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
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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/m 2), 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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Kurt William Swingle

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Date 25 November 1986

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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/m^2), 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 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.

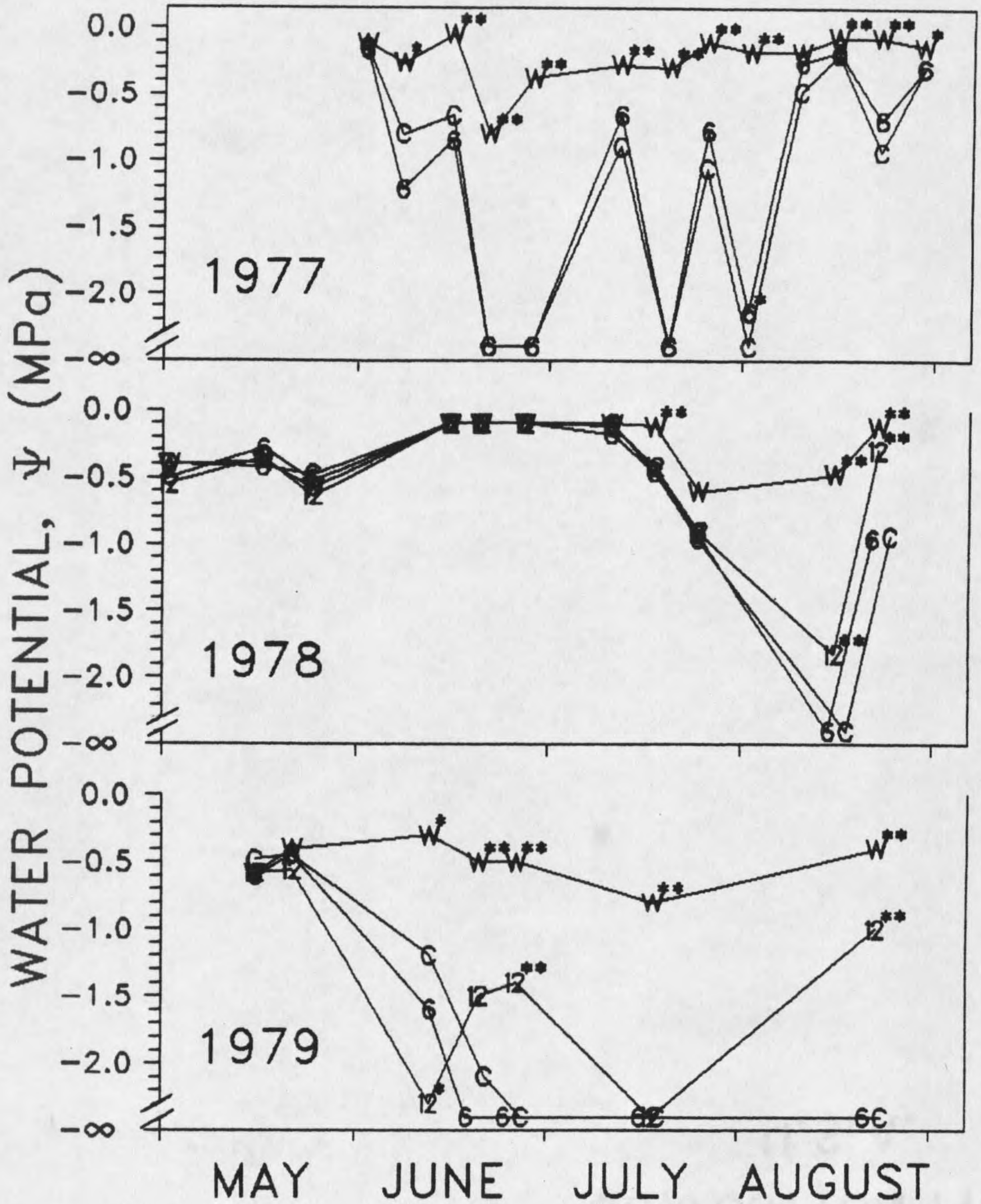

Figure 1. Agropyron smithii water potentials 1977 - 1979. The four irrigation treatments are: control (C), 6 mm (6), 12 mm (12), and wet (W). Points are means of five Scholander pressure bomb measurements. Significance of differences from the control on a given date are indicated by single ($p < .05$)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

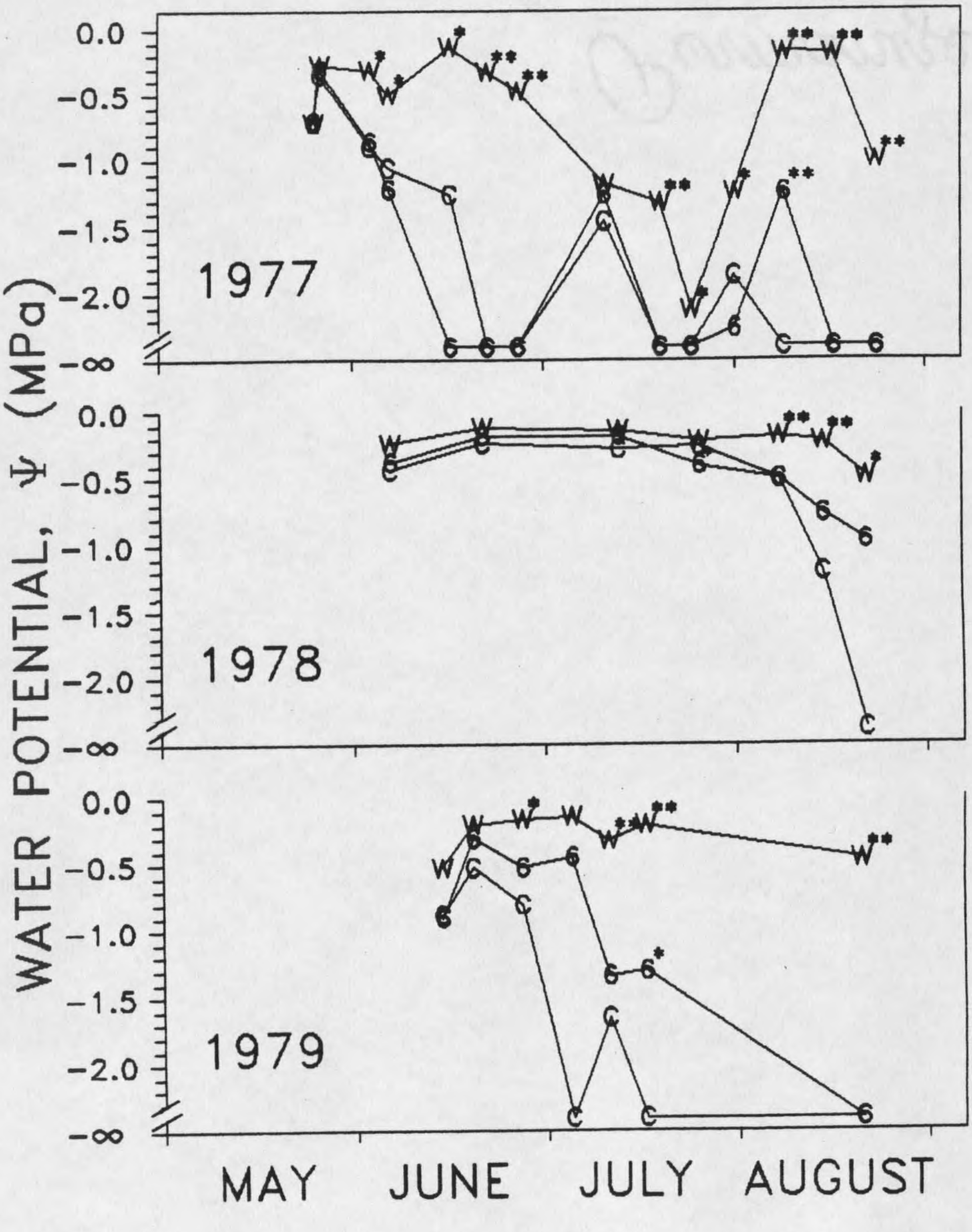

Figure 2. Bouteloua gracilis water potentials 1977 - 1979. The three irrigation treatments are: control (C), 6 mm (6), and wet (W). Points are means of five Scholander pressure bomb measurements. Significance of differences from the control on a given date are indicated by single (p <.05) and double (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: 1977-1985[1].

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 $\pm$1.9 S.E. for the control plot, 25.5/quadrat $\pm$2.1 S.E. for the 6 mm plot, and 26.3/quadrat $\pm$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 $\leq$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/m^2. 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.