6 mm (6), 12 mm (12), and wet (W). Comparisons of means are made for larger culms only. Significance of differences from the control on a given date are indicated by single ($p < .05$) and double ($p < .01$) asterisks.

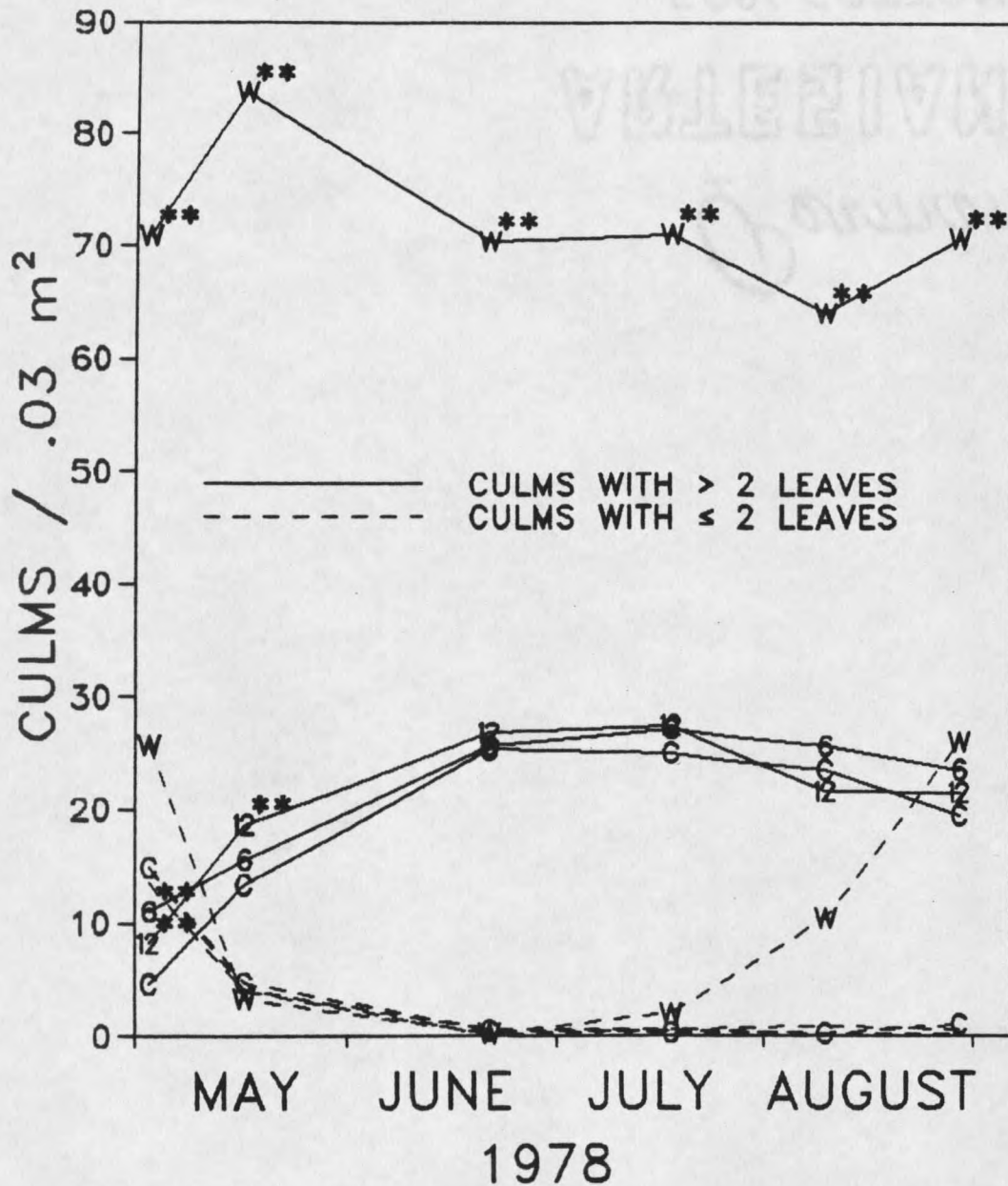


Figure 4. *Agropyron smithii* culm density 1978. The four irrigation treatments are: control (C), 6 mm (6), 12 mm (12), and wet (W). Comparisons of means are made for larger culms only. Significance of differences from the control on a given date are indicated by single ($p < .05$) and double ($p < .01$) asterisks.

6 mm Plot. Dynamics of culm populations in the 6 mm plot for 1977 parallel those of the control plot (Figure 3). Culm numbers for this year were slightly higher than those in the control plot except at the beginning of the season. During the entire 1977 season the density of large culms deviated only slightly from the initial value of 26 culms/quadrat. In early July, in the 6 mm treatment, the density of large culms fell (as it did in the control). By the end of August large culm densities in the 6 mm plot had increased to 24.7 culms/quadrat. The density of small culms in the 6 mm treatment was low and fluctuated little. In 1977, small culms increased in density at season's end, as in the control plot, from a low density of 0.2/quadrat on 26 July, to 16.2/quadrat on 30 August.

Seasonal density dynamics for 6 mm culms in 1978 were undifferentiable from those of the control. Density of large culms initially increased, leveled off, then decreased slightly. Density of small culms decreased from an early season maximum and stayed at low densities for the remainder of the season.

Initially, in 1979 (Table 3 in the following section), the 6 mm plot had a large culm density of 8.9 culms/quadrat, not significantly different from the control. By the end of the field season this density had increased to 12.9 culms/quadrat. Small 6 mm treatment

culms also increased over time from 0.9 culms/quadrat to 1.7 culms/quadrat.

12 mm Plot. Measurements of culm density in the 12 mm plot were initiated in 1978 (Figure 4). Seasonal dynamics for this treatment in 1978 were not significantly different from either the control or the 6 mm plot. This was true for both the large and small 12 mm treatment culms.

In 1979 (Table 3), the 12 mm plot had an early season density of 26.8 large culms/quadrat. This was significantly higher than the control. At season's end the density was essentially unchanged with 17.7 large culms/quadrat. Small culms increased slightly from densities of 2.0 culms/quadrat to 7.0 culms/quadrat.

Wet Plot. A spectacular increase in culm density resulted from the wet treatment. In the spring of 1977 (Figure 3), the density of large culms in the wet plot was similar to that in the control at 26 large culms/quadrat. This density increased continually through the season and by 30 August was 60.8 culms/quadrat or 2027 culms/m². Small culm numbers did not show the same rapid increase as did the large culms, but paralleled those of the other treatments. Initial small culm density was 0.8 culms/quadrat which increased only slightly through the summer. At the very end of the season however the small

culms showed an increase similar to that seen in both the control and 6 mm treatments with an end of season value of 21.7 small culms/quadrat.

In 1978 (Figure 4), culm density in the wet plot continued to increase for the first quarter of the season, reaching a maximum density of 83.3 culms/quadrat on 16 May. This is an increase of 625% over the control plot on the same observation date. After that maximum, culm density in the wet plot decreased gradually for the rest of the season except for a slight increase at season's end. In 1978 small culms were initially 25.7/quadrat. This value fell to low densities and remained low for most of the summer. In August small culm densities increased again to values similar to the early season. The wet plot was the only treatment in 1978 to show the late August increase in small culm density seen in all treatments in 1977.

The early season 1979 wet plot density was 40.8 large culms/quadrat and 2.6 small culms/quadrat. End of season figures were little changed from these values.

Intraseasonal Dynamics

Because small culms represent only a pool of potential recruitment prospects with unknown overwintering potential, results in this section consider only large culms.

1977 vs. 1978. In 1977 the control plot exhibited a net decrease in culm density (Figure 3). In 1978 the end of season control plot density (large culms) had increased both over the course of the summer and in comparison to the end of season 1977 (Figure 4). The difference in natural rainfall between the two years and the absence of water stress for the first half of 1978 can account for these observations.

In the dry summer of 1977, a small amount of supplemental water (conditions of the 6 mm treatment) appeared to inhibit the decrease in culm density experienced by the control plot. In the 6 mm treatment plots, there was little change in density over the course of the year. In 1978, the culm density of the 6 mm plot increased until some water stress was experienced; then it, like the control plot, stopped its increase but at a density higher than at season's start.

The wet plot started 1978 with a density similar to that which it had at the end of season in 1977 (large culms). While the wet plot showed some early season increases its net 1978 change was very slight. This suggests that at the end of two years of treatment limiting factors other than water may have exerted the dominant influence on density.

1979. Early in the season of 1979 all treatments, with the exception of the 12 mm, supported fewer culms

than their respective end of season values in 1978 (Table 3). By the end of 1979, as in the previous dry year 1977, the control density had decreased while the 6 mm treatment density had changed little. The wet treatment showed no net increase for 1979. Culms in the 12 mm plot in 1979 also showed no net yearly density increase.

Table 3. Large culm density (culms/.03 m²) during treated (1977 - 1980) and post-treatment (1981 - 1986) stand development. Statistically (Student's t) significant differences from control means are indicated. A single asterisk (*) indicates $p < .05$, a double asterisk (**) indicates $p < .01$.

Date	Treatment				
	Control	6 mm	12 mm	Wet	
6-21-77	24.8	26.1	----	30.4	Irrigated
7-26-77	15.9	21.7	----	37.9**	
8-30-77	12.9	24.7**	----	60.8**	
6-21-78	25.3	25.6	26.8	70.4**	
7-18-78	25.0	27.1	27.4	71.0**	
8-30-78	20.8	23.5	22.8	70.7**	
5-16-79	10.7	8.9	26.8**	81.6**	
8-28-79	3.3	12.9**	27.8**	82.2**	
8-21-80	2.0	9.5**	19.3**	75.2**	Non-Irrigated
6-28-81	9.1	15.6*	27.4**	89.3**	
7-20-81	4.6	4.5	6.1	55.0**	
8-27-81	0.5	0.1	2.0	62.5**	
7-25-82	9.0	16.2*	21.7**	64.5**	
6-15-83	6.7	11.6*	17.6**	44.6**	
6-24-86	16.0	19.2	15.2	35.8**	

1980. Only one data point exists for 1980, allowing only an end of season comparison with 1979 (Table 3). Density in the wet treatment still far exceeded that found in the other treatments.

1981, 1982, 1983, & 1986. Supplemental irrigation was discontinued at the end of 1980. After this, occasional measurements were made of culm density to document the rate of return to equilibrium.

In June 1981, all irrigated plots had higher culm densities than the control. For large culms in the wet plot, end of season culm density was 125 times higher than that found in the control plot.

In 1982, 1983, and 1986, the effect of previous irrigation remained detectable. In the wet plot, large culms for these years were respectively seven, six, and two times more numerous than the control. Even six years after supplemental water was no longer being provided, culm density remained significantly higher in the wet plot than the control.

DISCUSSION

Changes in culm density can result from changes in rates either of culm mortality or of culm emergence. The time required for a response from either factor to supplemental water need not be constant over the course of a season. Root and rhizome density may be altered by the treatments and these density changes may persist after termination of the treatment. For these reasons, the results of the treatments must be evaluated in terms of intra- and inter- seasonal effects.

Intraseasonal Dynamics

Because each year experienced a different natural rainfall, during some periods the amount of irrigation required to provide the required treatment was 0 mm whereas at other times it required considerable additions of water. In order to compare the effect of the treatment with the control, only contrasts with the control at a given date are strictly appropriate.

We cannot assume that a fixed percentage of small culms mature into the class of large culms. It is possible that a culm may emerge, reach a stage of growth of 2+ leaves and then either die, remain in a stable immature

phase or "oscar" (Silvertown 1982, p. 20), or grow into the large culm class.

From Figure 3 it can be seen that only during the times when the small culms are above 0 density does the density of the large culms increase. This suggests that the number of small culms in a plot is a measure of culm emergence. This emergence seems to have an interseasonal dynamic in that small culms are primarily formed only at the beginning and end of the season.

Interseasonal Dynamics

Reducing and maintaining water stress at low levels might have a cumulative effect which was carried over to the following years. This would influence comparisons made between years. Even if no moisture were retained in the soil from the previous summer, the plants might exhibit a plastic response to water presence that would take several seasons to disappear.

After the irrigation treatments were discontinued in 1980, culm density continued to be higher in the wet plots (Table 3). That a growth response persisted has been corroborated by clip measurements (Weaver 1983). Possible reasons for this phenomena are that large amounts of supplemental water: 1.) increased the root depth which allowed a different horizon of the water table to be exploited. 2.) increased ground litter which inhibited

soil water evaporation. 3.) increased the stand density past a threshold beyond which plants might be more successful in excluding invading weedy species.

This aspect of the project deserves further study. In addition to the possible value for models of successional processes, land use managers might benefit from the knowledge that pasture productivity is increased above normal levels for years after either a wet seasons' end or after cessation of heavy irrigation.

CONCLUSIONS

Supplemental water generally increases culm density. Large water supplements (wet treatments) significantly increased culm density both under relatively wet, and dry, background climatic conditions. In dry years (1977 & 1979), small to moderate amounts of supplemental water (6 mm and 12 mm treatments) produced a significant increase by season's end. In a wet year (1978) small (6 mm treatments) and moderate (12 mm treatments) amounts of supplemental water produced no observable density effects. After three years (two dry and one wet) application of supplemental water to Agropyron smithii grasslands, the effect of large (wet) and moderate (12 mm) amounts of water was a significant increase in culm density over that found in control plots. The application of small amounts of water (6 mm), however, produced no significant changes in culm density from controls.

New growth of small culms starts frequently at the end of summer. Water treatments did not appear to influence this phenomena consistently. This end-of-season growth took place in all treatments in 1977, but only in the wet treatment in 1978.

Small amounts of water had little effect on culm density. Large amounts of supplemental water had large

results. The effects of large amounts of supplemental water applied over a period of four years, were still observable six years after water supplements were discontinued.

PART II

The Effect of Supplemental Water on Culm Mortality In
Stands of Agropyron smithii and Bouteloua gracilis

INTRODUCTION

Culms of perennial grass plants are subject to various risks in the course of a summer. A culm may be eaten, mechanically damaged, shaded out, or exposed to physiological stresses. Among physiological dangers, lack of water is of major importance as a factor limiting yields of grassland plants (Simpson 1981 pp. 14-16).

If water stress were eliminated or lessened, would culms persist without appreciable mortality during the course of a summer? Could small amounts of water (such as might result from cloud seeding, or small climatic shifts) ameliorate mortality? Would large amounts of water (such as heavy irrigation) prove to have an even greater efficacy? Would the responses of two major grasses of the Northern Great Plains, Agropyron smithii and Bouteloua gracilis, to supplemental water be the same? The purpose of this section is to answer these questions.

Water stress was artificially relieved in separate stands of Agropyron smithii and Bouteloua gracilis by supplementing natural rainfall with measured amounts of irrigation water. Irrigation treatments were designed to mimic normal conditions, light periodic showers, and heavy irrigation. Survival was recorded for individual culms within each irrigation treatment.

METHODS

In order to study culm mortality of Agropyron smithii and Bouteloua gracilis plants under varying water regimens, irrigation water was applied to four separate plots in two fields each dominated by one of these grasses. Culms were tagged in late spring and their survival was recorded during the course of the summer.

Plants were observed at approximately one week intervals during the years 1977, 1978, and 1979 for Agropyron smithii; 1978 and 1979 for Bouteloua gracilis. Early in the season, individual culms (20 for Agropyron smithii and 30 for Bouteloua gracilis) were selected approximately 75 cm apart within a central untrampled 2 x 14 m strip within the treatment. Culms were selected at regular intervals along the center of the strip as representative of those found in the stand. Tags of cotton thread were tied around their bases and development of these plants was followed from May until late August. Unless mortality took place within the first three weeks of the season, plants which died were not replaced.

Individual leaves on each culm were periodically evaluated for physical condition (green and developing, damaged tip, brown and dead etc.) (Appendix A). As long as a culm had any leaves which contained some green tissue,

the culm was classified as being alive. As these culms were all roughly the same size and possessed roughly the same number of leaves early in the season, they are assumed to be approximately the same age (from date of emergence in early spring). Thus, all culm mortality calculations are based on observations of an early season cohort of culms. Results are expressed as the percentage of this cohort which remain alive at a given date.

On 18 July, 1978 a severe hailstorm knocked down many of the culms at the Agropyron smithii site. Some culms never recovered from the shock of the mechanical damage, others were lost from the sample set, and presumed dead. This culm death fell nonuniformly on the treatments (six in the wet plot, four in the 12 mm, zero in the 6 mm, and two in the control) and could have no correlation to supplemental water. For this reason, these deaths have been removed from the analysis.

Statistical interpretation of the results of this survey were made using a Chi-square analysis, testing the expectation of equal mortality occurring within each irrigated treatment and the non-irrigated plots. Expectations were weighted to compensate for the different sample sizes involved.

RESULTS

Agropyron smithii Control

In 1977, mortality of Agropyron culms did not begin until mid July (Table 4). Leaf water potential had fallen below -1.4 MPa 21 days earlier (Figure 1). After the onset of mortality, culm death continued steadily for the rest of the season. By the end of August, 50% of the original 20 culms had died.

The summer of 1978 was wet (Table 2). Leaf water potentials in the control plots first fell below -1.0 MPa only in early August. This may have affected the control plot mortality because while slight culm mortality did occur in July and August, end-of-season survival was only 79% of the original early season cohort.

In 1979, as in 1977, mortality began in mid July (Table 5); about three weeks after leaf water potentials fell below -1.4 MPa. Culm death continued at a high rate until early August when the culm deaths slowed. Although leaf water potentials continued to be below -2.0 MPa, culm death did not continue. This mortality may have been prevented by a large rain event (2.8 cm) which took place in the week of August 5-12. While the water was

insufficient to reduce leaf water stress (as measured), it may have inhibited culm death.

Table 4. Agropyron smithii culm survivorship as % of original culms alive at a given date for four irrigation treatments, 1977 - 1978. Single (*) and double (**) asterisks indicate, respectively, $p < .05$ and $p < .01$ probability of significant differences existing between treatments and the control plots.

Date	Treatment			
	Control	6 mm	12 mm	Wet
<u>1977</u>				
5-24-77	100	100	---	100
6-01-77	100	100	---	100
6-07-77	100	100	---	100
6-15-77	100	100	---	100
6-24-77	100	95	---	100
7-05-77	100	95	---	100
7-12-77	100	95	---	100
7-19-77	90	95	---	100
7-26-77	85	95	---	100
8-02-77	85	95	---	100
8-10-77	75	95	---	100*
8-16-77	75	95	---	100*
8-25-77	50	95**	---	100**
8-30-77	50	90**	---	100**
<u>1978</u>				
5-24-78	100	100	100	100
6-06-78	95	95	100	100
6-15-78	95	95	94	100
6-20-78	89	95	94	100
6-27-78	89	95	94	100
7-05-78	89	95	94	100
7-11-78	89	95	94	100
7-18-78	89	95	94	100
7-25-78	79	90	88	93
8-09-78	79	90	81	86
8-16-78	79	86	81	86
8-23-78	79	86	81	86
8-30-78	79	86	81	79

Table 5. Agropyron smithii culm survivorship as % of original culms alive at a given date for four irrigation treatments (1979). Single (*) and double (**) asterisks indicate, respectively, $p < .05$ and $p < .01$ probability of significant differences existing between treatments and the control plots.

Date	Treatment			
	Control	6 mm	12 mm	Wet
1979				
5-14-79	100	100	100	100
5-21-79	100	100	100	100
6-05-79	100	87	100	100
6-12-79	100	87	100	100
6-20-79	100	83	100	100
6-26-79	100	83	100	100
7-03-79	100	83	95	100
7-11-79	80	83	95	90
7-18-79	65	83	90	90
8-02-79	30	78**	90**	75**
8-09-79	30	78**	90**	70*
8-14-79	30	78**	90**	70*
8-24-79	20	70**	85**	60**

Agropyron smithii 6 mm

Even small amounts of water delayed culm death in dry years. In 1977 and 1979, end-of-season mortality for the plots receiving 6 mm of water was significantly less than that of the control (90% vs. 50% in 1977 and 70% vs. 20% in 1979) (Tables 4 and 5). In 1978, end-of-season culm mortality did not differ significantly from the control.

Agropyron smithii 12 mm

During the two years when measurements were taken in the plot receiving 12 mm water supplements, results

paralleled those observed on the 6 mm treatment. In 1979, a dry summer, culm death was reduced relative to the control (Table 5). End-of-season survival was 85% with mortality starting in the first week of July, four weeks after leaf water potential fell below -1.0 MPa (Figure 1). In wet 1978, end-of-season culm death was 81% in the 12 mm treatment and did not differ significantly from the control treatment.

Agropyron smithii Wet

Addition of large amounts of water appeared to slow the death of Agropyron culms relative to the control, but did not have any greater effects than did applications of lesser amounts of water (6 mm and 12 mm treatments). During 1977, there were no culm deaths in the wet plot. This did not differ significantly from the 6 mm. In 1978, after compensation for hail mortality, the end-of-season culm mortality was indistinguishable from that of other treatments. End-of-season culm deaths in the wet treatment, in 1979, were significantly lower than those in the control, but were not higher than those in either the 6 mm or 12 mm treatments.

Bouteloua gracilis Control, 6 mm, and Wet

Bouteloua culm mortality was not influenced by additional water (Table 6). End-of-season culm mortality

was slightly higher in all treatments during (wet) 1978 than in (dry) 1979. In both years, wet treatment end-of-season culm mortality was 10% higher than in the control.

Table 6. Bouteloua gracilis culm mortality expressed as % of original culms alive at a given date for three irrigation treatments. No significant differences were found between treatments and the control plots.

Date	Treatment		
	Control	6 mm	Wet
<u>1978</u>			
6-05-78	100	100	100
6-14-78	100	100	100
6-21-78	100	100	100
7-03-78	100	100	100
7-12-78	100	100	93
7-26-78	90	80	70
8-02-78	83	77	67
8-08-78	80	77	60
8-15-78	80	73	60
8-29-78	60	63	50
<u>1979</u>			
6-13-79	100	100	100
6-19-79	100	100	97
6-27-79	100	100	97
7-05-79	100	100	97
7-11-79	100	100	97
7-17-79	100	100	97
8-08-79	97	97	87
8-21-79	90	97	80

DISCUSSION

The term mortality in this section does not have the same meaning it would have in a discussion of animal mortality. By culm death I refer to the presumptive death of above-ground tissue; but this is only a fraction of the plant. Roots are a major component of plant biomass and this tissue may or may not die depending on the severity and duration of the adverse conditions. What has been called death (of above-ground tissue) may also be seen as a retreat from harsh conditions on the surface.

Through the years of the experiment, conditions did not remain constant. Culm density varied significantly in many instances (Section I) and increased culm density has been shown to be linked with increased culm mortality (Kays and Harper 1974, Antonovics & Levin 1980 pg. 418).

Mortality in Agropyron smithii was slowed by small amounts of supplemental water and slowed equally by large amounts. This effect was most noticeable in dry summers (1977, 1979).

The decreased culm mortality of Agropyron smithii in wet treatments is expected, since physiological water stress was essentially eliminated for these plots. What was not expected was that culm mortality would be greatly

reduced by treatments (6 and 12 mm) which fell short of eliminating water stress as conventionally measured.

In the case of Bouteloua gracilis, culm mortality was unaffected by supplemental water. In the control plot climatic conditions which provided a more mesic environment (1978) resulted in an end-of-season mortality which was higher than the dry year (1979).

CONCLUSIONS

Agropyron smithii

In dry summers (1977 and 1979), small amounts of supplemental water were sufficient to reduce culm mortality. During wet years (1978) mortality did not differ significantly among control, light (6 and 12 mm), and heavy treatments (wet).

Bouteloua gracilis

Bouteloua culm mortality did not appear to be influenced by either large or small amounts of supplemental water. During (wet) 1978, culm mortality was slightly higher than in (dry) 1979 for all treatments. If anything, the data suggest that supplemental water may actually increase the death rate of Bouteloua gracilis culms.

PART III

Effect of Supplemental Water on Leaf and Culm
Morphology In Agropyron smithii and
Bouteloua gracilis

INTRODUCTION

The ability to capitalize on transitory periods of favorable conditions is an important component of an organism's success in a variable environment. For plants, given their limited behavioral repertoire, this is expressed in modification of physiology and morphology. These changes must be flexible in magnitude to accommodate a changing environment. Plastic morphological changes may include alteration in 1.) numbers of shoots, leaves, and flowers, 2.) the size of vegetative parts, and 3.) degree of hairiness (Bradshaw 1965).

This section describes plastic responses of two economically important grasses (Agropyron smithii and Bouteloua gracilis) to water supplements such as might result from minor climatic changes, cloud seeding, light irrigation, or heavy regular irrigation. The morphological characters include culm height, number of leaves per culm, number of leaf nodes on each culm, maximum length of leaves, and total length of green leaf tissue per culm.

Water stress generally causes reduction of growth. Stunted plants have smaller stature, and fewer and smaller leaves (Kramer 1969). Since supplemental water can alleviate drought stress, the results expected from adding water are that by the season's end the plants would be

taller, have more nodes, have more and larger leaves on each culm, and carry more green tissue than control plants.

METHODS

In order to study water-induced morphological modifications of Agropyron smithii and Bouteloua gracilis, field plots were treated with four levels of irrigation. The realized water stress for plants within the plots was monitored (Figures 1 & 2) to document the effectiveness of the treatments; and plant morphology within the study plots was measured periodically with nondestructive methods.

Early in the spring, culms selected as representative of the plot were chosen at regular intervals along a 2 x 14 m strip and tagged with cotton thread. Through the summer, individual leaves on each culm were periodically evaluated for physical condition (green and developing, damaged tip, brown and dead) (Appendix A). As these culms were all roughly the same size and possessed roughly the same number of leaves early in the season, they are assumed to be approximately the same age (from date of emergence in early spring). All culm morphology calculations are based on this early season cohort of culms.

As long as a culm had any leaves which contained some green tissue the culm was classified as being alive. Leaf lengths were measured as the distance from the

outstretched apex of the leaf, along the blade and sheath, to the ligule of the next lower leaf. Culm height was measured as the distance from the ground to the tip of the uppermost outstretched leaf. For a more complete description of leaf evaluation methods and data management, see Appendices A and B.

In the data analysis the following conventions were used: 1.) Mean culm height was calculated by summing the heights of all plants alive at the sampling date and dividing this value by the number of plants. 2.) Mean number of leaves/culm was calculated by counting the number of green leaves on each culm, summing these counts and dividing the sum by the number of plants alive at the sampling date. 3.) Maximum leaf length was calculated by finding the largest length recorded that season. Only those maxima which occurred at least one observation before season's end were included. Similarly, only those maxima which occurred at least one observation before the death of the plant were used for analysis. This allowed confidence that these values were a measurement of the maximum potential leaf length and not biased by culm mortality or seasonal effects. Leaf conditions other than death (brown and lost leaf tips for example) were not considered as leaf mortality. 4.) Mean number of nodes per culm was calculated by counting the number of nodes on each live culm and dividing by the number of culms alive

at the sampling date. 5.) Mean total length of green tissue per culm was calculated by summing the lengths of all leaves with green tissue on a given culm. These sums were totaled and the grand sum divided by the number of plants alive.

Culm height measurements were made on Agropyron and Bouteloua plants in 1978 and 1979. Leaf condition measurements were made on Agropyron and Bouteloua plants for the years 1977, 1978, and 1979. Leaf length measurements were made on only Agropyron plants for the same three years.

The results of these calculations were evaluated by comparing results from each irrigation treatment with the control results, using Student's t comparison of weighted means from unequal sample sizes and unequal sample variances (Snedecor and Cochran 1980 chapter 12).

RESULTS AND DISCUSSION

This section is divided into five parts, each concerned with a single morphological character. These are culm height, mean number of nodes per culm, mean number of green leaves per culm, mean length of green leaf tissue per culm, and maximum leaf length.

Culm Height

By season's end, large amounts of supplemental water (wet treatments) made culms taller in both the wet year (1978) and the dry year (1979). Smaller water supplements had only slight effects.

1978. In a wet year (1978) (Table 2), culm height for Agropyron smithii in the wet plots remained indistinguishable from the control until early June (Table 7). After that time, culm height increased rapidly in the wet plot, with maximum heights being attained in mid-July. At maximum height, Agropyron culms in the wet plots were 55 cm (or 47%) taller than the control culms. Any decrease in mean culm height shown over the latter half of the field season is due to mortality of taller culms during this period.

Table 7. Mean culm height for Agropyron smithii in 1978 & 1979. Comparisons are made against the control plot only. Single asterisk (*) indicates $p < .05$, double asterisks (**) indicate $p < .01$.

Date 1978	Treatment			
	Control	6 mm	12 mm	Wet
5-02-78	127.3	109.2	117.2	133.5
5-10-78	138.0	127.6	131.3	152.2
5-16-78	151.7	141.2	139.1	172.6
5-24-78	184.3	180.8	189.4	216.4*
6-06-78	235.5	236.6	257.1	294.6**
6-15-78	281.0	270.6	324.2	377.1**
6-20-78	308.7	-----	357.3	417.5**
6-27-78	341.5	308.0	395.8	478.7**
7-05-78	370.2	336.7	427.1	533.4**
7-11-78	381.4	343.8	440.5	551.1**
7-18-78	384.9	-----	443.9	564.7**
7-25-78	-----	351.8	400.5	552.2
8-09-78	364.6	353.3	-----	546.8**
8-10-78	-----	-----	407.0	-----
8-16-78	-----	358.2	407.0	546.8
8-23-78	364.6	358.2	407.0	546.8**
8-30-78	364.6	-----	407.0	565.8**
1979				
5-14-79	116.7	105.5	122.8	139.7**
5-21-79	138.5	131.6	142.6	163.0**
6-05-79	173.6	159.9	170.9	230.4**
6-12-79	185.1	168.2	175.3	269.0**
6-20-79	189.5	174.1	176.3	316.6**
6-26-79	190.2	174.3	176.9	354.8**
7-03-79	190.2	174.3	179.8	379.4**
7-11-79	187.6	174.3	179.6	406.5**
7-18-79	192.3	174.3	185.4	407.8**
8-02-79	201.0	183.8	185.4	385.7**
8-09-79	204.7	178.2	185.6	384.0**
8-14-79	204.7	178.2	185.6	382.0**
8-24-79	211.2	182.8	186.6	390.7**

Table 8. Mean culm height for *Bouteloua gracilis* in 1978 & 1979. Comparisons are made against the control plot only. Single asterisk (*) indicates $p < .05$, double asterisks (**) indicate $p < .01$.

Date 1978	Treatment		
	Control	6 mm	Wet
6-05-78	89.6	95.2	129.5**
6-14-78	96.7	103.8	145.6**
6-21-78	101.4	109.8	148.6**
7-03-78	140.6	136.7	169.2
7-12-78	156.5	163.8	184.6
7-26-78	150.4	165.9	154.0
8-02-78	147.9	167.3	156.9
8-08-78	142.0	167.3	144.1
8-15-78	141.9	171.5	144.5
8-29-78	106.4	174.2	152.9
<u>1979</u>			
6-13-79	96.1	104.3	140.8**
6-19-79	101.0	110.2	149.3**
6-27-79	101.3	111.4	155.9**
7-05-79	102.8	115.2	166.3**
7-11-79	102.1	116.3	178.5**
7-17-79	103.0	117.1	190.7**
8-08-79	102.2	122.8*	202.4**
8-21-79	100.6	122.9*	207.5**

Mean height of culms in the 12 mm treatment showed intraseasonal dynamics similar to those in the wet plots. At no time did the mean culm height differ significantly from the control plot heights (Table 7).

Water treatments of 6 mm also caused no significant increases in culm height relative to the control in 1978. Culm growth proceeded until early July, after which growth slowed and then stopped. Mean culm height was not significantly less than the control after mid-June.

In 1978, Bouteloua gracilis was not significantly affected by heavy irrigation (wet treatments). This may be due to the wet year and the xerophytic nature of Bouteloua. Through June plants growing under the wet treatment were significantly taller than the control plants (Table 8), but the differences disappeared by early July.

1979. In (dry) 1979, the wet treatment produced larger effects upon culm height relative to the control in Agropyron smithii (Table 7) than it did in 1978. However, the maximum culm height was not as great as that in 1978. This was probably due to the lower humidity of 1979. Interseasonal dynamics were very similar to 1978, with maximum height attained in mid-July. At that time, wet plot culms were 112% taller than the control plot culms.

Neither 12 mm nor 6 mm plot culm heights were significantly different from control in 1979. At season's end, 6 mm and 12 mm plot culms were roughly 15% shorter than those of the control. This figure was not statistically significant and no explanation is offered for the observation.

In 1979, Bouteloua gracilis height responded to heavy watering (Table 8). By the end of August, wet treatment culms were 107% taller than those in the control plots. Small amounts of water (6 mm) in this dry summer (1979) caused no significant effects on culm height.

Culm Height Conclusions. Culm heights in Agropyron and Bouteloua can respond to supplemental water. Large amounts of water made the culms taller. This effect was more pronounced in dry years than in wet years. Small amounts of supplemental water had little effect on culm height for either species in both moist and dry years.

Mean Number of Nodes per Culm

Nodes in grass plants are produced at the junction of each leaf with the stem. While individual leaves may die or detach, the nodal structure will remain as long as the stem is intact. Since Agropyron smithii and Bouteloua gracilis grow from apical meristems, the number of nodes on a culm is a record of the cumulative number of leaves produced by the culm since emergence in early spring.

Agropyron smithii. In the dry summers of 1977 and 1979, by the end of the year, mean numbers of nodes on each culm of Agropyron smithii were highly influenced by supplemental water (Table 9). In wet 1978, however, the end of season mean node number differed little among treatments.

In 1977, start-of-season node number in the 6mm and wet plots was not statistically different from the control (Table 9). By the end of the year, mean node number was 6.7 in the control, 7.6 in the 6 mm, and 11.2 in the wet plot.

Due to the early season rainfall in 1978 (Table 2 and Figure 1), the mean node number did not differ significantly from the control for any irrigation level except the wet treatment during 1978. End-of-season means were $9.1 \pm .27$ S.E. for the control and $11.5 \pm .61$ S.E. for the wet plot (Table 9).

In 1979, node number at the beginning of the season did not differ among the treatments (Table 9). With the onset of drought stress in early June, the rates of leaf production were slowed in all but the wet plot. The mean number of nodes on each culm differed between the wet plots and all other treatments after that time. End-of-season values for the four treatments were $6.5 \pm .29$ S.E. in the control, $6.8 \pm .19$ S.E. in the 6 mm plot, $6.7 \pm .33$ S.E. in the 12 mm plot, and 8.3 ± 5.4 S.E. in the wet (Table 9).

Table 9. Mean nodes per culm in Agropyron smithii during 1977 - 1979. Comparisons are made against the control plot only. Single asterisk (*) indicates $p < .05$, double asterisks (**) indicate $p < .01$.

Date 1977	Treatment			
	Control	6 mm	12 mm	Wet
5-24-77	4.3	4.6	----	4.6
6-01-77	5.0	4.8	----	5.1
6-07-77	5.4	5.3	----	5.9*
6-15-77	5.4	5.3	----	6.8**
6-24-77	5.4	5.3	----	7.1**
6-28-77	---	---	----	7.9
7-05-77	5.4	5.4	----	8.3**
7-12-77	5.7	6.1	----	9.0**
7-19-77	5.8	6.3	----	9.4**
7-26-77	5.8	6.4	----	9.9**
8-02-77	6.1	6.5	----	10.1**
8-10-77	6.0	6.9*	----	10.7**
8-16-77	6.1	7.2**	----	10.8**
8-25-77	6.4	7.4*	----	11.0**
8-30-77	6.7	7.6	----	11.2**
1978				
5-02-78	3.7	3.5	3.5	3.4
5-10-78	4.1	3.7	3.9	3.9
5-16-78	4.3	4.1	4.1	4.4
5-24-78	5.1	4.9	4.9	5.0
6-06-78	6.0	5.9	5.7	5.9
6-15-78	6.7	6.6	6.4	6.5
6-20-78	7.1	---	6.8	6.7
6-27-78	7.7	7.4	7.2	7.3
7-05-78	8.2	8.2	7.8	7.8
7-11-78	8.4	8.6	8.2	8.3
7-18-78	8.6	---	8.5	8.6
7-25-78	---	9.1	9.2	9.4
8-09-78	9.0	9.3	9.5	10.3*
8-16-78	---	9.4	9.5	10.7
8-23-78	9.1	9.5	9.5	11.0*
8-30-78	9.1	---	9.7	11.5**

Table 9 Continued

Date 1979	Treatment			
	Control	6 mm	12 mm	Wet
5-14-79	3.7	3.7	3.7	3.5
5-21-79	4.3	4.2	4.1	4.1
6-05-79	5.3	5.1	5.0	5.2
6-12-79	5.7	5.6	5.1**	5.7
6-20-79	5.8	6.0	5.2*	6.3*
6-26-79	5.8	6.0	5.5	6.5**
7-03-79	5.8	6.0	5.6	6.9**
7-11-79	5.9	6.0	5.8	7.2**
7-18-79	6.0	6.0	5.9	7.4**
8-02-79	6.2	6.4	6.4	7.7**
8-09-79	6.2	6.6	6.6	7.8*
8-14-79	6.2	6.7	6.7	8.0**
8-24-79	6.5	6.8	6.7	8.3*

Bouteloua gracilis. Mean node number for Bouteloua gracilis was little affected by supplemental water in either the dry or the wet year (Table 10).

In 1978 initial node numbers were $4.4 \pm .13$ S.E., $4.7 \pm .10$ S.E., and $4.2 \pm .12$ S.E. for the control, 6 mm, and wet plots respectively. End-of-season values were $6.6 \pm .28$ S.E., $6.7 \pm .34$ S.E., and $7.2 \pm .35$ S.E. for the same three treatments.

During the dry year (1979), mean node numbers for Bouteloua plants differed little from the wet year of 1978 (Table 10). Initial values did not differ among the treatments; end-of-season values were only slightly higher for the wet plots (Table 10).

Table 10. Mean nodes per culm in Bouteloua gracilis during 1978 - 1979. Comparisons are made against the control plot only. Single asterisk (*) indicates $p < .05$, double asterisks (**) indicate $p < .01$.

Date 1978	Treatment		
	Control	6 mm	Wet
6-05-78	4.4	4.7	4.2
6-14-78	5.0	5.3	4.9
6-21-78	5.4	5.7	5.2
7-03-78	5.7	6.1	5.5
7-12-78	5.9	6.1	5.8
7-26-78	6.1	6.4	6.0
8-02-78	6.1	6.5	6.3
8-08-78	6.1	6.5	6.4
8-15-78	6.2	6.6	6.6
8-29-78	6.6	6.7	7.2
<u>1979</u>			
6-13-79	5.0	4.8	4.6*
6-19-79	5.3	5.0	5.0
6-27-79	5.7	5.5	5.5
7-05-79	5.8	5.9	5.9
7-11-79	5.8	6.0	6.1
7-17-79	5.9	6.0	6.3
8-08-79	6.1	6.2	6.6
8-21-79	6.2	6.2	7.0*

Mean Number of Leaves per Culm

The number of leaves sustained by an individual culm might be expected to increase with water supplements which relieve water stress. The net number of leaves borne on a culm may be constant through a season, while, at the same time, considerable turnover in leaves may occur through leaf emergence and death. Constraints on numbers of leaves sustained by a culm may be imposed by desiccation. Numbers

of green leaves may have to be limited in times of water stress to prevent desiccation of the entire plant. If water stress were eliminated, would the plant continue to add leaves through the year?

Initial Values. Initial numbers of leaves on culms did not differ significantly among the treatment plots for either Agropyron smithii or Bouteloua gracilis. Mean numbers of Agropyron leaves/culm were 3.5, 3.9, and 3.7 respectively for the control, 6 mm and wet plots on 24 May, 1977 (Table 11). The pre-treatment mean leaf numbers for Bouteloua gracilis are 3.9, 4.2, and 4.1 (Table 12). Mean leaf numbers for the season's first observation were not different among the various treatments in any of the years studied for either species. Since perennating tissue of these plants dies back each winter, pre-irrigation growth conditions are similar. There apparently is no cumulative effect of supplemental water on accelerating early growth in leaf numbers.

Table 11. Green leaves/culm in Agropyron smithii during 1977, 1978, and 1979. Comparisons are made against the control plot only. Single asterisk (*) indicates $p < .05$, double asterisk (**) indicates $p < .01$.

1977 Date	Treatment			
	Control	6 mm	12 mm	Wet
5-24-77	3.5	3.9	----	3.8
6-01-77	4.1	4.2	----	3.8
6-07-77	4.1	4.3	----	4.5
6-15-77	3.6	3.8	----	5.2**
6-24-77	3.5	3.5	----	5.3**
6-28-77	---	---	----	6.1
7-05-77	2.8	3.1	----	6.3**
7-12-77	3.0	3.7**	----	6.8**
7-19-77	2.7	3.9**	----	7.0**
7-26-77	2.5	3.8**	----	7.4**
8-02-77	2.6	3.8**	----	7.4**
8-10-77	2.7	4.2**	----	7.9**
8-16-77	2.8	4.4**	----	7.9**
8-25-77	3.2	4.3*	----	8.0**
8-30-77	3.5	4.6*	----	8.2**
1978				
5-02-78	3.3	3.1	3.3	3.2
5-10-78	3.0	3.0	3.1	3.1
5-16-78	3.2	3.0	2.9	3.1
5-24-78	3.6	3.8	3.8	3.4
6-06-78	4.2	4.4	4.2	3.8
6-15-78	4.8	4.8	4.7	4.2*
6-20-78	5.2	---	5.0	4.2**
6-27-78	5.2	4.8	4.9	4.4*
7-05-78	5.1	5.3	5.2	4.4
7-11-78	5.1	5.4	5.1	4.6
7-18-78	4.9	---	5.2	4.7
7-25-78	---	4.8	5.0	5.2
8-09-78	3.9	3.7	4.0	5.3*
8-16-78	---	3.4	3.4	5.5
8-23-78	2.8	3.0	3.2	5.8**
8-30-78	2.4	---	2.6	5.4**

Table 11. Continued

Date 1979	Treatment			
	Control	6 mm	12 mm	Wet
5-14-79	3.6	3.7	3.6	3.5
5-21-79	3.8	3.9	3.6	3.6
6-05-79	4.3	4.2	3.7*	3.8*
6-12-79	4.6	4.2	3.6**	3.8**
6-20-79	4.0	4.0	3.0**	4.1
6-26-79	3.6	3.4	3.0*	3.9
7-03-79	2.8	3.3	2.8	4.0**
7-11-79	2.3	2.9*	3.1**	4.2**
7-18-79	2.2	2.6	3.1**	4.3**
8-02-79	2.0	3.0**	3.3**	4.3**
8-09-79	2.0	3.1**	3.4**	4.2**
8-14-79	1.7	3.1**	3.5**	4.4**
8-24-79	1.8	3.1	3.5*	4.4**

1977 Agropyron smithii. In 1977, numbers of leaves per culm stayed within fairly narrow limits for the control and 6 mm treatments, ranging from 2.5 to 4.1 leaves for the control and 3.1 to 4.6 for the 6 mm (Table 11). These numbers are far lower than those in the wet plot. Wet plot mean culm numbers increased throughout the 1977 season. End-of-season mean number of leaves was 8.2 for plants in the wet plot, 4.6 for plants in the 6 mm, and 3.5 for plants in the control. Comparison of means for these end-of-season figures show leaf numbers for both the 6 mm and the wet treatments to be significantly larger than those in the control.

1978 Agropyron smithii. Early in 1978, mean leaf numbers were very similar for all four treatments (Table

11). Leaf numbers increased for all treatments until the middle of the season. After July 10, mean leaf numbers decreased for the control, 6 mm and 12 mm plots. The number of leaves per culm in the wet plot continued to increase through the year, reaching a maximum number of 5.7 leaves on August 23. This number was significantly greater than that of the control. End-of-season mean leaf numbers did not differ among the control, the 6 mm, and 12 mm plants.

1979 Agropyron smithii. In 1979, initial leaf numbers were similar for all four treatments (Table 11). Wet plot leaf numbers increased only slightly during the course of the year, with end-of-season mean numbers of 4.4 leaves/culm. The 6 mm and 12 mm treatments had end-of-season mean leaf numbers of 3.1 and 3.5 leaves/culm. Initial leaf numbers in the control increased during the first 3 weeks of May and after that decreased for the rest of the season. End-of-season leaf numbers for the control were 1.7 leaves/culm. All three irrigation treatments had numbers significantly higher than the control during the last half of the season (beginning in the last week of July).

1978 Bouteloua gracilis. Mean number of leaves/culm did not differ significantly among the three treatments in 1978 (Table 12). In general, the number of leaves decreased over the season.

Table 12. Green leaves/culm in Bouteloua gracilis during 1977 (start-of-season only), 1978, and 1979. Comparisons are made against the control plot only. Single asterisk (*) indicates $p < .05$, double asterisks (**) indicate $p < .01$.

Date 1978	Treatment		
	Control	6 mm	Wet
5-26-77	3.9	4.2	4.1
6-05-78	4.3	4.6	4.2
6-14-78	4.3	4.7	4.1
6-21-78	4.4	4.8	3.9*
7-03-78	4.4	4.8	3.8
7-12-78	4.5	4.4	3.9
7-26-78	3.9	3.7	3.5
8-02-78	3.6	3.7	3.6
8-08-78	3.4	3.5	3.4
8-15-78	3.1	3.1	3.2
8-29-78	3.2	3.1	3.4
<u>1979</u>			
6-13-79	4.6	4.6	4.3
6-19-79	4.4	4.6	4.5
6-27-79	4.3	4.7	4.5
7-05-79	4.1	4.7**	4.7**
7-11-79	3.9	4.3*	4.6**
7-17-79	3.5	4.0**	4.3**
8-08-79	3.3	3.5	4.2**
8-21-79	2.9	3.0	4.0**

1979 Bouteloua gracilis. This year was much drier than the previous year. Mean leaf numbers per culm decreased through the season in the control and 6 mm treatments, while the wet treatment numbers changed little

from start-of-season values (Table 12). End-of-season mean leaves/culm in the wet treatment were significantly higher than the control treatment with 4.0 vs. 2.8 leaves/culm (Table 12).

Mean Leaf Number Conclusions

Supplemental water increased the mean number of leaves per culm of Agropyron smithii in dry years. This was true for small amounts of water as well as large ones. In wet years, light addition of supplemental water did not increase the leaf numbers, but heavy irrigation did.

For Bouteloua gracilis, supplemental water increased the mean leaves/culm only if the year was dry and large amounts of irrigation were applied.

In no case was the early season leaf number morphology changed by addition of water. All plants showed the same numbers of leaves early in the spring regardless of previous water treatment. This is in contrast to Agropyron smithii culm density which showed strong interseasonal cumulative effects (Section I).

Maximum Leaf Length- Agropyron smithii

As leaf surface area is both critical to net photosynthetic gain and desiccation potential, it was anticipated that supplemental water would make the leaves of Agropyron smithii larger. To eliminate the effects of

differential rates of leaf maturation on size measurements, only leaves at maximum elongation were considered. As leaves are also expected (Robson 1973) to differ in maximum size based on their ranking in acropetal order (from the base of the plant upward), it was necessary to compare leaves which were of equivalent rank order.

Maximum lengths of leaves were calculated by scanning the records for maximum leaf lengths for leaf positions #3, #4, and #5 (Table 13). Leaves in these ranks generally were still growing at the start of the field season but had enough time before summer's end to reach maturity. In cases where insufficient numbers of undamaged leaves existed to make valid estimations for a particular rank order of leaves, the rank order was dropped from the survey.

Because leaves mature in acropetal order, in certain cases the leaf in position #3 was fully developed before treatment effects could be felt, and effects of the supplemental water are not seen. For example this was probably the case for the wet plot in 1977 (Table 13).

In 1977, the only leaf position which differed from the control plot's leaves of the same rank was position #5 in the wet plot. Its mean length was 26% longer than that found in the control (Table 13).

In 1978, leaves in the 4th and 5th positions in the wet plot were significantly longer (131% and 121% respectively) than those in the control (Table 13). The mean length of the 4th leaf in the 12 mm plot was also significantly larger. Leaves in the 6 mm plot were not appreciably larger than control leaves in any year.

Table 13. Mean maximum length (mm) of Agropyron smithii leaves subjected to four irrigation treatments. Comparisons are made against the control plot only. Single asterisk (*) indicates $p < .05$, double asterisks (**) indicate $p < .01$.

Leaf #	Year	Treatment			
		Control	6 mm	12 mm	Wet
#3	1977	143	138	-	138
#3	1978	-	-	-	-
#3	1979	111	109	101	144*
#4	1977	-	-	-	-
#4	1978	150	162	178*	196*
#4	1979	135	123	123	170*
#5	1977	119	120	-	150*
#5	1978	185	171	200	223*
#5	1979	121	122	121	195*

In 1979, only the wet plot had leaves which were larger than the control leaves. In this year, leaves at all three positions grew larger. The percentage of additional growth was of the same general order as those in previous years at 130%, 127%, and 163% longer than the control leaves.

Heavy irrigation clearly promotes larger leaves on Agropyron plants. This effect was observed in both wet and dry years. Lighter water supplements had less dramatic or negligible effects although there is some indication (1978, 12 mm treatment) that smaller amounts of water might marginally increase the size of leaves.

Mean Green Tissue per Culm

The total length of green tissue on a culm is determined by both the number of leaves on each culm and the size of those leaves. Since it has been shown that the number of leaves per culm increased as a result of increased water and that selected leaves had larger leaves when large amounts of supplemental water were added to a natural grassland- it is reasonable to conclude that the total length of green tissue per culm should also have increased as a result of adding large amounts of water.

1977. Wet plots showed dramatic changes in the morphology of Agropyron smithii culms this year (Table 14). Total length of green tissue, which is highly correlated with total photosynthetic area (Newbauer 1985), increased over the entire year (Table 14). By the end of the season, wet treatment culms had a green tissue length of 1135 mm/culm. This was 308% of the control plants at the same date. Large increases in total culm leaf length were found in the first two observations of the 6 mm and

Table 14. Green leaf tissue length (mm/culm) of Agropyron smithii 1977-1979. Comparisons are made against the control plot only. Single asterisk (*) indicates $p < .05$, double asterisk (**) indicates $p < .01$.

Date 1977	Treatment			
	Control	6 mm	12 mm	Wet
5-24-77	298	312	---	335**
6-01-77	394	378	---	435*
6-07-77	467	460	---	538*
6-15-77	417	421	---	656**
6-24-77	415	388	---	734**
6-28-77	---	---	---	830
7-05-77	334	349	---	910**
7-12-77	357	397	---	959**
7-19-77	300	420**	---	1004**
7-26-77	278	401**	---	1052**
8-02-77	279	409**	---	1068**
8-10-77	284	430**	---	1097**
8-16-77	302	455**	---	1110**
8-25-77	350	443	---	1123**
8-30-77	368	471*	---	1135**
<u>1978</u>				
5-02-78	236	198	---	284
5-10-78	272	304	221	298
5-16-78	307	191	256	323
5-24-78	397	419	385	429
6-06-78	541	548	537	588
6-15-78	681	681	712	735
6-20-78	774	---	746	793
6-27-78	805	757	812	843
7-05-78	851	856	893	905
7-11-78	881	859	896	933
7-18-78	850	---	940	980
7-25-78	---	785	890	1040
8-09-78	619	557	668	1002**
8-16-78	---	485	532	917
8-23-78	410	413	500	982**
8-30-78	328	---	372	867**

Table 14 Continued

Date 1979	Treatment			
	Control	6 m	12 mm	Wet
5-21-79	281	242	282	328
6-05-79	392	364	361	484**
6-12-79	437	386	378	530*
6-20-79	422	384	326*	607**
6-26-79	390	341	315	633**
7-03-79	310	327	301	658**
7-11-79	246	279	316	730**
7-18-79	238	255	333*	748**
8-02-79	235	301	342	716**
8-09-79	241	308	345	693**
8-14-79	192	306	354*	709**
8-24-79	205	301	361	726**

control plots. Plants in the latter two treatments had leaves which first experienced water stress greater than -0.8 MPa on 7 June and after that the mean green tissue length decreased for both these treatments. By the end of the season, control plot green leaf length was little changed from the beginning of the season and had exhibited a narrow range of values. This was also true for the 6 mm plots. Leaf length on 6 mm treatment culms, however, was greater than that on control plants by the end of the season.

1978. All four treatments showed marked increases in green tissue length for the first half of 1978- the period of abundant natural water. Water stress first exceeded -0.8 MPa on 24 July for the 12 mm, 6 mm, and control treatments. After the end of June, the wet plot culms

continued to increase their green tissue length for several weeks while the accumulation of green tissue under other treatments slowed. After 19 July and for the last half of the summer, mean culm leaf length decreased. The response of these plants to ample water resources was a rapid increase in photosynthetic area and the response to water stress was a decrease in green tissue.

In 1978, there was no significant response over the control by the 6 mm and 12 mm treatments. Wet plots showed significant responses after 1 July when water stress appeared in the other plots.

1979. In the third year of the treatment, early season increases in green tissue were identical to those of previous years. Onset of water stress was much earlier in this year, however, and for all treatments but the wet, maximum leaf length occurred on 11 June. Wet plots continued to increase green tissue until mid-July. Plants in the 6 mm, 12 mm, and control plots lost mean green leaf tissue/culm after 11 June. The rate of decrease slowed in the 6 mm and 12 mm plots by the third week in July, when culms in all three irrigated treatments had significantly more green tissue than the control.

Green Tissue Length Conclusions. Supplemental water did increase the photosynthetic area of Agropyron smithii culms. For those years in which summer rain was scarce,

large amounts of supplemental water produced culms with much greater leaf area than culms which received only natural rainfall. Smaller amounts of supplemental water had less dramatic results (Table 14).

Density Effects

Analysis of the effect of supplemental water on culm morphology is complicated by the non-uniform density which resulted from water supplements (Section I). Density has been shown to affect plant morphology (Kays 1974). Antonovics and Levin (1980 p.418) have shown that plants will respond to medium densities with a reduction in growth rate. In a study of this kind in which perturbation of the plant community occurs at many levels, it quickly becomes difficult to differentiate between effects which are the direct result of relief from water stress and those effects which are secondary to the treatment.

CONCLUSIONS

In general, the morphological changes which resulted from supplemental water confirmed the expectations which resulted from previous studies of water stress (Simpson 1981, Kramer 1969). Agropyron smithii grew taller with addition of large amounts of water (wet treatments), less so with lighter irrigation treatments. Numbers and size of leaves on Agropyron culms was increased by large amounts of water, smaller amounts had little effect. Total length of green leaf tissue on culms of Agropyron smithii was only affected by large amounts of irrigation.

Supplemental water had a much less marked effect on Bouteloua gracilis. While culm height was affected by irrigation, leaf numbers were not.

PART IV

Senescence, Emergence, and Maturation Rates in Leaves
of Agropyron smithii and Bouteloua gracilis

INTRODUCTION

Scope of the Study

A differential in the rates of leaf emergence and senescence will result in increased or decreased numbers of leaves found on a culm. Having shown that supplemental water can produce morphological changes in the number of leaves sustained on grass culms (Section III), records of leaf condition and survival were analyzed to determine relative magnitudes of the processes which resulted in the change.

Investigation of emergence and senescence also has the capacity to disclose turnover in a leaf population which might otherwise go unnoticed. Simple counts of the numbers of individuals present at a given time may answer questions of density but will tell nothing of the dynamics in the populations involved (Nobel et al. 1979). New individuals may be emerging while older individuals are disappearing and the net change in the community is zero. Without knowledge of turnover rates a dynamic community might appear static.

Both emergence and senescence have relationships to plant physiology (Hsiao 1973, Webster 1973) and may reasonably be expected to be correlated with the water

status of plants. One might wish to correlate the rates of senescence and emergence with the degree of water stress experienced by the grass plant. One might also look for a differential seasonal response in leaf emergence. Since the energy invested in leaf production at the end of the season might not have time to be repaid by the resulting increased photosynthetic production, one might expect a decrease in leaf emergence with season.

Other questions which present themselves at this juncture are whether supplemental water would delay or accelerate the developmental time of leaves.

These questions will be considered in this section.

Concepts Related to Leaf Dynamics

To view leaf emergence and senescence as independent processes occurring simultaneously within a plant, it is necessary to recognize the metameric nature of leaves. Plant growth is largely indeterminate and the major changes of plant form occur by varying the number of modular units (leaves, buds, phytomers, tillers) which make up a plant.

The practice of viewing a plant as an aggregate population of leaves has a long history (White 1979). Plant population biology as discussed by John Harper (1977) has made use of the leaf population concept to

elucidate processes (such as emergence and senescence rates) in plant biology which required this approach.

A simple model of leaf population numbers has been given by Harper (1977) which describes both the current population size as well as the turnover rate of the individual members. Here N_0 is the population size at time 0 and the subscripted variable N_{t+1} is the population size after the next unit of time has elapsed.

$$N_{t+1} = N_0 + \text{Births} - \text{Deaths} + \text{Immigrants} - \text{Emigrants}$$

In the case of leaves, with the few exceptions of vegetative cloning, either to immigrate or emigrate is to die and the equation becomes an even simpler one of births and deaths or emergence and senescence.

METHODS

To determine how the dynamics of Agropyron smithii and Bouteloua gracilis leaf populations react to supplemental water, a field study was conducted in which natural rainfall was augmented with irrigation. Leaves within the study plots were measured periodically with nondestructive methods and the degree of water stress was monitored (Figures 1 & 2). General details of the experiment have been described in the General Introduction under the sections "The Study Site" and "Irrigation Regimen".

Rates of leaf emergence were calculated by counting the number of leaves which had emerged since the last observation and scaling the rates to the common unit of number of leaves emerged per 100 culms per week. Leaf senescence rates were calculated in an analogous fashion. Mean weekly rates of leaf emergence and senescence for a particular year were calculated by averaging the scaled weekly rates over a given field season.

To correlate the rates of leaf emergence and senescence with plant water status it was necessary to pair the leaf water potential observation with the interval over which the emergence and senescence rates were affected. Because reported leaf emergence and senescence data was the result of processes which had happened since the previous

observation, leaf water potential data for a given date was matched with the following emergence or senescence date. In this way it was possible to test leaf water potential as a predictor of leaf population dynamics.

Tests of seasonal trends in emergence and senescence rates were made by segregating observations for the months June, July, and August and comparing the mean rates measured in these periods.

The time it took a newly emerged leaf to reach it's maximum length was defined as the leaf's juvenile period. To measure this interval: 1.) A date was selected which was early enough in the year that leaves appearing then could reach maturity. 2.) Data on all leaves which emerged at that date were scanned, and the Julian date at which the leaf was first recorded as being present was subtracted from the last date it showed growth. This interval was called the juvenile period of the leaf. Use of a particular cohort of leaves in these calculations was necessary to remove the possible confounding effects of season and weather on the duration of the elongation process.

Leaf condition measurements, which form the basis of the leaf emergence and senescence rates, were made for both Agropyron smithii and Bouteloua gracilis. Leaf length measurements, which form the basis for the leaf maturation calculations, were made only for Agropyron plants.

RESULTS

Mean seasonal emergence and senescence rates will be discussed first, comparing years, treatments and net change brought about by these two opposing processes. Second, two factors which may influence senescence and emergence rates, seasonal effects and water potential, are considered. Finally, the duration of two phases of a leaf's existence: 1.) the time from first emergence until cessation of expansion, and 2.) the time from cessation of growth until senescence, will be contrasted among irrigation treatments.

Seasonal Averages of Emergence
and Senescence Rates

Emergence and senescence rates were averaged over the entire field season for each treatment. By doing this one may show the mean rate of leaf production and leaf death in each treatment for each year. Leaf turnover was prorated to compensate for the uneven time elapsed between observations. The rate variance was calculated as a binomial distribution of plants which produced (or lost) leaves since the previous observation.

Comparison of Treatments. Comparison (Student's t) of irrigated seasonal means with the control could not show

significant differences in emergence or senescence rates in any instance for either Agropyron smithii or Bouteloua gracilis (Table 15 and 16). This result was unexpected in light of the significant differences between treatments shown by mean leaf numbers in Section III.

Table 15. Mean weekly leaf emergence and senescence rates for Agropyron smithii under four different irrigation regimens in the summers of 1977-1979. Rates are calculated as the mean number of leaves emerged or senesced for 100 culms in a one week interval. Difference between the two rates is given.

<u>24 May-30 Aug. 1977</u>			
	Emergence	Senescence	Difference
Control	18.2	22.0	-3.8
6 mm	23.4	18.2	+5.2
12 mm	----	----	----
Wet	47.2	14.3	+32.9
<u>3 May-30 Aug. 1978</u>			
	Emergence	Senescence	Difference
Control	32.7	34.7	-2.0
6 mm	36.7	40.6	-3.9
12 mm	35.2	40.8	-5.6
Wet	43.7	36.2	+7.5
<u>14 May-24 Aug. 1979</u>			
	Emergence	Senescence	Difference
Control	18.2	40.6	-22.4
6 mm	16.5	27.9	-11.4
12 mm	17.2	22.1	-4.9
Wet	32.1	26.9	+5.2

Table 16. Mean weekly leaf emergence and senescence rates for Bouteloua gracilis under three different irrigation regimens for the years 1978 to 1979. Rates are calculated as the mean number of leaves emerged or senesced for 100 culms in a one week interval. Difference between the two rates is given.

<u>5 June-29 Aug. 1978</u>			
	Emergence	Senescence	Difference
Control	17.0	30.0	-13.0
6 mm	16.4	30.5	-14.1
Wet	22.3	36.5	-14.2

<u>13 June-21 Aug. 1979</u>			
	Emergence	Senescence	Difference
Control	13.5	34.7	-21.2
6 mm	17.2	34.3	-17.1
Wet	29.0	31.5	-2.5

Comparison of Years. Wet 1978 generally showed the highest leaf emergence rates at both the Agropyron and the Bouteloua field sites. The single exception was the wet treatment rate in that year, which was slightly lower than the 1977 rate. Dry 1979 exhibited the lowest emergence rates. Given the relative natural moisture levels of these two years, this is an indication of a positive correlation between water and emergence rates even though comparison of irrigation treatment seasonal means could prove no such correlation.

Senescence rates showed no comparable relationship with natural rainfall. The year with the lowest rate was 1977 for Agropyron smithii, while wet 1978 and dry 1979 had very similar leaf death rates. Bouteloua gracilis also had senescence rates which were very similar in both 1978

and 1979. Within each year, senescence rates varied less among the treatments than did the emergence rates.

Difference Between the Two Rates. The net result of the actions of emergence and senescence may be seen in the "difference" column of tables 15 and 16. Agropyron smithii wet treatments in all years had a net increase in leaf numbers over the start-of-season value (Section III). It can be seen from table 15 that this increase was due to a higher mean emergence rate. In 1977, the first year of irrigation treatments and a time when culm density was still increasing rapidly in the wet plot (Section I), the difference between emergence and senescence was larger than in any other year.

For other treatments in the Agropyron smithii plots, with one minor exception, mean senescence rates were higher than emergence rates. The plants lost leaves more rapidly than they produced them. This is confirmed by the net intraseasonal decline in mean leaf numbers per culm shown in Section III.

Bouteloua gracilis plants lost more leaves in the course of the summer than they gained for both years studied and in all treatments.

Seasonal Influence on Leaf Emergence
and Senescence Rates

Although there was a large weekly fluctuation in both emergence and senescence rates, preliminary graphical analysis (not shown) indicated a general seasonal decline in both rates for both species. In order to document this trend, rates from all treatments were grouped by month and the monthly rates were compared. In order to prevent complication by water stress effects, comparison of mean monthly emergence rates (Table 17) was made using only those observations of minimally stressed plants which had water potentials between 0 and -0.49 MPa.

Table 17. Mean monthly leaf emergence rates for Agropyron smithii (1977-1979) and Bouteloua gracilis (1978-1979). Observations are of plants with water potentials of 0-0.49 -MPa. Means within each row with different letters indicate significant differences with $p < .05$.

Species	June	July	August
<u>Agropyron</u>	51.8 A	30.8 B	19.6 B
<u>Bouteloua</u>	35.1 A	9.8 B	17.0 B

Both species had the highest rate of leaf emergence in June. The rate dropped significantly in July and rates in July and August could not be differentiated.

Leaf senescence rates for both species were also grouped by month in a manner analogous to the emergence rates (Table 18). These means did not seem to have come

from different populations so no significant effect of seasonal trend could be shown.

Table 18. Mean monthly leaf senescence rates for Agropyron smithii (1977-1979) and Bouteloua gracilis (1978-1979). Observations are of plants with water potentials of 0-0.49 -MPa. Differences between means within rows did not have significance levels with $p > .05$ in all comparisons.

Species	June	July	August
<u>Agropyron</u>	32.4	40.4	22.8
<u>Bouteloua</u>	33.4	35.4	26.3

Effect of Water Potential on Emergence and Senescence Rates

Graphical Analysis of Emergence. Irrigation

treatments were shown earlier to affect emergence rates (see above). For this reason, an examination of the specific correlation of plant water stress and leaf dynamics was desirable. Figures 5 and 6 illustrate the relationship between leaf emergence and plant water potential for Agropyron smithii and Bouteloua gracilis. Observations have been grouped by month to avoid confounding effects of water and season on leaf dynamics.

For both species, leaf emergence never took place at a high rate when water stress was high. When water stress was low (0-1.0 MPa) leaf emergence rates showed a broad range of values (Figure 5 and 6).

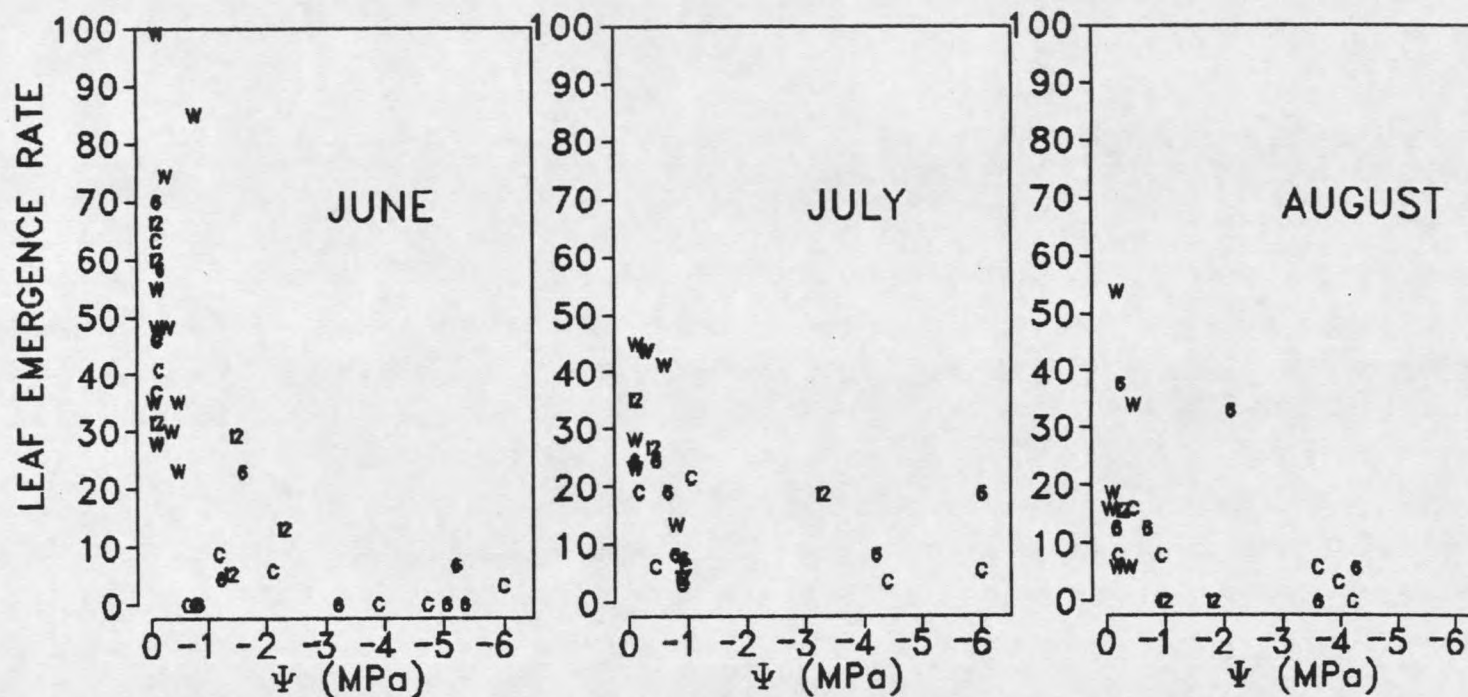


Figure 5. *Agropyron smithii* leaf emergence rate vs. water potential. Data from 1977 - 1979 are pooled. Emergence rate is calculated as the number of leaves born in one week per 100 culms. Water potential applies to the period during which emergence was taking place.

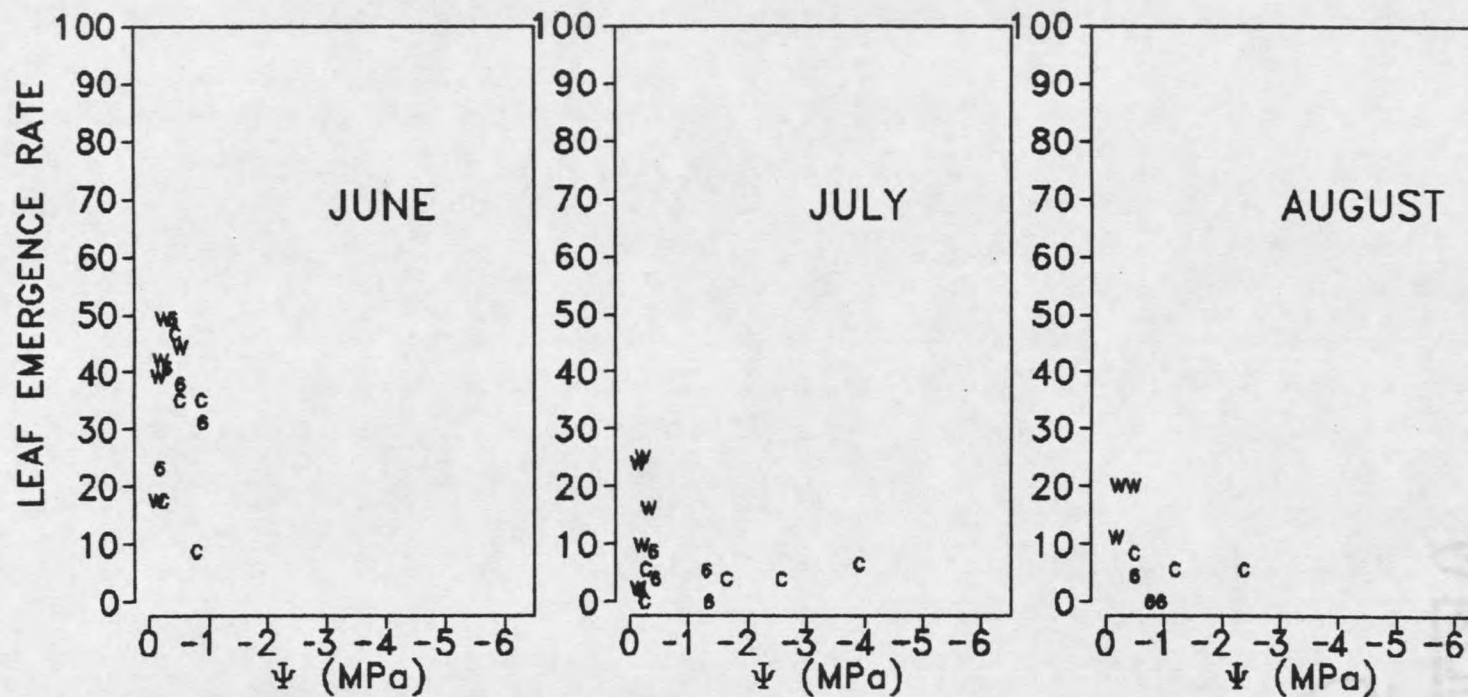


Figure 6. *Bouteloua gracilis* leaf emergence rate vs. water potential. Data from 1978 - 1979 are pooled. Emergence rate is calculated as the number of leaves born in one week per 100 culms. Water potential applies to the period during which emergence was taking place.

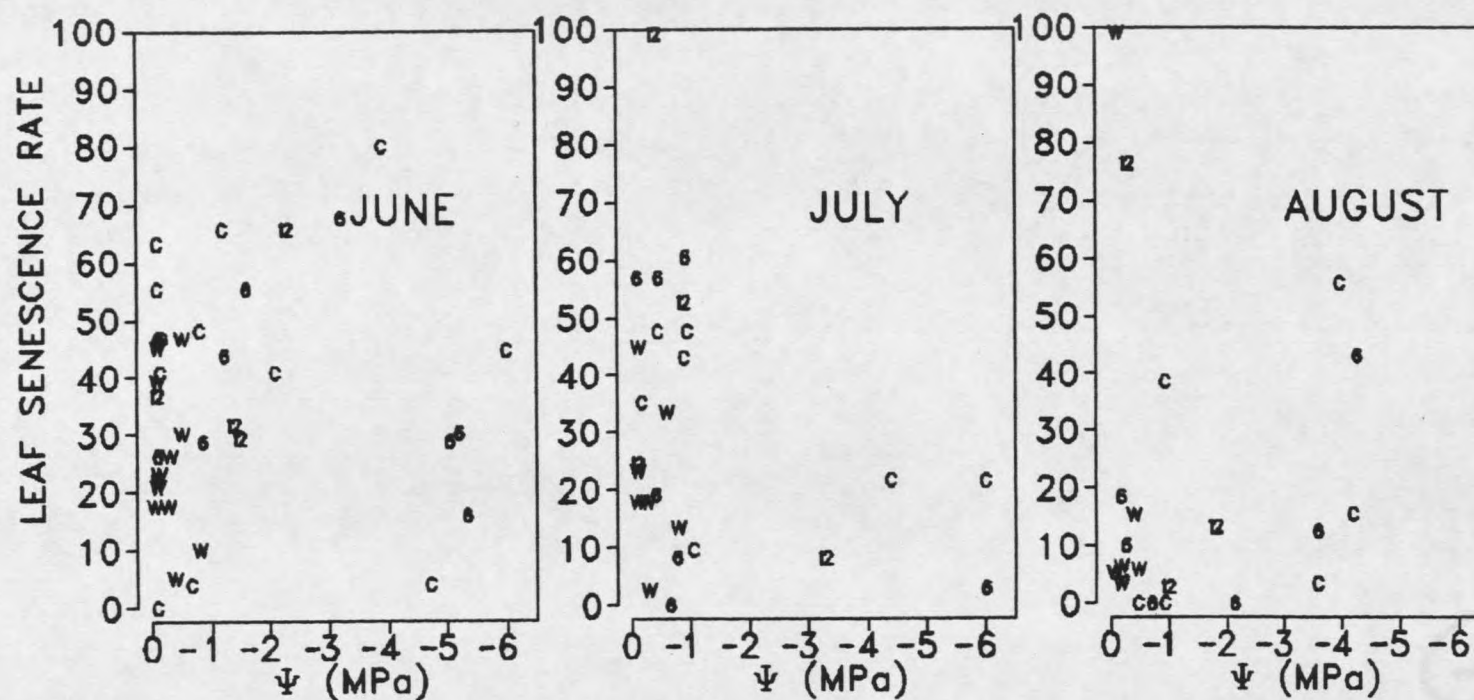


Figure 7. *Agropyron smithii* leaf senescence rate vs. water potential. Data from 1977 - 1979 are pooled. Senescence rate is calculated as the number of leaves which died in one week per 100 culms. Water potential applies to the period during which senescence was taking place.

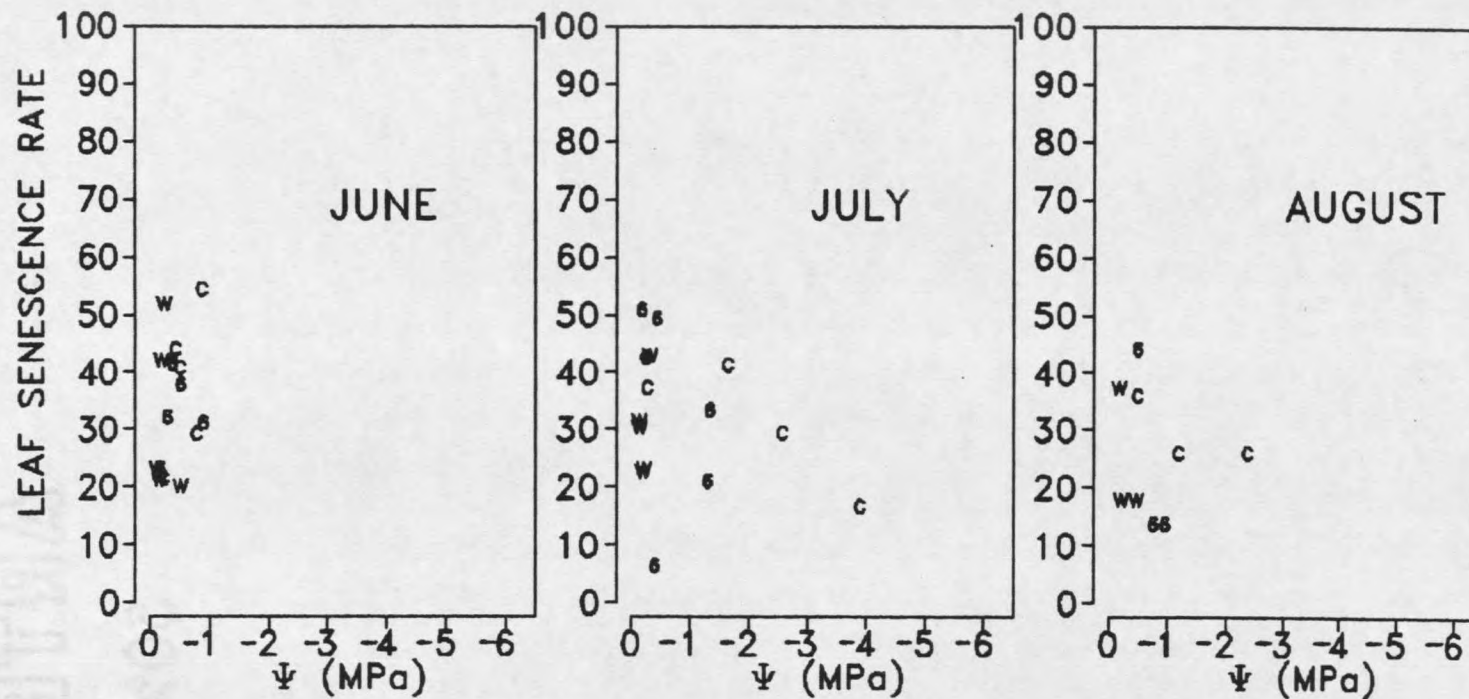


Figure 8. *Bouteloua gracilis* leaf senescence rate vs. water potential. Data from 1978 - 1979 are pooled. Senescence rate is calculated as the number of leaves which died in one week per 100 culms. Water potential applies to the period during which senescence was taking place.

Graphical Analysis of Senescence. Grouping senescence observations by month and pooling all treatments, figures 7 and 8 show there was little correlation of water stress with senescence rate for either Agropyron smithii or Bouteloua gracilis. Leaf senescence rates showed much less correlation with water stress than did emergence. While high senescence rates were expected when plants were highly water stressed, this was not found consistently. High rates of senescence took place at all levels of water stress for both species.

Statistical Analysis. To lessen the confounding effect of season on the relationship between water potential and leaf dynamic rates, only data from June were used for statistical analysis. Tables 19 and 20 compare mean emergence and senescence rates at for Agropyron smithii and Bouteloua gracilis at three levels of water stress.

Table 19. Mean June leaf emergence and senescence rates for three levels of water stress in Agropyron smithii. Rates are calculated as leaves emerged (or senesced) per 100 culms in a one week period. Different letters within the same column indicate means with a probability of belonging to the same population at $p < .05$.

Water Potential (MPa)	Emergence rate	Senescence rate
0 to $-.49$	51.8 A	27.7 A
-0.5 to -1.99	19.5 B	26.4 A
< -2.0	3.2 B	27.2 A

Table 20. Mean June leaf emergence and senescence rates for three levels of water stress in Bouteloua gracilis. Rates are calculated as leaves emerged (or senesced) per 100 culms in a one week period. Different letters within the same column indicate means with a probability of belonging to the same population at $p < .05$.

Water Potential (MPa)	Emergence rate	Senescence rate
0 to -.19	26.7 A	22.6 A
-0.2 to -.49	39.4 A	38.9 B
-0.5 to -.99	32.0 A	32.1 AB

A comparison of means confirms conclusions of the graphical analysis for Agropyron smithii. Although the emergence rates were variable at high water potentials (0 to -0.49 MPa) the mean was significantly higher for this class. Between lower water potential classes (-0.5 to -1.99 MPa and below -2.0 MPa) effect of water stress on emergence was not statistically differentiable. Senescence rates did not differ statistically among the three levels of water stress.

The Bouteloua gracilis study had a narrower range of water potential values to be matched with observed emergence rates than Agropyron smithii study had. With the values available, no effect of water stress on leaf emergence could be shown statistically. Senescence rates were significantly higher in the -0.2 to -.49 MPa range of water potentials than the more stressed -0.5 to -.99 MPa range. No explanation for this unexpected observation is offered.

Leaf Juvenile Period

The juvenile period of a leaf was defined as the time between a leaf's emergence and the time when the leaf ceased to grow longer. Because this period is expressed in days and measurements were taken at approximately weekly intervals the reader should recognize the possibly overstated precision of these figures.

At any given moment there were rarely more than two or three immature leaves on a single culm. Leaves tended to be produced sequentially; each leaf at least nearing attainment of it's ultimate size before a new leaf emerged.

The hypothesis that supplemental water would decrease the time required for leaf elongation is supported by the results of 1977 (Table 21). The control plants required the longest time for leaf development, the 6 mm plants took less time than those in the the control plots, and the wet treatment plants took the least time of all.

Table 21. Mean juvenile period (days) for leaf cohorts of Agropyron smithii.

Emergence date	Treatment			
	Control	6mm	12mm	Wet
7 June 1977	56	44	----	17
15 June 1978	18	17	21	19
5 June 1979	16	27	27	19

Data from the year 1978, which had above normal rainfall in the spring, are also consistent this hypothesis. Plants in all treatments took roughly the same time for their leaves to mature, 18 days. This interval is also roughly the same as that for the 1977 wet treatment plants, 17 days.

Data from 1979 tends to refute the development rate hypothesis. With weather conditions in this year dryer than normal, control plants had the shortest mean juvenile period observed. Plants in the 6 mm and 12 mm plots had leaves with the longest mean juvenile period, while plants in the wet treatment had an intermediate maturation time. I have no explanation for this discrepancy, and on the basis of the conflicting results, the hypothesis that supplemental water will decrease leaf juvenile intervals cannot be accepted.

Leaf Adult Interval

The interval between the moment when a leaf reaches its maximum length and the moment at which the leaf has senesced was defined as the leaf's "adult phase". The hypothesis was advanced that plants which received supplemental water would have leaves which had longer adult phases. For example, leaves of non-water-stressed plants might persist until the first frosts while plants with stress might shed leaves to conserve water. This wet

plot culm behavior would be possible only as long as culm density was low enough to prevent lower leaves from being shaded out. If the culm density became higher, leaf adult phase would be shortened due to shading of the leaves.

To test this hypothesis on Agropyron smithii, it was necessary to use leaves of the same rank order, as was done in Section III for maximum leaf elongation analysis. Robson (1973) demonstrated a possible relationship between leaf rank and leaf adult duration in the perennial ryegrass Lolium perenne. If leaves of different rank were grouped the factor of leaf rank would confound analysis of adult period. Unfortunately this restriction reduced the number of leaves available for consideration to such a small sample size that analysis was deemed unfeasible.

DISCUSSION

Because both Agropyron smithii and Bouteloua gracilis produce new leaves only at the apical meristem, leaf emergence was calculated on the basis of a standard number of culms producing a variable number of leaves in a standard interval. One might calculate leaf senescence rates differently, reasoning that those culms (and treatments) with more leaves would also have more leaves which were at risk of death and thus be biased towards higher senescence rates. This would be inappropriate for these grass species since virtually without exception, leaves died in order - from the bottom up. This allows calculation of senescence rates to be exactly analogous to that for emergence.

When comparing the mean weekly rates of leaf dynamics between years, interpretation of leaf emergence and senescence dynamics is complicated by both culm density variation and seasonal changes. First, because of the higher culm density which developed as the irrigation progressed (Section I), the high rate of leaf production shown by plants in the wet plot in 1977 could not be maintained in 1978 even though conditions were more moist. Second, due to different seasonal rainfall levels, plants

in unwatered plots are expected to perform differently in wet and dry years.

For both species, leaf emergence rates were positively correlated with low plant water potential. This was expected because water stress inhibits many of the functions required by plant growth (Hsio 1973). The absence of even moderate emergence rates when water stress was high shows that water is a true limiting factor whose absence limits the ability to produce new leaves. The wide range of emergence rates which accompanied low water stress indicates that water is not the only limiting factor.

A decline in emergence rate with season was expected on the basis of plant energetics. Energy investment in leaf production at the end of the year makes little evolutionary sense. Conditions then are less favorable for photosynthesis due to xeric conditions and the increased possibility of tissue killing frost minimizes the potential for return on the energy investment.

That leaf senescence was not correlated with season can also be explained in terms of plant energetics. The energy required to produce a leaf is undoubtedly greater than the energy required to let the leaf wither. Once the investment of energy required for leaf synthesis is expended, it is reasonable that a plant might allow the leaf to remain green as long as the leaf can produce a net

energetic surplus. Consideration of the anatomy of grass plants supports this conjecture in that grass leaves lack the abscission layer used by many angiosperms to remove leaves from the main structure of the plant.

CONCLUSIONS

Under non-water-stressed conditions, leaf emergence was highly correlated with season for both Agropyron smithii and Bouteloua gracilis. Emergence rates in June were higher than those found in the rest of the season. Leaf senescence rates were not correlated with season.

Emergence rates were correlated with plant water potential for Agropyron smithii, but were not correlated for Bouteloua gracilis. The wide range of emergence rates found when the plants had plenty of water suggests that several factors other than water stress influence this process. When water stress was high emergence rates were always low, as expected if water were a limiting factor. Leaf senescence rates were no higher under dry than wet conditions.

The time required for a newly emerged leaf to elongate fully was shortened by addition of supplemental water in 1977 but was not in 1978 and 1979. No explanation for the discrepancy is offered, but this negates the hypothesis of accelerated leaf development.

Data from this study did not permit comparison of the duration of the mature phase of leaf life history among irrigation treatments.

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APPENDICES

APPENDIX A

Field Observations

The following descriptions of methods pertain to details of field observations.

Early in the field season, representative culms (20 for Agropyron smithii and 30 for Bouteloua gracilis) were selected for observation and marked. Due to the clonal nature of these plants it is impossible to ascertain the genetic diversity represented by this sample. As these culms were all roughly the same size and possessed of roughly the same number of leaves early in the season, I have assumed them to be of the same age. Thus all leaf measurement samples are based on an early season cohort of culms. This same cohort was followed for the rest of the season.

Plants were observed at approximately one week intervals during the years 1977, 1978, and 1979 for Agropyron smithii, 1978 and 1979 for Bouteloua gracilis. Early in the season, individual culms were selected as being representative of the stand, tags were inserted at their base and their development was followed from roughly mid May until 30 August. These culms were spaced down the middle of the treatment row and spaced approximately 75 cm apart.

Leaves on each culm were evaluated for physical condition and length. Each leaf was also assigned a number designating the leaf's relative position on the culm, with "#1" being the leaf closest to the ground and counted acropetally in ascending order. In this way, subsequent observations could be made on the same leaf for the entire season. Leaf length was measured with a ruler and was defined as the distance from the ligule of the lower leaf to the outstretched tip of the measured leaf, held along the culm axis. Culm height was measured by lifting the grass away from the ground and measuring the distance between the ground and the tip of the most outstretched leaf.

Collection of this field data was done principally by John Newbauer, who was assisted by various personnel on the weather modification project.

Field sheets were transcribed to a computer readable format with alpha numeric codes used to designate leaf condition. (Appendix B)

Approximately three or four weeks into the field season, specified leaves (usually leaf #3 or #4) of these plants were trimmed at an angle in order to facilitate identification of the other leaves based on their relative position along the culm. These leaves have been marked with an "X" in the third column of their four character condition code. The first appearance of the "X" designates the date at which the cut was made. Once cut, the leaf continued to be marked with the "X" to indicate that the leaf was altered.

Each data file represented a year's observations for a species-treatment. After entry was complete, data were proofread for transcription errors by reading from the original field sheets and checking them against the computer print out.

Further data checking was performed by sorting the data by plant number and running a "transition error" checking program (CHKDAT) on the sorted data. This program read evaluations of leaf conditions for paired dates. If the data revealed that on successive dates the leaf changed condition in a manner that was deemed not to be obviously part of the naturally occurring maturation process of leaf development, the pair of observations was written to a file for later evaluation and correction.

The corrections were made on a case by case basis, using the following assumptions.

- 1.) Leaves were not able to shrink except as a result of damage and lost tissue.

- 2.) A leaf once lost must remain lost.

- 3.) A leaf once turned brown was not able to regenerate.

- 4.) In a series of observations, if a leaf turns brown, then appears to turn green again, the observation with the brown designation is the suspect one.

- 5.) If a leaf's length measurement was deleted for some reason, its condition designation could be allowed to stand. The inverse was not allowed to occur.

Certain plants were replaced during the course of the field season, usually during the first three observation dates. In cases where notes were provided stating that marking tags were missing (eg. rodent damage to tags) past information on these plants was discarded and the newly marked plants were put in their place with the assumption that the new plants were alive early in the season, but with unknown condition. The newly marked plants have a "B" placed after the plant number.

Certain plants died early in the field season and were replaced with new plants. The dead plants were kept in the sample population, designated "DEAD", and an "A" was placed after the plant number. The new plant, as in the case with the rodent damaged tags, was given the

suffix of "B" after its number and assumed to be alive early in the season but with unknown condition.

Some plants were replaced for reasons that remain unclear. If the plant's previous condition was healthy, it was assumed not to have died, and was simply removed from the sample. Its replacement was given the suffix "B" and assumed to be alive on the date of the season's first observation. If the plant did not appear healthy, but was replaced without explicitly being called dead, death was presumed. If several leaves were marked as green but damaged, death was assumed to occur one observation following the introduction of the new, remarked plant. The dead plant was given the suffix "A" and the replacement "B" as in the previous situations.

APPENDIX B

Coding of Observations and Data Files

The following codes were used on the field sheets. In cases where the code was modified during computer data entry, the new code is indicated with an "=" symbol.

- A- developing leaf in the highest position on culm.
- AB- mature leaf in the highest position on culm
- AC- developing leaf in highest position with damage in excess of 2 mm.
- ACL- developing leaf in highest position with a damaged tip which has been lost
- FH=F- Flag leaf
- CF- damaged flag leaf.
- ABC- mature leaf in highest position that was damaged.
- B- mature leaf.
- CLF- flag leaf with a damaged tip that has been lost.
- C- leaf with more than 2 mm damage.
- CL- leaf that has lost more than 2 mm from tip.
- D- yellow leaf. -
- Red=D- yellow leaf.
- E- leaf more than 75% brown.
- F=G- grey leaf.
- L- leaf that has become lost.
- H- seed head.

Leaves were assigned the following character codes to describe their condition. No other codes are possible in the data set. To verify that this was in fact the case program CHKSYMB was run on all the data files to verify that no other symbols were used. For some cases where the height of seed heads were available from the Bouteloua files the height was recorded in mm directly following the "H" symbol.

- "A" "- green developing leaf in the highest position on the culm.
- "F" "- flag leaf, always in the highest position on culm
- "CF" "- damaged flag leaf
- "EF" "- flag leaf over 75% brown
- "CLF" "- flag leaf with more than 2 mm lost from tip
- "AB" "- green mature leaf in highest position on culm
- "ACL" "- green developing leaf in highest position with more than 2 mm lost from tip

"ABC "- green mature leaf in highest position with more than 2 mm damage
 "ABCL"- green mature leaf in highest position with more than 2 mm damage on tip that has been lost
 "B "- green mature leaf
 "CL "- leaf that has lost more than 2 mm from tip
 "C "- leaf with damage done to it
 "G "- gray leaf
 "E "- leaf more than 75% brown
 "D "- yellow or red leaf
 "L "- lost leaf
 "B X "- green mature leaf that has been clipped for marking
 "C X "- damaged leaf that has been clipped for marking
 "CLX "- leaf with damaged tip that has been clipped
 "D X "- yellow leaf that has been clipped
 "E X "- brown leaf that has been clipped
 "L X "- lost leaf that has been clipped
 "H "- seed head
 "? "- leaf with unknown condition, might not even exist, missing data
 "? X "- leaf with undetermined condition that had been clipped in past

The data were entered from field notes onto computer disks in 20 data files.

1977	1978	1979	1981
ASCN77.DAT	ASCN78.DAT	ASCN79.DAT	ASCN81.DAT
AS6M77.DAT	AS6M78.DAT	AS6M79.DAT	
ASWT77.DAT	AS1278.DAT	AS1279.DAT	
	ASWT78.DAT	ASWT79.DAT	
		ASFC79.DAT	
		ASFW79.DAT	
	BGCN78.DAT	BGCN79.DAT	
	BG6M78.DAT	BG6M79.DAT	
	BGWT78.DAT	BGWT79.DAT	

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