Growth response of Agropyron smithii individuals to increased summer water availability
by John Joseph Newbauer

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

Abstract:
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JOHN JOSEPH NEWBAUER, III

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John Joseph Newbauer, III

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VITA

John Joseph Newbauer, III was born November 10, 1943 in Washington, D.C. His father is John J. Newbauer, Jr. and his mother, Eleanor W. Newbauer. Following graduation from Miller School of Albermarle, Miller School, Virginia, in 1963, he moved to Whitefish, Montana, where he met and married his wife, Sydney L. Newbauer in January 1965. He received a Bachelor of Science degree in Zoology from Montana State University in June 1973. He has worked as a Range Biologist for the Montana Department of Natural Resources and Conservation on the High Plains Experiment in Miles City, Montana since 1974. He began Graduate studies at Montana State University, in the Department of Biology, winter 1980.

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ABSTRACT

Four irrigation treatments -- 0, 6, 12, and approximately 25 mm/week -- were applied to a homogeneous stand of Agropyron smithii to determine the response of individual plants to differences in water availability. Sigmoid growth curves were observed. From these and records of green leaf area, unit leaf rates for major growth stages were calculated. Across treatments these averaged 78, 32, 4, and 7 $mg.dm^{-2}.day^{-1}$ for early-rapid-growth, peak-of-green, early-quiescent-period and season's end, respectively. Aboveground production of individual plants read from growth curves averaged 156, 151, 150, and 307 mg in dry 1979 and 301, 209, 431, and 343 mg in wet 1978 in the 0, 6, 12, and 25 mm treatments respectively. Replacement of unit leaf rates with estimated photosynthetic rates suggested that belowgrowth production was at least half and probably not much more than twice aboveground production. Production seems to be controlled both by water stress--with slowing of growth at -5 bars and halting at -20 bars--and by another seasonally correlated factor, perhaps daylength.

INTRODUCTION

Agropyron smithii ranges from Alberta and British Columbia south to Texas and Arizona (Hitchcock 1950) and is a dominant grass in 437,000 km^2 of the North American Great Plains (Kuchler 1964). It is a major range grass in the northern and central Great Plains and is used for early pasture, hay, and erosion control (USDA 1972). Its importance east of the Mississippi has been increased by agricultural planting (Hitchcock 1950). Interest in its management is therefore high.

I have examined the effects of water availability on the performance of *Agropyron smithii* because the manager might modify water availability by a variety of processes including cloud seeding (Hess 1974) or reallocation of water by pitting, water spreading, or irrigation (Valentine 1980). Detailed measurements of *Agropyron smithii* growth allowed me to describe the seasonal pattern of above- and below-ground growth, the control of that growth by water availability and perhaps photoperiod, and the growth responses to treatments bracketing those that might be achieved by irrigation or cloud seeding: repeated supplementation of rainfall to 6 mm per week, 12 mm per week, or at least 25 mm per week.

LITERATURE REVIEW:

EFFECTS OF WATER STRESS ON PLANT PERFORMANCE

The growth of native forage species in the northern Great Plains is often limited by lack of water. The growth process is the most sensitive of plant processes to moisture stress (Acevedo et al. 1971; 1979; Haiao 1973; Fischer and Hagan 1965). Among the first effects of plant water stress are reduction in shoot and leaf growth (Hsiao 1973). Brown (1977) and others have reported that a continuing decline in plant water potential (ψ_p) causes a substantial reduction in respiration (Henckel 1964), carbon translocation (Hsiao 1973; Henckel 1964), cytokinin titer (Itai and Vaadia 1971), and an increase in abscisic acid level (Ackerson 1980). When water stress becomes severe, proline accumulation occurs (Haglund 1980; Stewart 1978) and CO_2 assimilation ceases (Hsiao 1973). Senescence induced by drought may become visible at severe water stresses. If water is added to the system after severe stress, growth may resume, but it will never return to the rates of unstressed plants (Noggle and Fritz 1976; Hsiao 1973; Fischer and Hagan 1965; Acevedo et al. 1971).

Translocation of photosynthates continues under water stress (Wardlaw 1974) and is primarily to below-ground portions of the plant (Sosebee and Wiebe 1971; Moser 1977). The storage of resources in perennating organs (roots and crowns) allows the plant to recall resources for growth when moisture conditions improve. During moderate water stress photosynthate accumulates in the leaf -- or in other portions of the plant -- and, since accumulation occurs, growth may be more vigorous for a short time after a period of water deficiency than before (Boyer 1970). Translocation to storage depots is generally most active in the fall and these will be drawn on during either fall regrowth or in initiation of spring growth (Trlica 1977). Carbohydrate reserves therefore show a significant decline during spring growth, with the extent and duration of the decline differing among species (Trlica 1977). For example, using ^{14}C techniques in _Phleum pratense_, Balasko and Smith (1973) found that at initiation of stem elongation, mobile carbohydrates were found primarily in roots and leaves; at flowering, the stems and inflorescences contained most of these carbohydrates; and at anthesis, stems and roots contained 73% of the labeled soluble carbohydrates. The results of such transport should be observable as changes in the relative masses of plant parts. Sims and Singh (1978a) report that, in a variety of grasslands, crown biomass decreased in the early season period of initial growth, increased thereafter, and peaked after the live shoot biomass peaked.

Generally, moisture stress is the dominant environmental factor affecting photosynthetic rates in semi-arid regions (Moore 1977). Photosynthesis is less sensitive to initial reductions in $_p$ than is leaf elongation (Fischer and Hagan 1965; Acevedo et al 1971) but it is severely inhibited with continued declines in water potential (Boyer 1970). The photosynthate produced is transferred in a prioritized manner to 1) initiation and development of leaves, 2) increase in the dry weight of shoots and elongation of internodes, and 3) accumulation of carbohydrate reserves (Begg and Wright 1964). The carbon allocation pattern changes with phenological development and with root and rhizome growth (Moser 1977).

Any influence that slows the growth rate might be expected to delay the onset and reduce the intensity of competitive stress among plants (Harper 1977). In addition to various environmental factors, age of the plant and time of year may affect the growth rate. The juvenile plant is capable of exponential increases in size, but as it matures the growth rate declines (Leopold 1975). Dahl and Hyder (1977) suggest that the end of the juvenile stage can only be defined by the development of spikelet buds and that the differentiation to reproductive status is preceded by a rapid elongation of the shoot apex.

MATERIALS AND METHODS

Site and Plot Description. The study site was a homogeneous stand of *Agropyron smithii*, located on an alluvial fan of Kobar Silty Clay Loam soil. The USDA/SCS classified the soil as a Brollic camborthid fine, montmorillonitic. The texture is a silty clay loam through the B_{3Ca} horizon at 41 cm; loam through the C_2 horizon at 84 cm; and very fine sandy loam in the C_3 horizon between 84 and 152 cm. The site has a slope of approximately 2% and a northerly aspect. It is located on the U.S. Livestock and Range Research Station, Miles City, Montana (latitude 46°21'15" N, longitude 105°55'00"W). A detailed description of the study site and the experimental plots is given by Weaver et al (1981).

Water treatments on four experimental plots were: control--no rainfall augmentation throughout the study period; six millimeter--a minimum of 6 mm . wk^{-1} guarantee; wet--plots in which the soil moisture at 25 and 75 cm was maintained between 0 and -2 bars. The low water stress condition could generally be maintained with 25 mm . wk^{-1} additions. Irrigations occurring between 1 May and 1 September are summarized in Figure 2 (p. 28).

Irrigation water was applied with sprinklers located approximately 50 cm above the ground surface. Water applications were made between 0300 and 0900 MDT to minimize evaporation and wind effects on water distribution. Irrigation was halted when winds exceeded 13 cm . sec^{-1} to avoid an irregular distribution pattern and unacceptable overspray.

Drop sizes were determined using a method described by Mason (1971). Shallow rectangular pans approximately 31 x 61 cm with a layer of uncompacted flour on the bottom were exposed, at canopy height, to sprinkling for 10-20 seconds and the dough balls produced were measured to determine the drop size distribution and mean drop size. The sprinklers tested (N=50) delivered drops in the range of 0.5 to 3.0 mm with a mean of 1.8± 0.1 mm. These sizes are within the limits expected from summer rain showers in the northern Great Plains (Edmond Holroyd, 1978).

<u>Growth Measurement and Analysis</u>. Plant growth was measured in three treatments (control, six millimeter, and wet) in 1977 and in all four treatments in 1978-79. In each plot 20 individuals were marked approximately 0.75 m apart, in a line across the center of each plot. Numbered metal reference tags were tied to the base of each plant.

The growing leaves of <u>Agropyron smithii</u> were measured at weekly intervals from approximately 1 May to 1 September of each year. On the first sampling date of each year all except the lowermost leaf were measured; thereafter only the upper elongating leaves of the plant were measured. Measurements originated at the tip of the leaf and terminated at the ligule of the next leaf below. This method of measuremment included the growth of the entire leaf (blade and sheath) and therefore, the total above-ground growth. All measurements were made to the nearest 1 mm.

Analysis of variance (ANOVA) was used to test for significance of differences among treatments. Rate matrices of 3 treatments x 13 dates in 1977, 4 treatments x 15 dates in 1978, and 4 treatments x 12 dates in 1979 were used. Each cell contained 20 individuals for a total of 780, 1200, and 960 observations in 1977, 1978, and 1979 respectively. The Kolmogorov-Smirnov goodness-of-fit test was employed to assess deviations of data distributions from normality on selected data sets (Ostle and Mensing 1975). The data sets used for the examination of distributions were from the control and wet treatments, the most diverse plots studied, on the assumption that if the normality criterion was met in these plots it would also be met in the remaining plots. The data were not normally distributed ($P>0.20$) so a logarithmic transformation was applied to better satisfy the assumptions of ANOVA. This yielded data sets that fit normal distributions well ($P<0.01$, Dixon and Massey 1969).

The transformation used was log (x+1) to eliminate zero values in the rate matrix.

Leaf Weight and Area Determinations. Leaves from randomly collected *Agropyron smithii* plants were dissected into sections equivalent to those used in growth determinations (ie, a phytomer). The units isolated included the sheath, blade, and associated stem (=internode) of each leaf which was cut away at the ligule of the leaf below. The dry weight of each section was determined to the nearest 0.1 mg. Leaves were then soaked in detergent solution to facilitate unrolling the blades, blotted dry, and mounted on clear laminating film. Length, area, and condition of individually mounted leaves were recorded. The condition was recorded as developing, fully developed and green, fully developed with brown tip > 5 mm but < 75% of total leaf surace, damaged (leaf area reduced because of loss) or dead (75% or more of the leaf surface brown).

The area of individual leaves was calculated using the method of trapezoidal area approximation (Beyer 1979), on a Tektronix 4051 minicomputer interfaced with a Tektronix 4956 digitizing tablet. The areas were recorded to the nearest 0.01 mm^2 and lengths were recorded to the closest 1 mm.

Water Potential Measurements. Soil water potential (ψ_s) was determined in the field using gypsum blocks (Taylor et al 1961) buried at three locations in each plot at depths of 10, 25, and 75 cm. The blocks were read weekly and mean values for each depth were determined to obtain a mean $_s$ for each plot and depth at each measurement date.

Plant water potential ψ_p was measured with a Scholander-type pressure chamber (Scholander et al 1965) using procedures recommended by Ritchie and Hinkley (1978) except as noted below. Measurements were made weekly, within one hour of sunrise, on five plants selected from predetermined locations randomly placed within each of the treatments. The ψ_p presented are the means for each treatment. Dawn measurements were used because ψ_p should be close to its maximum at that time (Slayter 1967; Ritchie and Hinkley 1978). Plants were observed through a dissecting scope, with magnification capabilities of 7-30x, within seconds of being cut. Generally, 10x provided sufficient magnification for determination of the end point. Pressure was increased at less than 1 bar $\cdot$ sec^{-1} until water was expressed from the cut end.

RESULTS AND DISCUSSION

Above Ground Growth Rates. In all treatments and years *Agropyron smithii* plants show a sigmoidal growth curve (Fig. 1) with an early season lag phase followed by a rapid growth phase, and finally a quiescent or stationary phase. This growth pattern has been observed in most plants (e.g. Golubev 1971; Erickson 1976; Larcher 1975; Evans 1972; and Milthorpe and Moorby 1974). Growth is initiated each spring when conditions (light, water, temperature) become suitable. During the lag phase (first period) plant growth is limited by a small photosynthetic area, and must, therefore, be determined by food reserves. The rapid growth phase (second period) begins when root and leaf formation are adequate for high photosynthetic rates (Noggle and Fritz 1976). Since growth rate is an index of the plant's photosynthetic capabilities under prevailing environmental conditions, the rapid growth period indicates the season of optimum growing conditions (Sims and Singh 1978a; Hunt 1970). Figure 1 suggests that the rapid growth phase begins by 15 May or earlier. Canopy generation is rapid during this period but ceases suddenly at its end. The quiescent phase (third period) could be due to exhaustion of water or nutrients,

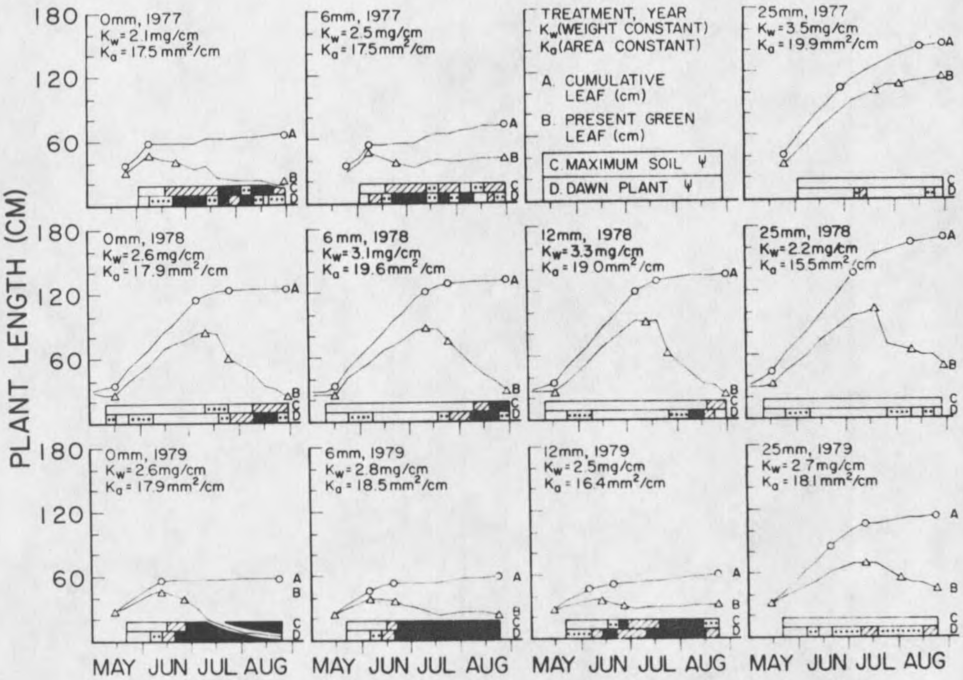

Figure 1. Cumulative growth (cm, solid line), green leaf length (cm, broken line), soil water status (A), and plant water status (B) of Agropyron smithii plants subjected to four water treatments (supplementation of natural rainfall to 0, 6, 12, and 25 mm/week) in three years (1977-1979). Growth and green leaf expanse expressed in mm (as measured) can be converted to weight or area by application of the constants provided (K_w and K_a). The shading in bar 'A' indicates the lowest soil water stress present in the upper 75 cm of the soil (clear = 0-5 negative bars, dots = 5-10 bars, hatching = 10-15 bars, and solid = 15+ bars. Shading in bar 'B' summarizes weekly measurements of dawn plant water potential (clear = 0-2 negative bars, dots = 2-10 bars, hatching = 10-20 bars, and solid = over 20 bars). Unit leaf rate calculations (Tables 1 and 2) are based on the leaf areas indicated by triangles on the green leaf curve and time periods between circles on the cumulative leaf curve.

accumulation of toxic substances (inhibitors or waste materials), increased respiration relative to photosynthesis, or to diversion of photosynthate from vegetative growth to seed or storage reserves.

<u>Unit Leaf Rates (mg.dm^{-2}.day^{-1}).</u> Aboveground production per unit of green surface, unit leaf rate (ULR), is calculated by dividing the rate of production by green leaf area. The necessary data appear in Fig. 1 and the process is demonstrated with formulae and sample calculations in Table 1. The term 'unit leaf rate' is preferred over the once popular phrase 'net assimilation rate' (NAR) because it clearly relates to leaf growth and doesn't suggest any relationship to total production (Evans 1972 and Thomas 1980).

Table 1. Calculation of unit leaf rate.

Unit leaf rate = rate of above ground production/per unit of photosynthetic area (= ULR).

= (W/ T) (1/A) where:

T = a specified time period

W = change in weight in mg during that time period
= (change in leaf length read from Fig. 1, upper curve) X (K_w, a weight conversion constant (mg/cm) reported in Fig. 1).

A = area in dm^2
= (green length at the time considered from Fig. 1, lower curve) X (K_a, an area conversion constant [mm^2/cm] reported in Fig. 1) X ($1/10^4$ dm^2/mm^2).

Examples:

Unit leaf rate for the early rapid growth phase of control 1977 is calculated as:

$$ULR = 60 \frac{mg}{dm^2 . da} = \frac{(570\ mm - 360\ mm)\ (0.21\ mg/mm)}{(day\ 158 - day\ 144)}$$

$$X \quad \frac{1}{(300\ mm)\ (1.75\ mm^2/mm)(0.0001\ dm^2/mm^2)}$$

Similarly unit leaf rate for the peak of green phase of control 1977 is calculated as:

$$ULR = 39 \frac{mg}{dm^2 . da} = \frac{(570\ mm - 360\ mm)\ (0.21\ mg/mm)}{(day\ 158 - day\ 144)}$$

$$X \quad \frac{1}{(465\ mm)\ (1.75\ mm^2/mm)\ (0.0001\ d^2/mm^2)}$$

At a given season ULR varies relatively little among treatments and the variation shows no consistent pattern (Table 2). Production averaged 78 $mg.dm^{-2}.day^{-1}$ in the early season, 32 $mg.dm^{-2}.day^{-1}$ at peak green area, 4 $mg.dm^{-2}.day^{-1}$ approximately two weeks past peak green area, and 7 $mg.dm^{-2}.day^{-1}$ at the end of August (Table 2). Because these rates differ relatively little and inconsistently among treatments, I deduce that the principal effect of irrigation has been on the area of the producing unit (leaf surface) rather than on its condition (photosynthetic capacity).

Since ULR is primarily a function of photosynthesis (Potter and Jones 1977), I speculate that the maximum net photosynthetic rate of <u>Agropyron smithii</u> is equal to or greater than the ULR observed early in the log phase (78 $mg.dm^{-2}.day^{-1}$). Equality would occur if 1) storage depot subsidies to shoot growth have ceased by the time the log phase of growth has begun, 2) roots present in the early season support the sparse canopy adequately so there is no transport downward to support root growth, and 3) stem respiration is a constant proportion of total respiration.

The decline in ULR later in the log phase of growth (32 $mg.dm^{-2}.day^{-1}$) and the low production rate per unit of leaf surface observed late in the season (7 $mg.dm^{-2}.day^{-1}$), probably understate the actual photosynthetic rates for these seasons. The presumed understatement of production

Table 2. Unit Leaf Rates of <u>Agropyron smithii</u>.

	ULR (mg.dm^{-2}.day^{-1} aboveground)			
	Early Rapid Growth	At Peak Green	After Peak Green	At Season's End
Control				
1977	60	39	3	7
1978	87	26	1	3
1979	53	31	1	13
6 mm				
1977	69	43	9	8
1978	106	29	2	5
1979	64	40	4	6
12 mm				
1977	--	--	-	-
1978	110	31	3	9
1979	46	29	6	7
Wet				
1977	107	27*	-	3
1978	84	24	5	6
1979	69	28	4	6
Mean	78	32	4	7
Standard Error	8	2	1	1

-- Measurements not taken

* Green material never peaked, but continued to increase to the last measurement period in this year.

is due to increased allocation of photosynthate to storage areas. Reallocation is probably the major factor determining the declines recorded in the control, 6, and 12 mm plots where the canopy never closed. It is likely that declines in wet plot ULR are due both to reallocation and to competition for light -- ie reduced photosynthesis -- after canopy closure.

The very lowest ULR (4 $mg.dm^{-2}.day^{-1}$) was observed just after the end of the log phase when growth rates were low but green leaf areas and available water were high. Because it seems very unlikely that photosynthesis per unit of leaf area should plunge at mid-season -- from high rates to rates lower than end-of-season rates -- I speculate that, despite unit leaf rates, net photosynthetic rates were, at a minimum, between the preceeding and succeeding unit leaf rates (ie 32 and 7 $mg.dm^{-2}.day^{-1}$) and, at a maximum, equal to the early season ULR (78 $mg.dm^{-2}.day^{-1}$). The excess photosynthesis predicted, but not observed in above-ground production, should appear as growth or storage in crowns, rhizomes, and roots. This is consistent with the report (Sosebee and Wiebe 1973) that, in _Agropyron smithii_, almost all translocation during the quiescent phase is to the roots.

Estimation of production. The following paragraphs review two methods for estimating aboveground production and two methods for calculating total production. Table 3 summarizes these methods and Table 4 compares the results of all methods.

Leaf measurements made between mid-May and the end of August permit us to calculate net aboveground production for any sub-period by either of two methods. First, production can be estimated by multiplying the change in plant length during any period (mm, Fig. 1) by the weight per unit of length (K_w, Fig. 1). Such estimates are summarized in Table 4.

Second, for any very short period aboveground production is the product of unit leaf rate (ULR, $mg.dm^{-2}.day^{-1}$) and leaf surface (mm, Fig. 1 lower curve). Unit leaf rate is, of course, the product of leaf extension rate ($mm.day^{-1}$, from the slope of the upper curve of Fig. 1) and the weight of a unit of length ($mg.mm^{-1}$ Fig. 1) divided by the green leaf area producing it (lower curve, Fig. 1). For longer periods, one can estimate total production by plotting instantaneous production, estimated in this matter, over a series of periods and integrate under the curve. Identical estimates must result if the same data base is used. Either estimate is more accurate than those made by harvest methods because material lost before harvest to either grazing or senescence is included (Sims and Singh 1975).

Aboveground production might occur before or after the measurement season. We doubt that post season

Table 3. Calculation of seasonal production, a demonstration of methods.

Method 1, read it directly from production graphs of Figure 1.

Seasonal production = P (mg/plant/season) = change in leaf length ($mm_{final}-mm_{initial}$, from

Fig. 1, upper curve) X K_w (a constant converting mm to mg, (presented) in Figure 1).

Method 2, calculate it from graphs in Figure 1.

Instantaneous production (mg/plant/day) = ULR x green leaf area

ULR ($mg/dm^2/day$) is read from Table 2 or calculated from Fig. 1 by methods illustrated in (Table 1).

green leaf area = green leaf length (mm, from lower curve, Fig. 1) X K_a (mm^2/mm, presented in Fig. 1).

Seasonal production = instantaneous production (mg/plant/da) x days

This was estimated by plotting instantaneous rates over time and integrating under the curve by cutting out the area and comparing its weight with weights of known areas. Three sets of rates were considered.

If we assume ULR = those actually observed (Fig. 1 and Table 1), production calculated from method 1 equals that calculated by method 2.

If we assume (see text) that the initial ULR persists until the peak of green leaf area and end-of-season ULR applies for the remaining time, the seasonal production by method 2 exceeds that calculated by method 1 significantly. Table 4 summarizes the differences in production for the rapid growth and quiescent periods; we believe the unobserved production contributes to below ground growth Table 5.

If we assume (see text) that the initial ULR persists until the peak of green leaf area and that ULR after that time is actually ten times end-of-season-ULR (approximately initial growth rates) production is further increased, but without violation of possible root growth rates.

Table 4. Production (mg/plant) of individuals of *Agropyron smithii* grown under four irrigation regimes.[1]

Parameter[2]		Aboveground production				Minimum total production				Maximum Total production			
Season[3]		P	E	Q	T	P	E	Q	T	P	E	Q	T
Treatment and year													
0 mm	1977	76	44	19	139	76	55	31	162	76	55	312	443
	1978	78	202	16	301	78	523	16	61	78	523	160	761
	1979	70	74	12	156	70	100	34	20	70	100	343	513
6 mm	1977	86	53	49	188	86	62	49	197	80	62	485	633
	1978	88	112	9	209	88	351	30	469	88	351	301	740
	1979	67	46	38	151	67	81	38	186	67	81	380	528
12 mm	1977	-	-	-	-	-	-	-	-	-	-	-	-
	1978	94	302	35	431	94	621	35	750	94	621	350	1065
	1979	71	53	26	150	71	73	26	170	71	73	260	404
Wet	1977	42	357	11	510	142	1324	11	1477	142	1324	110	1576
	1978	69	241	33	343	69	588	33	690	69	588	250	907
	1979	85	202	20	307	85	323	29	437	85	323	292	700

---

[1] Irrigation regimes were an unirrigated control (0 mm), a plot guaranteed 6 mm per week (6 mm), a plot guaranteed 12 mm per week (12 mm), and a plot in which soil water potentials were maintained above -2 bars with irrigiations of 25 mm per week or more.

[2] Aboveground production was estimated by multiplying leaf length (mm) produced in the period by the weight per mm. Total production was estimated by integrating under a curve of leaf production rate created by multiplying observed green leaf areas by either a minimum or maximum estimate of the photosyynthetic rate.

[3] Production was estimated for the period before measurements began in May (preseason = P) for the period of exponential growth before the peak-of-green (E), for the quiescent period after peak-of-green (Q) and for the total season (T).

production was significant because the soils dried and the plants turned brown (Fig. 1). Preseason growth was observable as green plant material present when measurements were initiated. Preseason aboveground production is easily estimated by the first method. Estimates are presentated in Table 4. Our data cannot provide the rate estimates needed for the second method.

Belowground production must occur in <u>Agropyron smithii</u> grasslands since belowground masses exceed aboveground masses (Weaver et al 1981). Consideration of the second method of estimating production outlined above and the unit leaf rate discussion suggests a way of estimating this belowground production: one should integrate across time the product of green leaf area (Fig. 1, lower curve) and its production rate. For aboveground production the production rate was the unit leaf rate (ULR) calculated as above. For total production a production rate including belowground transport is needed. Two possibilities, labeled maximal and minimal, are outlined and applied below.

A minimal estimate of total production was made by summing production in three subseasons; the preseason, the period before maximum green leaf area, and the period after maximum green leaf area. Preseason production is assumed to be entirely aboveground and therefore calculated as the product of aboveground growth (mm) and weight per unit of length (K_w=mg/mm). Early season production is calculated as the integral of green leaf area (Fig. 1) and a maximal unit leaf rate (Table 2) calculated from the curves in Figure 1. This assumes that the observed drop in ULR during the log growth phase is due to increasing transport to belowground organs. Late season production is calculated as the integral of green leaf area (Fig. 1) and the ULR at season's end. The results appear in Table 4. Our minimal estimate of total production is about 150% of measured aboveground production.

While we suspect that the preceeding procedure underestimates total production, we believe that the following procedure will give us a maximal estimate of total production. We assume, as above, that preseason production is entirely aboveground (for lack of data to do otherwise) and therefore underestimate total production if actual carbon transport is downward and overestimate it if carbon transport is upward. We assume again that calculation of early season production based on early season ULR and actual green leaf areas is correct. Our maximal estimate differs, then, only in late season production which we estimated as ten times the minimal estimate for two reasons: 1) it is generally believed that most late season photosynthate is stored (Sosebee and Wiebe 1973); and 2) early season unit leaf rates are about ten times late season unit leaf rates (Table 2) so, if photosynthetic rates do not actually fall, 90% of the photosynthate would be transported below ground. We call our estimate maximal because, while it is based on actual green leaf areas, estimated photosynthetic rates may be high since water and nutrient resources per unit of leaf area are probably less available late in the summer than in the spring. Maximal production estimates presented in Table 4 are about 300% of aboveground production rates measured by method 1.

Belowground production. Belowground production (root, rhizome, and crown) is easily calculated by substracting aboveground production from total production and is presented in Table 5. In the preseason our assumptions of no downward transport implies that there will be an absence of root growth. To the extent that net carbon flows are upward, belowground production may actually be negative. During the log phase transport downward is calculated similarly for both minimal and maximal estimates; therefore similar belowground production is observed, ie an average of 43 ±6 SE % of total net production (Table 6). Quiescent phase transport averages 19 ± 8 SE % of total net production in the minimal estimate and 92 ± 1 SE % in the maximal estimate. The latter seems more reasonable since 98, 96, 95, and 56% of the roots are belowground in our 0, 6mm, 12mm, and wet

Table 5. Belowground production[1] (mg/plant) calculated using minimum or maximum estimates of photosynthetic rates.

Parameter[2] Season[3]		Production, minimum				Production, maximum			
		P	E	Q	T	P	E	Q	T
						mg/plant[1]			
Treatment and year									
0 mm	1977	0	11	12	23	0	11	293	304
	1978	0	316	0	316	0	316	144	460
	1979	0	26	22	48	0	26	331	357
6 mm	1977	0	9	0	9	0	9	436	445
	1978	0	239	21	260	0	239	242	531
	1979	0	35	0	35	0	35	342	377
12 mm	1977	-	-	-	-	-	-	-	-
	1978	0	319	0	319	0	319	315	634
	1979	0	20	0	20	0	20	234	254
Wet	1977	0	997	0	967	0	997	99	1066
	1978	0	347	0	347	0	347	217	564
	1979	0	101	9	130	0	101	272	393

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[1] Belowground production = total production (Table 4) minus above ground production (Table 4).

[2] Production was estimated for the period before measurements began in May (preseason = P), for the period of exponential growth before the peak-of-green (E), for the quiescent period after peak-of-greenn (Q), and for the total season (T).

[3] Irrigation regemes were an unirrigated control (0 mm), a plot guaranteed 6 mm per week (6 mm), a plot guaranteed 12 mm per week (12 mm) and a plot in which soil water potentials were maintained above - 2 bars with irrigations of 25 mm per week or more.

Table 6. Belowground production[1] (% of total) calculated using minimum or maximum estimates of photosynthetic rates.

Parameter Season[2]		Production, minimum				Production, maximum			
		P	E	Q	T	P	E	Q	T
					% of Total[2]				
Treatment and year									
0 mm	1977	0	20	38	14	0	20	94	69
	1978	0	60	0	51	0	60	90	60
	1979	0	26	65	24	0	26	96	70
6 mm	1977	0	15	0	5	0	15	90	70
	1978	0	68	70	55	0	68	97	72
	1979	0	43	0	19	0	43	90	71
12 mm	1977	-	-	-	-	-	-	-	-
	1978	0	51	0	43	0	51	90	60
	1979	0	27	0	12	0	27	90	63
Wet	1977	0	73	0	65	0	73	90	68
	1978	0	59	0	50	0	59	87	42
	1979	0	6	8	6	0	6	1	3

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[1] Belowground production = total production (Table 4) minus above ground production (Table 4). Belowground production is expressed as a percentage of total production reported in Table 4.

[2] Production was estimated for the period before measurements began in May (preseason = P), for the period of exponential growth before the peak-of-green (E), for the quiescent period after peak-of-green (Q), and for the total season (T).

[3] Irrigation regimes were an unirrigated control (0 mm), a plot guaranteed 6 mm per week (6 mm), a plot guaranteed 12 mm per week (12 mm) and a plot in which soil water potentials were maintained above - 2 bars with irrigations of 25 mm per week or more.

treatments respectively (Weaver et al 1981). Summing across season one calculates that between 33 ± 6 SE % (minimal estimate) and 64 ± 3 SE % (maximal estimate) of total net production is deposited in the belowground compartment.

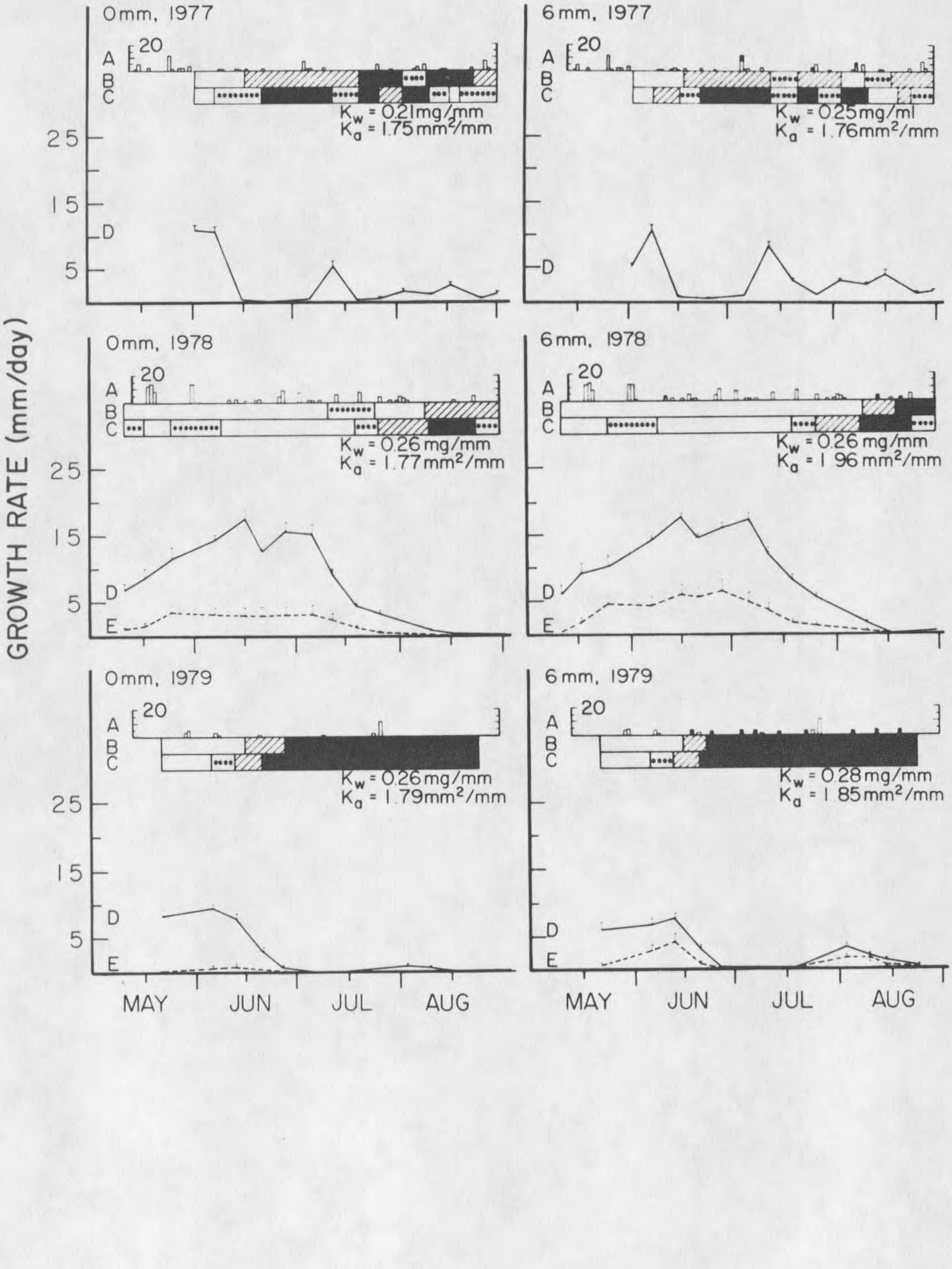
<u>Factors controlling production and growth.</u> Three observations support the conclusion that water availability is one major determinant of production. First, increased water availability slows the rate of loss of green leaf areas and results in maintenance of a larger photosynthetic surface (Fig. 1) which might function late in the rapid growth phase or after any rainstorms occurring during the quiescent phase. The amount of green leaf material on the average plant peaked before the end of the rapid growth phase of growth and was maintained for two to three weeks before it began to decline. In dry 1979, the decline in green leaf material was most rapid in the dry plot and progressively less rapid in the 6 mm, 12 mm, and wet plots. The same is true in dry 1977 when super-adequate water supplies, due to heavy watering and small populations, resulted in no decline in the wet plot. Even in the wet summer of 1978 when declines were similar in the control, 6 mm, and 12 mm treatments, the drop was least in the wet treatment.

Secondly, in relatively dry years (1977 and 1979) leaves began to die (Fig. 1), and growth stopped earlier in the dry control treatment than in the wet treatment (Fig. 2). Extending the period in which growth occurs has a dual positive effect -- first, on the length of the productive period and second, on any returns on additions to photosynthetic surface due to increased production, ie to a 'compound interest effect'. In contrast to the wet treatment, the 6 mm and 12 mm treatments had little or no effect on the length of the active growth period (Fig. 2). I tentatively conclude that the 6 mm and 12 mm treatments produced little additional plant material despite the additional water available.

Thirdly, in all seasons, growth rates declined with increasing plant water stress (Fig. 3). Maximum above-ground growth occurred when plant water stresses were less than -5 bars and cessation of growth occurred at plant water stresses near -20 bars. The scatter associated with higher stresses (Fig. 3) was probably caused by small spurts of growth after rainstorms. While such growth would have occurred in non-stress moments it would have been associated in our records with low plant water potentials (indicative of high stresses) read at the beginning and end of the measurement period.

While growth always ceased when water was exhausted, the fact that it always slowed markedly in mid-July, even though water was not limiting, suggests that other factors, perhaps season, also limit growth. The reader

Figure 2. (overleaf) Relationship of growth rate (mm/day) to water availability for _Agropyron smithii_ plants subjected to four water treatments (supplementation to 0, 6, 12, or 25 mm/week) for three years (1977-1979). A) Water added (mm): clear and shaded bars indicate summer rainfall and irrigiation respectively. B) Shading indicates soil water stresses of 0-5 (clear), 5-10 (dotted), 10-20 (hatched), and over 20 (solid) negative bars. C) Shading indicates dawn plant water potentials of 0-2 (clear), 2-10 (dotted), 10-20 (hatched), and over 20 (solid) negative bars. D) Mean growth rates (mm/day) of initial plants with their standard errors. E) to convert growth rates to weight or area multiply by the weight constant (K_w in mg/mm) or area constant (K_a in square mm/mm) respectively. E) Growth rates of tillers in mm/day.


GROWTH RATE (mm/day)
0mm, 1977
6mm, 1977
0mm, 1978
6mm, 1978
0mm, 1979
6mm, 1979
A
B
C
D
E
20
K_w = 0.21mg/mm
K_a = 1.75mm²/mm
K_w = 0.25mg/ml
K_a = 1.76mm²/mm
K_w = 0.26 mg/mm
K_a = 1.77mm²/mm
K_w = 0.26 mg/mm
K_a = 1.96 mm²/mm
K_w = 0.26 mg/mm
K_a = 1.79mm²/mm
K_w = 0.28 mg/mm
K_a = 1.85 mm²/mm
25
15
5
MAY
JUN
JUL
AUG

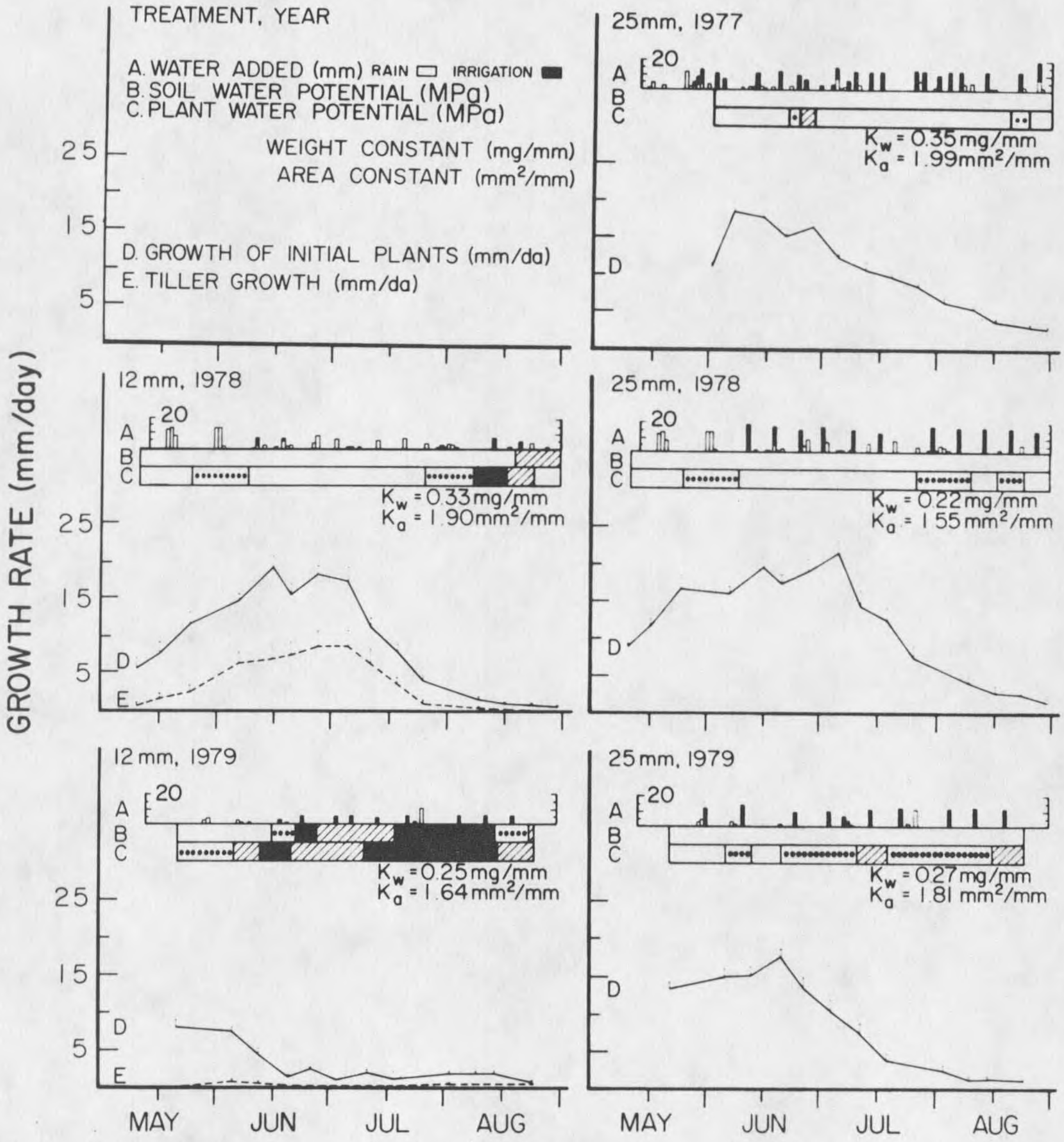


Figure 2. Continued.

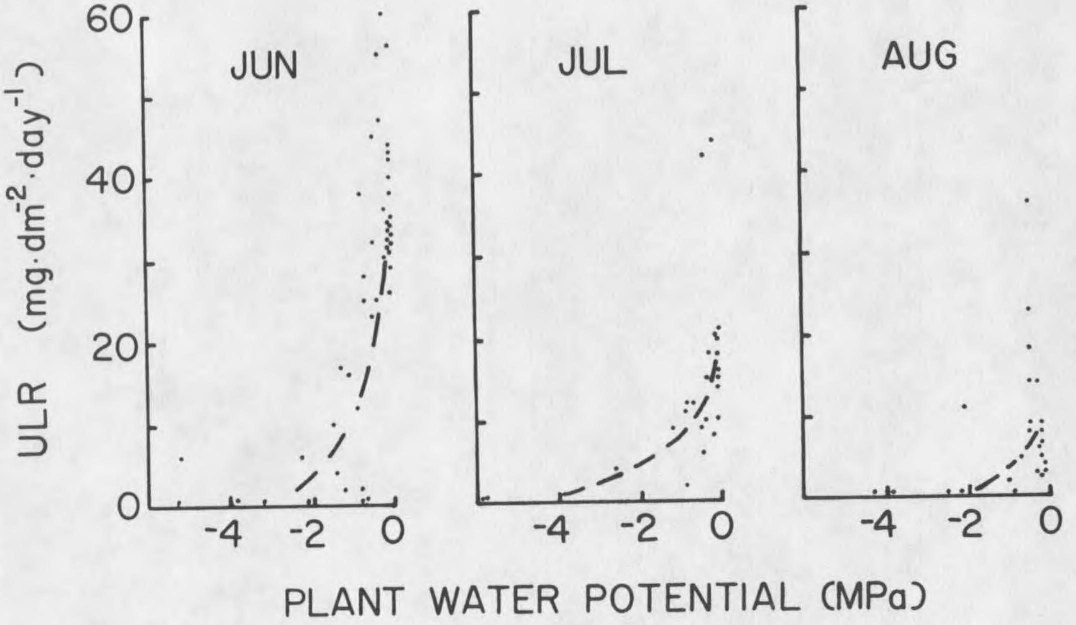


Figure 3. The effect of water potential and season on unit leaf rate. The dashed lines are hand fit.

should verify from Figure 2 that growth slowed in the wet plot in mid-July in all years despite moist soils that kept plant water potentials between 0 and -5 bars. Comparison of the wet and control plots shows that cessation of growth is probably not due to achievement of a maximum plant size, to internal shading, or to exhaustion of nutrients, since in 1978 it occurred concurrently in dry plots and in wet plots (which, with larger plants, had more internal shading and had consumed more nutrients).

I hypothesize, therefore, that the potential for above-ground growth, and therefore production, is reduced at mid-summer -- perhaps due to daylength-induced preparation for fall and winter. Three lines of evidence support the daylength-control speculation. First, above-ground growth ceases when no other factor seems to limit it. Second, the fact that growth rates associated with a given water stress fall as the season progresses (Fig. 3) suggests that photosynthate is being diverted from growth to storage (Trlica 1977, Moser 1977, and Brown & Blaser 1970). I do not accept the alternative hypothesis that photosynthetic capacity of healthy green leaves declines with season. Thirdly, under experimental conditions a variety of range grasses, including _Agropyron smithii_, _Bouteloua gracilis_, _Andropogon scoparius_, and _Stipa comata_, all grew more rapidly under energetically equal short night conditions than under long night conditions (Weaver and Forcella 1983).

While the capacity for growth was reduced at midsummer, drought-stressed plants apparently retain some capacity to respond to late summer showers. Plants from both dry control plots and 6 mm plots grew after showers in 1977 and 1979 (Fig. 2). In the 6 mm plots leaf extension rates were 150, 217, 170, and 400 percent greater ($P<0.01$) than those of the control plots in mid-July 1977, early August 1977, late August 1977, and early July 1979, respectively. Though growth continued throughout the summer in 12 mm and wet plots, no effects of summer showers could be detected. Late season growth responses in the wetter plots may have been masked by the irrigation treatments, or prevented by a physiological state (e.g. carbohydrate balance) induced by regular watering.

Growth response to water supplements. Leaf extension increased with increasing water availability. When compared with the control (100 %), the average 6 mm treatment culm was 107 %, the average 12 mm treatment culm was 106 %, while the average 25 mm treatment culm was 207 % in dry 1977 and 1979 and 135 % in wet 1978 (Fig. 1; Table 7). Statistical analysis --ANOVA after logarithmic transformation -- of the growth data summarized in Figure 2 show that plants in the control, 6 mm, and 12 mm plots

Table 7. Total aboveground yields, on culm length (mm) and biomass (mg) bases, of average *Agropyron smithii* plants from plots subjected to four water regimes. Each datum is reexpressed (in parentheses) as a percentage of the control.

	Treatments			
	Control	6 mm	12 mm	Wet
		Total length production (mm)		
1977	606 (100%)	735 (111%)	----	1455 (220%)
1978	1245 (100%)	1340 (106%)	1365 (110%)	1680 (135%)
1979	585 (100%)	600 (102%)	600 (102%)	1140 (195%)
		Total mass production (mg)		
1977	139 (100%)	188 (135%)	----	510 (367%)
1978	301 (100%)	209 (69%)	431 (143%)	343 (114%)
1979	156 (100%)	151 (97%)	150 (96%)	307 (197%)

grow less than those in the wet plots ($P<0.0001$) in all years. Plants from the control plots grew less than those in the 6 mm and 12 mm treatments in all years ($P<0.02$). Although growth rates were not different in the 6 mm and 12 mm treatments in wet 1978, they did differ in dry 1979 ($P<0.0001$).

When leaf length is multiplied by specific leaf weights (K_w) there is no clear pattern of yield increase with increasing water availability (Table 4 or Table 7). Despite increases in growth described above, we cannot therefore confidently conclude that per-plant yields were increased by 6 mm or 12 mm irrigation regimes. Total yields would increase, however, if plant densities increased (see below). Per-plant yield increases due to the wet treatment are obvious.

Tillers were present in every plot in every year. Although measurements were not taken in the 12 mm plot in 1977, it is assumed that since tillers appeared in the remaining three treatments under study, they were also present in the 12 mm plot. Tillers, as used here, are defined as lateral vegetative shoots, arising from a leaf axil, and growing upward within the leaf sheath, ie intravaginally (Moser 1977 and Thomas 1980). Tiller growth -- which was measured only in 1978 and 1979 -- while less than that of parent plants had a similar seasonal pattern (Fig. 2). Tiller growth declined more rapidly, however, in response to drought stress than did the growth of parent plants.

The reader will note (Table 7) that production of the average culm was less in 1979 than in 1977. This may be due, in part, to the fact that 1979 was drier than 1977, but is probably due also to increased competition, undoubtedly associated with increasing plant densities which were observed, especially in the wet plots.

The reader will realize that the effects of water supplements are a product of individual responses (discussed here) and population size (to be discussed elsewhere) and in so doing will conclude -- due to the omission of expected (and observed) increases in population density -- that this paper understates the benefits of added water.

CONCLUSIONS

The results discussed above suggest five major conclusions:

1) The cumulative growth of individual plants (gm/plant) followed the usual sigmoidal curve.

2) Green leaf area generally exhibited a bellshaped curve which peaked about the time the aboveground mass peaked and sometimes before significant plant or soil water stress developed.

3) Aboveground production per unit of leaf area was largest early in the season, fell to a low soon after the peak of green leaf area, and rose slightly in the late summer. The first growth must have been built with reserves from the previous season. The decline in unit leaf rates through the log growth phase to the post-peak-of-green-stage was probably due to allocation of increasing amounts of photosyntate to root growth and belowground storage. By growth analysis it is estimated that one to two thirds of net photosynthate is devoted to belowground growth; this is not inconsistant with the observation that 55-95% of the plant is belowground. Seasonal changes in allocation of photosynthate may be

triggered by exhaustion of water and/or changes in daylength.

4) On a plant length basis, per-plant growth increased 6-7% after light shower treatments (guarantees of 6-12 mm/week) and 33-107% when soils were kept moist. On a plant weight basis, however, aboveground yields were significantly increased only by the wet treatment.

5) Yield effects of water treatments are a product of per-plant effects (discussed here) and plant density effects (the subject of another study). It is doubtful that water supplements ever reduced plant densities. Until the density effects are multiplied in, one can only conclude that the effects reported here understate the magnitude of water treatment effects.

LITERATURE CITED

Acevedo, E., T. C. Hsiao, and D. W. Henderson. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48:631-636.

Acevedo, E., E. Fetetes, T. C. Hsiao, and D. W. Henderson. 1979. Diurnal growth trends, water potential, and osmotic adjustment of maize and soughum leaves in the field. Plant Physiol. 64:476-480.

Ackerson, R. C. 1980. Stomatal response of cotton to water stress and abscisic acid as affected by water stress history. Plant Physiol. 65:455-459.

Balasko, J. A. and D. Smith. 1973. Carbohydrates in grasses: V. Incorporation of ^{14}C into plant parts and nonstructural carbohydrates of timothy (Phleum pratense L.) at three developmental stages. Crop Sci. 13:19-22.

Begg, J. E. and M. J. Wright. 1964. Relative effectiveness of top and basal leaves for the growth of vegetative shoots and reed canary grass. Crop Sci. 4:607-609.

Beyer, W. H. 1979. CRC Standard Mathematical Tables. CRC Press, Fla.

Boyer, J. S. 1970. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. Plant Physiol. 46:233-235.

Brown, R. W. 1977. Water relations of range plants. Rangeland Plant Physiology (E. Sosebee ed.). Range Science Series No. 4. p. 98-140.

Brown, R. H. and R. E. Blaser. 1970. Soil moisture and temperature effects on growth and soluble carbohydrates of orchardgrass (Dactylis glomerata). Crop Sci. 10:213-216.

Charley, J. L. 1977. Mineral cycling in rangeland ecosystems. Rangeland Plant Physiology (R. E. Sosebee ed.). Range Science Series No. 4. p. 216-256.

Dahl, B. E. and D. N. Hyder. 1977. Developmental morphology and management implications. Rangeland Plant Physiology (E. Sosbee ed.). Range Science Series No. 4. p. 258-290.

Dixon, W. J. and F. J. Massey. 1969. Introduction to statistical analysis. McGraw-Hill: New York. p. 322-324.

Erickson, R. O. 1976. Modeling of plant growth. Ann. Rev. Plant Physiol. 27:407-434.

Evans, G. C. 1972. The quantitative analysis of plant growth. Studies in Ecology. Vol. 1. University of Calif. Press.

Fischer, R. A. and R. M. Hagan. 1965. Plant water relations, irrigation management and crop yield. Expl. Agric. 1:161-177.

Golubev, V. N. 1971. Growth of vegetative shoots in grasses and sedge under conditions of the southern Crimean Shore. Sov. J. Ecol. 2 (4):357-359.

Haglund, B. M. 1980. Proline and valine - cues which stimulate grasshopper herbivory during drought stress? Nature 288:697-698.

Harper, J. L. 1977. Population biology of plants. Academic Press: New York.

Henckel, P. A. 1964. Physiology of plants under drought. Ann. Rev. Plant Physiol. 15:363-386.

Hess, W. 1974. Weather and climate modification. J. Wiley and Sons, N.Y. 841 pgs.

Hitchcock, A. S. and A. Chase. 1950. Manual of the grasses of the United States. U.S.D.A. Misc. Pub. 200. p. 234.

Holroyd III, Edmund. 1978. Ph.D. meterologist. USDI Bureau of Reclamation Division of Atmospheric Resources Research. Skywater Office, Montrose, Colorado.

Hsiao, T. C. 1973. Plant response to water stress. Ann. Rev. Plant Physiol. 24:519-570.

Hunt, W. F. 1970. The influence of leaf death on the rate of accumulation of green herbage during pasture regrowth.

Itai and Vaadia. 1971. Cytokinin activity in water-stressed shoots. Plant Physiol. 47:87-90.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geo. Soc. Special Pub. 36. 154 p. and map.

Larcher, W. 1975. Physiological plant ecology. Springer-Verlag: New York. p. 252.

Leopold, A. C. 1975. Aging, senescence, and turnover in plants. Bio. Science 25:659-662.

Mason, B. J. 1971. The physics of clouds. Clarendon Press: Oxford. p. 602-603.

Milthorpe, F. L. and J. Moorby. 1974. An introduction to crop physiology. Cambridge University Press: New York. p. 202.

Moore, R. T. 1977. Gas exchange and photosynthetic pathways in range plants. Rangeland Plant Physiology (E. Sosebee ed.). Range Science Series No. 4. p. 1-46.

Moser, L. E. 1977. Carbohydrate translocation in range plants. Rangeland Plant Physiology (E. Sosebee ed.). Range Science Series No. 4. p. 48-71.

Noggle, G. R. and g. J. Firtz. 1976. Introductory plant physiology. Prentice-Hall: New Jersey.

Ostle, B. and R. Mensing. 1975. Statistics in research. Iowa State University Press: Ames, Iowa. p. 489-490.

Potter, J. R. and J. W. Jones. 1977. Leaf area partitioning as an important factor in growth. Plant Physiol. 59:10-14.

Ritchie, G. A. and T. M. Hinckley. 1978. The pressure chamber as an intrument for ecological research. Advances in Field Research. (J. Cragg, ed.). Academic Press: New York. p. 165-254.

Scholander, P. F., H. T. Hammel, D. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. Sci. 148:339-346.

Sims, P. L. and J. S. Singh. 1978a. The structure and function of ten western North American grasslands. II. Intra-seasonal dynamics in primary producer compartments. J. Ecol. 66:547-572.

Sims, P. L. and J. S. Singh. 1978b. The structure and function of ten western North American grasslands. IV. Compartmental Transfers and Energy Flow Within the Ecosystem. J. Ecol. 66:983-1009.

Singh, J., W. Lauenroth and R. Steinhorst. 1975. Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. Bot. Review 41:181-232.

Slayter, R. O. 1967. Plant-water relationhips. Academic Press: New York. p. 366.

Sosebee, R. E. and H. H. Wiebe. 1971. Effect of water stress and clipping on photosynthate translocation in two grasses. Agron. J. 63:14-17.

Sosebee, R. E. and H. H. Wiebe. 1973. Effect of phenological development on radiophosphorous translocation from leaves in creasted wheatgrass. Oecologia 13:103-112.

Stewart, C. R. 1978. Role of carbohydrates in proline accumulation in wilted barley leaves. Plant Physiol. 61:775-778.

Taylor, S., D. Evans, and W. Kemper. 1961. Evaluating soil water. Ag. Expt. Station Bull. 426. Utah State Univ., Logan. 67 pgs.

Thomas, H. 1980. Terminology and definitions in studies of grassland plants. Grass and Forage Sci. 35:13-23.

Trlica, M. J. 1977. Distribution and utilization of carbohydrate reserves in range plants. Rangeland Plant Physiology (E. Sosebee ed.). Range Science Series No. 4. p. 74-96.

U. S. Department of Agriculture, Agricultural Research Services. 1972. Grass varieties in the United States. U.S.D.A. Agricultural Handbook 170. U.S. Gov. Printing Office, Washington, D.C. p. 8-9.

Valentine, J. 1980. Range development and improvements. Brigham Young Univ. Provo, Utah. 545 pgs.

Wardlaw, I. F. 1974. Phloem transport: physical, chemical or impossible. Annu. Rev. Plant Physiol. 25:515-539.

Weaver, T., J. Birkby, J. Welker, and J. Newbauer. 1981. Short-term responses of an Agropyron smithii grassland to six water regimes. IN: G. Knutsen and R. Moy eds. State of Montana Act. activities in the High Plains Cooperative Program. 1975-1980. Helena, MT. 287 pgs.

Weaver, T. and F. Forcella. 1983. Nyctoperiod (photoperiod) control of vegetative growth of high plains grasses. p. 103-110. IN: L. Holman and G. Knutsen 198 eds. 1983 State of Montana activities in the High Plains Cooperative Program: 1981-1983. Mont. Dept. of Natural Resources and Conservation, Helena. 171 pgs.