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BROMEGRASS PRODUCTIVITY IN RELATION TO
PRECIPITATION, SHRUB CANOPY COVER AND
SOIL NITROGEN CONTENT

by

Lawrence G. Kline

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Range Science
(Ecology)

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1973

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ABSTRACT

Bromegrass Productivity in Relation to Precipitation, Shrub Canopy Cover and Soil Nitrogen Content

by

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Utah State University, 1973

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Department: Range Science

In seasons of above normal precipitation, populations of annual weedy species increase in great abundance in semi-arid desert plant communities. These increases in biomass tie up a considerable portion of the available nitrogen of such ecosystems and may depress subsequent annual grass germination.

A big sagebrush-annual bromegrass plant community was irrigated to simulate a spring growth period of abundant precipitation amenable to annual bromegrass productivity. Productivity and nitrogen content parameters were monitored throughout the spring and summer to evaluate the short and potential long term effects of this seasonal increase in "precipitation".

Irrigation increased annual bromegrass productivity almost 50 percent. This increase was a result of the combined factors of increased soil moisture content and increased nitrogen availability due, apparently, to increased soil microfloral nitrification activity under low water

water stress conditions.

The increased annual growth resulted in a greater nitrogen uptake despite an observed decrease in irrigated bromegrass percent nitrogen values. Both the tie up and irrigation effect were maintained throughout the summer and into the subsequent annual germination period. However, total soil nitrogen levels and bromegrass nitrogen mineralization rates suggest that soil nutrient conditions for subsequently germinating bromegrass seedlings do not differ because of previous spring irrigation treatment.

(70 pages)

INTRODUCTION

Cheatgrass, a winter annual also known as downy brome, (Bromus tectorum L.) was introduced to the North American continent from Europe in the middle of the nineteenth century. It made its first appearance in the western United States at the turn of the century and rapidly spread throughout the Great Basin and Columbia River Basins (Klemmedson and Smith, 1964).

The most probable causes of this invasion were the activities of the early pioneers. Their practices of over-grazing and indiscriminate burning led to the retrogression of the Palouse grassland climax and the resultant dominance of big sagebrush (Artemisia tridentata Nutt.) and B. tectorum (Stoddard, 1941).

LITERATURE REVIEW

The change in botanical composition associated with widespread land abuses has been most detrimental to the livestock industry. Hull and Pechanec (1947) reported that the invasion of B. tectorum was almost complete in southern Idaho and it is now considered an important although less desirable forage plant in that area. Similar findings have been reported for Utah (Pickford, 1932), Nevada (Fleming et al, 1942), and Oregon (Platt and Jackman, 1946) with the greatest problem area being Idaho (Stewart and Hull, 1949; Tisdale et al, 1969).

The semi-arid climate of the Great Basin greatly affects the annual productivity of B. tectorum due to the extreme variation in annual rainfall. The variable and unpredictable forage production associated with fluctuations in rainfall distribution in the critical fall and spring growth periods of the grass has necessitated a reduction of the stocking rate on these deteriorated lands (Stewart and Young, 1939; Hull, 1949).

The nutritive value of B. tectorum compares favorably with that of many desirable grass species (Bovey et al, 1961), but its short growing season and fluctuating annual productivity combine to reduce the value of the forage on invaded ranges. Thus lands dominated by B. tectorum frequently serve as marginal spring-fall ranges with fall range use requiring water and protein supplements. This situation has prompted the seeding of invaded ranges to exotic species of wheatgrasses--primarily crested wheatgrass (Agropyron spicatum) (Cook and Harris, 1952).

Attempts at seeding have had mixed results, usually at the expense of the more desirable perennial species (Rummel, 1946; Hull and Stewart, 1948; Evans, 1961; Hull, 1963, 1964; Kay and Evans, 1965; Evans et al, 1970).

Young et al (1969) studied the population dynamics of B. tectorum in an effort to clarify the failures of revegetation attempts. They concluded that variations in B. tectorum seed production and the phenomenon of continuous seed germination were primary factors in the competitive advantage enjoyed by B. tectorum.

Other studies dealing with the competitive advantage exhibited by B. tectorum indicate that complete utilization of available soil moisture is the primary reason for its success (Hulbert, 1955; Harris, 1967). Its shallow, but extensive fibrous root system, fall germination and establishment and early spring growth initiation provide a considerable advantage over slower growing perennial species (Hull, 1963). These factors are especially important in seasons of below average precipitation (Evans et al, 1970).

Studies by Hironaka (1961) disclosed that B. tectorum root growth preceeded that of medusahead (Taeniatherum caput-medusa Nev.) by one phenologic stage and that B. tectorum roots penetrated to a greater depth. Thus, B. tectorum enjoyed a competitive advantage for available soil moisture even against this weedy species.

The matter of interspecific competition seems quite clear but of intraspecific competition is more involved. Harris (1967) observed that

sparse and dense stands of B. tectorum underwent the same degree of soil moisture depletion. These observations suggest that factors other than soil moisture limit B. tectorum productivity.

Kay and Evans (1965) reported increases in B. tectorum productivity due to the addition of nitrogen fertilizer. Fertilization also increased competition for soil moisture between B. tectorum and Agropyron intermedium. They concluded that nitrogen stimulated root growth and therefore the depletion of soil moisture. Similar studies by Smika et al (1961) and D'Aoust and Tayler (1968) support this hypothesis.

Early studies by Muller (1953) revealed that two desert shrub genera (Encelia and Franseria) were capable of producing toxins which killed other plant seedlings in laboratory cultures. However, the effect of these toxins in natural systems was overcome by the ability of the longer lived Franseria crowns to intercept and collect airborne soil and other debris which provide suitable environments for herbaceous plant germination and growth. Robertson (1947) noted much the same phenomenon with A. tridentata. The shrub crown reduced wind movement and evaporation of soil moisture. Shrub influence over B. tectorum growth was positively correlated with crown canopy area and extended to a distance of one meter from the crown center. No causative agent for this effect was suggested.

Garcia-Moya and McKell (1970) studied the relation of shrubs to the nitrogen economy of a desert wash ecosystem. They found that in such arid regions the shrubs and their immediate environs acted as reservoirs

of the community's nitrogen supply. Bjerregaard (1971) reported that while the soil was the greatest reservoir of nitrogen in salt desert shrub communities, the nitrogen existed in forms which were "microbial in origin and thus a very stable terminal residue of decomposition not subject to further transformation of any consequence by microorganisms". He concluded that the small quantities of nitrogen present in litter and its partly decomposed residue served as the most available sources of nitrogen for the plant community.

The present study was undertaken to investigate the nutrient relationship of a shrub-annual grass plant community with respect to precipitation and shrub canopy cover.

Specific objectives were as follows:

- 1) To study the utilization of added seasonal precipitation by B. tectorum, B. japonicus, and A. tridentata.
- 2) To compare A. tridentata understory and interspace habitats with respect to B. tectorum and B. japonicus productivity and nitrogen content.
- 3) To compare A. tridentata understory and interspace habitats with respect to soil moisture content and total soil nitrogen content.

METHODS

Study Site

A relatively homogeneous A. tridentata-winter annual bromegrass desert plant community served as the study site. It was located 33 kilometers west of Logan, Utah, on the benchlands of the Wasatch Front at a latitude of $41^{\circ} 42' 31''\text{N}$ and longitude of $112^{\circ} 5' 1''\text{W}$.

The soil is a gravelly loam of the Sterling Series. It is a member of the loamy-skeletal, mixed, mesic, family of Typic Calciustolls (Soil Survey, Davis-Weber, 1968: Soil Survey, Box Elder-East, No date). Sterling Series soils are formed on mixed lake sediments predominantly from limestone and quartzite. The upper 36 cm is a gravelly loam and is underlain by highly calcareous gravel beds. The slope is 10 to 20 percent. Annual precipitation is 510 mm at this particular site (U.S. Geological Survey, No date) and the frost-free period is 120 to 150 days. Elevation is 1400 meters above sea level.

Six study plots were established within a 75 x 35 meter cattle-proof fenced area located one kilometer southeast of the highway intersection in Deweyville, Utah. Each plot measured 10 x 10 meters and was at least 5 meters distance from all other plots.

The study site was stratified into shrub understory and interspace to account for the observation that understory bromegrass biomass greatly exceeded that in the interspace. Shrub canopy cover, soil bulk density and soil texture were measured to quantify and differentiate the habitats.

Shrub canopy cover was estimated by running two line transects diagonally across each 10 x 10 meter study plot. Cover estimates ranged from 24 to 59 percent. The mean shrub canopy cover of 43 percent coincided with the observation made by Robertson (1947) that a shrub canopy cover in excess of 40 percent results in a decided reduction in interspace B. tectorum productivity.

Soil bulk density cores were taken from surface (1 cm) and sub-surface (15 cm) depths in both shrub understory and interspace habitats. The mean bulk density values were 1.25 with sampling variation (values ranged from 1.13 to 1.34) overshadowing any habitat or depth difference.

Soil samples were analyzed for particle size distribution by the hydrometric method (Bouyoucos, 1962). No differences due to depth (1 and 15 cm) or habitat were observed. The soil was 40 percent sand, 40 percent silt and 20 percent clay.

No grazing was observed on this site during the study period. The landowner had grazed his livestock at higher elevations for several years prior to this study. Local residents attested to the indiscriminate burning practice of the past and also to the excellent condition of the range prior to grazing pressure.

Treatment

An irrigation treatment was applied to three of the six study plots. This treatment simulated conditions of above normal rainfall during the spring growth period from March through May.

Water was trucked from the town of Deweyville and then pumped via a system of plastic irrigation hoses to four Rainbird sprinklers placed one to a corner of each treated plot.

Irrigation water was added at a calculated average rate of 12-15 mm per week per 10 x 10 meter plot. The irrigation treatment was applied for eight weeks.

Water Status

Since irrigation was the treatment used to stimulate a year of abundant annual grass growth, it was essential that the amount of natural precipitation and soil moisture content be monitored.

Precipitation

Natural precipitation was measured using two 20-cm diameter rain gauges. The gauges were placed at the north and south ends of the study

area. Measurements were taken monthly except during the spring when readings were taken every two weeks.

Soil moisture

Soil moisture content was measured gravimetrically on a dry weight basis. Soil samples were collected at 1-cm and 15-cm depths in both understory and interspace habitats every two weeks during the spring and monthly thereafter.

Productivity

Annual plant growth was assessed in relation to nitrogen content within this shrub-annual bromegrass plant community. To determine productivity a means of quantifying the biomass of each plant system component was developed. The biological system was divided into four components: 1) annual bromegrasses; 2) shrubs; 3) annual forbs; and 4) soil. Each component was further subdivided into ecologically significant parts as described in the following sections.

The basic sampling unit for the biomass of each system component was an individual A. tridentata shrub. Each shrub from which samples were to be collected was randomly selected from a plot according to a grid system. A random numbers table was used to select individual points on a one-meter interval grid. The closest living shrub to each grid point was then used as the plant biomass sampling unit.

Bromegrass biomass

The shrub community was stratified into shrub understory and interspace habitats to reduce the variability in assessing bromegrass productivity due to competitive effects of the shrub canopy. The understory was considered to be that area immediately under the shrub canopy as well as the area extending 20 cm out from the shrub canopy perimeter. The 20-cm distance was used to reduce the edge effect of the shrub canopy. Shrub interspace habitat was the area not defined as shrub understory (Figure 1).

Ten A. tridentata shrubs were selected in each plot using the grid system. Placement of the bromegrass sampling quadrat entailed the selection of a quadrant adjacent to the shrub which would permit it to be located along a single line radiating outward from the shrub center. Each quadrant was chosen randomly and if it did not meet the sampling criteria due to the sample shrub's proximity to another shrub in that quadrant, the next quadrant in the numerical sequence was chosen. The northeast quadrant was number 1 and the northwest quadrant was number 4. The number of the quadrant selected was not recorded as the intent of this project was not to investigate the effect of aspect on bromegrass productivity.

A 20 x 20-cm quadrat was used to obtain bromegrass biomass samples from each habitat about the sample shrub. In the shrub understory the quadrat frame was butted against the shrub's main stem. The grass was hand-pulled from the area within the quadrat and placed in a

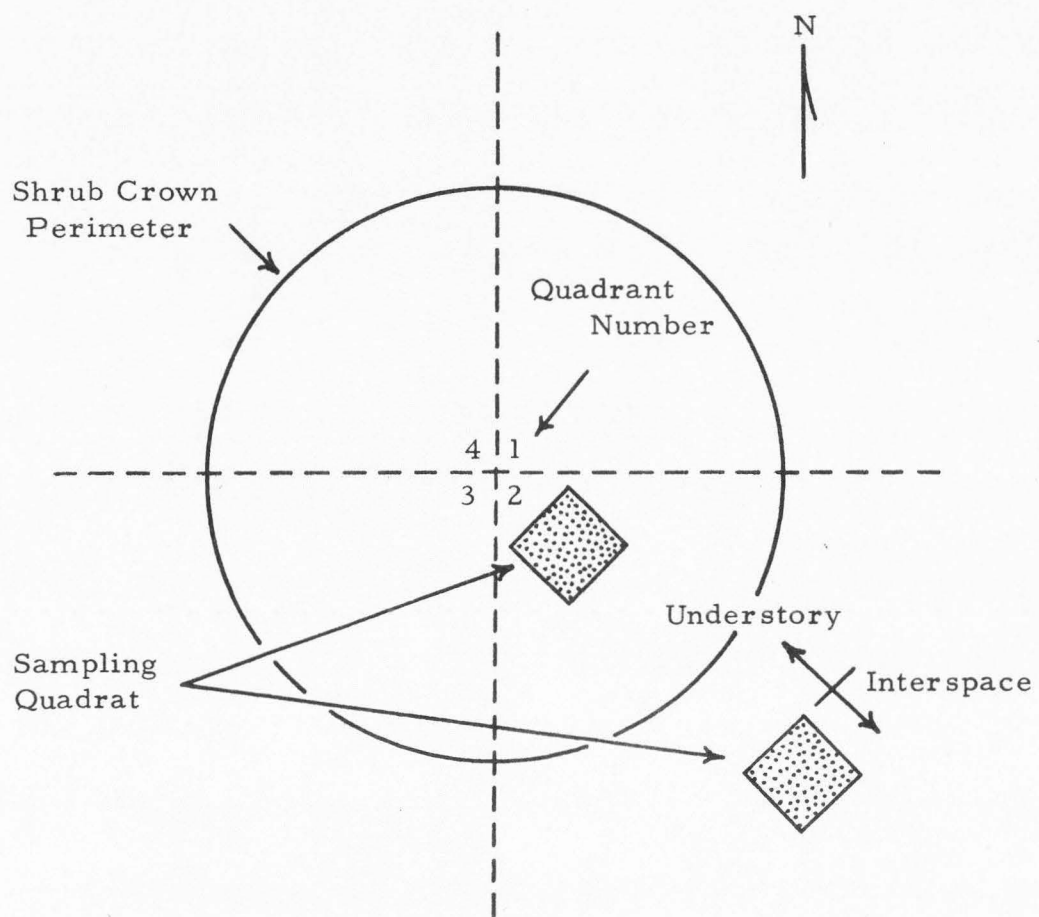


Figure 1. Bromegrass biomass sampling scheme.

paper bag for transfer to the laboratory. The inclusion of root material was negligible since the fine roots of the grasses were easily broken at the surface.

Interspace biomass samples were obtained by placing the quadrat edge at a distance of 20 cm from the shrub canopy perimeter. Quadrat placement was also in the same shrub quadrant as the understory bromegrass sample. Samples were bagged for transfer to the laboratory.

Location of each bromegrass sampling site was marked to prevent inadvertent resampling. In the event the same shrub quadrant was selected for sampling at a later date, an adjacent quadrant was sampled.

Biomass samples were collected on three separate dates. The first was in mid-April at the beginning of the experiment. Early June sampling at bromegrass maturity provided a measure of productivity by species. A final biomass sampling period in late September provided an estimate of decomposition loss for the summer period. The final biomass sample was collected after the fall germination of new bromegrass seedlings.

Bromegrass samples were also collected at frequent intervals between biomass sampling dates. These samples were used for nitrogen content analysis and no biomass estimates were made. From April to June samples were collected twice a month. From June to September a monthly collection was made. Only two shrubs per plot were used as sampling units during these intermediate sampling periods.

In the laboratory the bromegrass samples were separated into new (living plants) and old growth (litter) fractions. Only in June was it possible to identify the bromegrass by species based on the emergence of the inflorescences and the development of coloration caused by differences in maturity. After separation the samples were oven-dried and weighed.

Shrub growth rate

To determine the effect of irrigation treatment on shrub growth an investigation into the relative rate of vegetative growth was conducted. A small spot of red paint was applied to the bud scales of the new portion of two living stems on each of four randomly selected A. tridentata plants per plot. Stem length measurements were recorded monthly. Measurement was to the nearest one half centimeter from the paint spot to the tip of the stem.

The absolute shrub growth measurements were converted to a relative growth rate defined as the rate of increase in stem length per unit of stem length present (Kvet et al, 1971). Relative growth rates in irrigated and control plots were then compared for statistical differences.

Forb biomass

An estimate of the biomass of the annual forb Ranunculus testiculatus was made. Samples were collected from both interspace and understory habitats before maturity in early spring (15 April 1972). Forb samples were collected coincident with bromegrass samples and were separated from them in the laboratory.

Nitrogen

All vegetative material and soil samples were analyzed for percent total nitrogen content. The Semimicro-Kjeldahl method described by Bremner (1965) and modified by Bjerregaard (1971) to deal with the low nitrogen levels in desert soils was used to analyze the 1500 samples collected during this project. Modification included use of sample weights containing at least twice the recommended 1 mg N, elimination of the water pre-treatment for clay soils, reduction of the digestion period from five hours to two hours since 98 percent of the nitrogen is assumed to be liberated in this short time, collecting of condensate in double the amount of boric acid-indicator solution, and titration with 0.1N sulfuric acid rather than 0.01N.

Plant material

On a given sampling date bromegrass biomass samples from each plot were composited by habitat and species (June only). Duplicate samples of bromegrass material were then analyzed for total nitrogen content. Forb biomass samples from each plot were composited by habitat. Single samples were analyzed for total nitrogen content.

Soil

Soil samples were obtained from the shrub understory and inter-space habitats at depths of 1 and 15 cm. These depths were selected on the basis of being areas of major change within the rooting zone of the annual bromegrasses. The cobbly nature of the soil profile also

limited the depth to which samples could be easily obtained.

Soil samples were collected every two weeks during the spring and monthly thereafter. Vegetation was removed from the surface and the 1-cm depth soil sample was collected from each habitat. A hole was then dug at the same site to obtain the 15-cm depth sample.

Soil samples were transferred to the laboratory in paper bags and allowed to air dry on a work bench for several days. This procedure prevented the volatilization of nitrogen compounds that would occur if dried at high oven temperatures. Drying time was sufficiently short that biological activity was curtailed soon enough to prevent major changes in nitrogen status (Bremner, 1965). The dried soil was then screened and bottled before duplicate samples were analyzed for total nitrogen content.

RESULTS

An A. tridentata-mixed annual bromegrass plant community was irrigated during the spring of 1972. Estimates of bromegrass biomass and nitrogen content, forb biomass and nitrogen content, shrub stem length, soil moisture and nitrogen content, and natural precipitation levels were recorded during the spring and summer of the study year. Factorial analysis of parameter values is presented in this section. The Neuman-Keuls test was employed to determine valid differences for all mean comparisons.

Precipitation

Natural precipitation was recorded monthly and is presented graphically in Figure 2. The 20-year (1951-1970) monthly average values are adjusted means computed from records at the Garland, Utah, weather station (8 kilometers NW of the study site) where the mean annual precipitation is 380 mm compared with the 510 mm mean for the study site (U. S. Geological Survey, No date). The irrigation treatment is incorporated in the graph as the calculated amount (12-15 mm/week/plot) added per month.

During the first fall germination period (Sept-Oct 1971) the study site received abundant rainfall (140 mm). Spring and summer months were drier than normal except for April; however, the 1972 fall germination period received ample rainfall for seedling establishment (41 mm). The irrigation treatment in March, April and May was sufficient to boost the "precipitation" received on irrigated plots to values well above the 20-year average.

Bromegrass Biomass

The results of the irrigation treatment were manifest as differences in bromegrass biomass (Figure 3). No significant difference existed between biomass in treated and control plots (68 versus 74 g/m²) when irrigation began in April. However, after eight weeks of irrigation treatment a significant treatment effect was observable. June

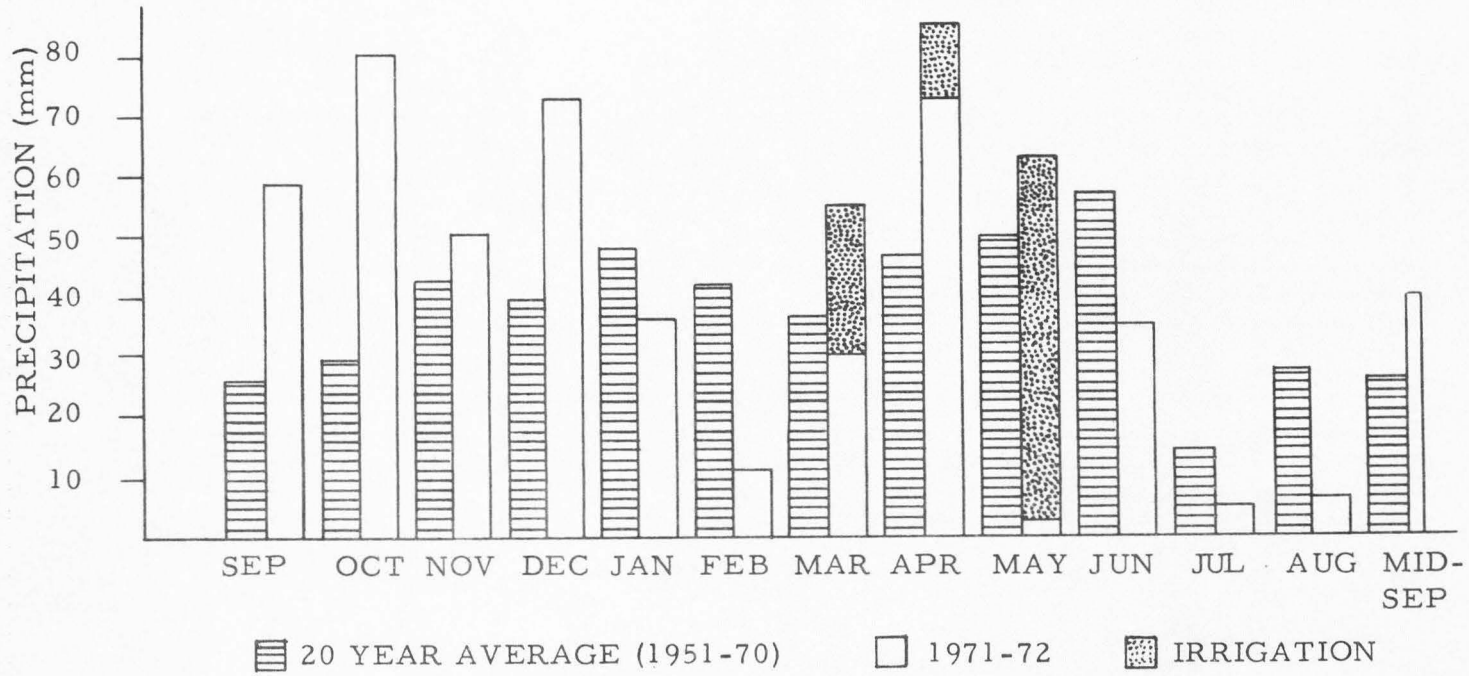


Figure 2. Monthly precipitation record for study site.

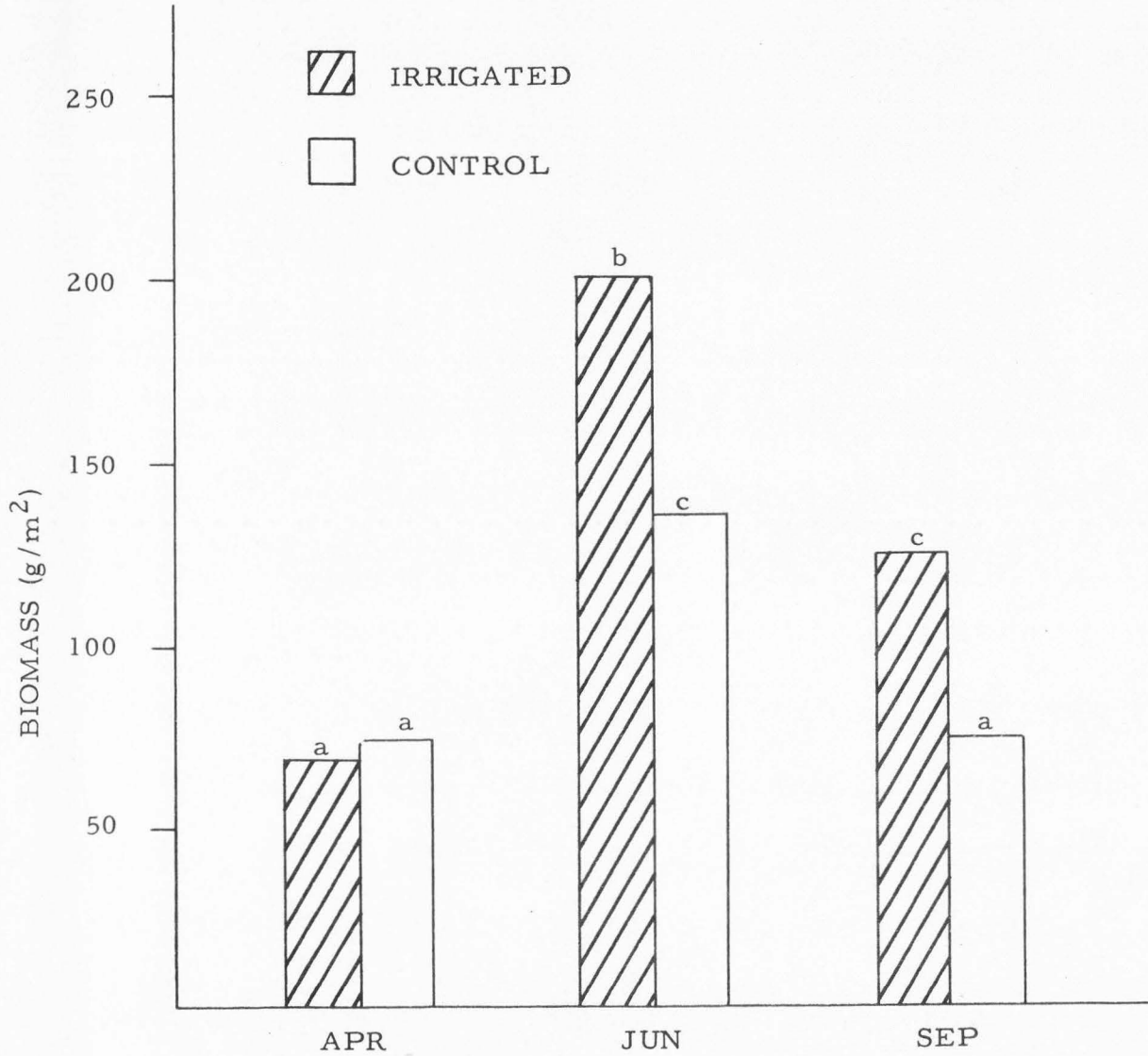


Figure 3. Bromegrass biomass compared by date and treatment for 1972. Like lower case letters denote statistically equivalent (.01) mean values.

bromegrass biomass in irrigated plots was significantly (.01) greater (200 g/m^2) than that in control plots (134 g/m^2) regardless of habitat. September bromegrass litter biomass also remained greater in treated plots (123 g/m^2) than in control plots (72 g/m^2). The interaction between date and treatment was significant indicating a greater bromegrass productivity in irrigated plots than in control plots after the initial April sampling data.

Regardless of treatment the shrub understory (Figure 4) maintained about a fourfold biomass advantage over the interspace (118 versus 23 g/m^2 in April; 262 versus 72 g/m^2 in June; and 154 versus 41 g/m^2 in September). Understory bromegrass biomass increased from 118 g/m^2 in April to 262 g/m^2 in June whereas interspace biomass increased from 22 g/m^2 in April to 72 g/m^2 in June regardless of treatment. A significant interaction existed between date and habitat indicating a greater increase in bromegrass productivity in the shrub understory than the interspace after the initial April sampling data regardless of treatment.

Bromegrass biomass in the understory (Figure 5) was significantly (.01) greater in irrigated plots (210 g/m^2) than in control plots (153 g/m^2) regardless of date. A significant difference also existed in interspace bromegrass biomass when irrigated plots (57 g/m^2) were compared to control plots (33 g/m^2) regardless of date. Also, the interaction between treatment and habitat was significant (.05) again indicating a greater bromegrass productivity response to irrigation in the understory than in the interspace habitat regardless of date.

Mean comparisons between species and treatment (Figure 6) for the June sampling period show that B. tectorum grew equally well in irrigated and control plots (106 and 80 g/m^2 respectively) while

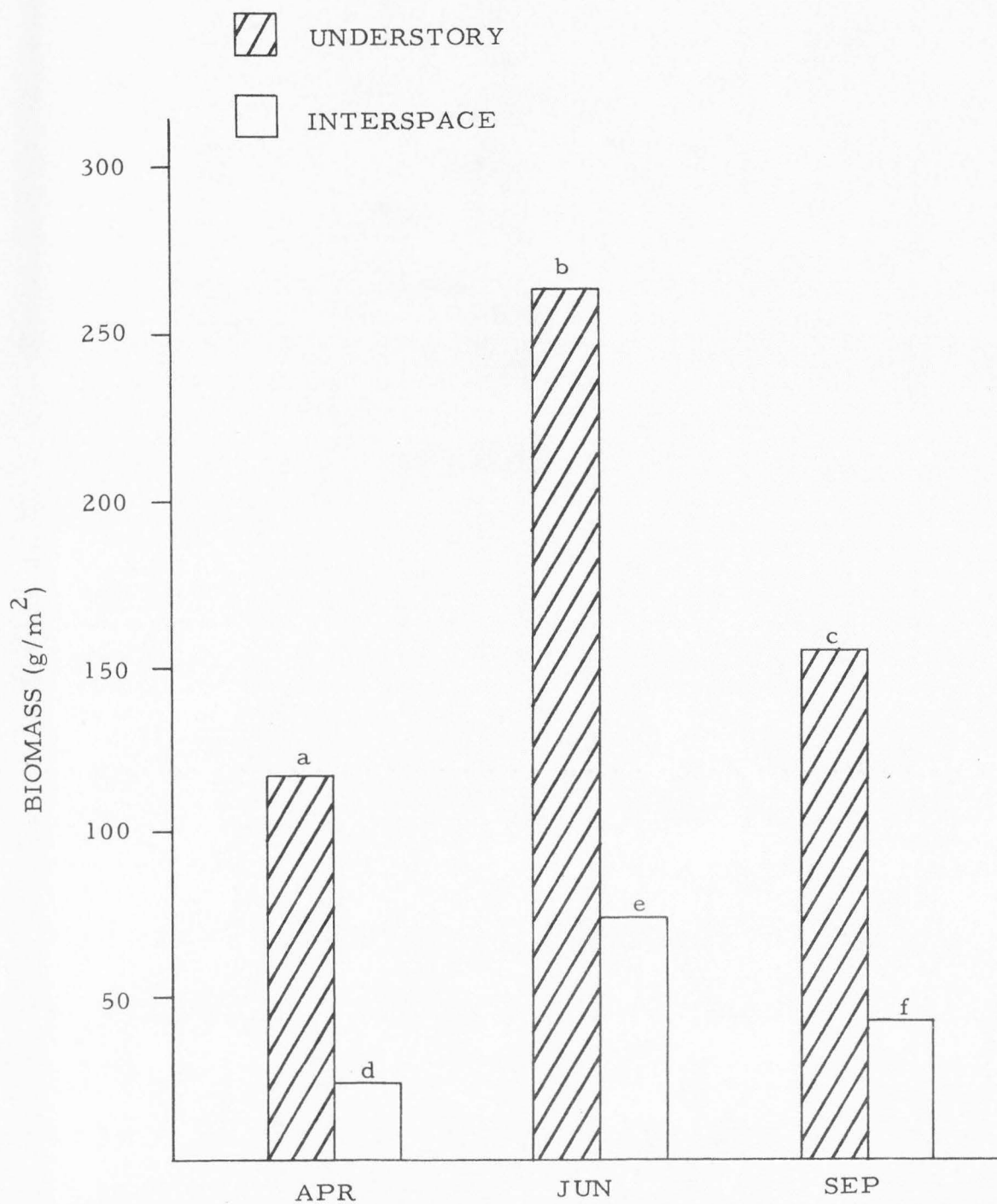


Figure 4. Bromegrass biomass compared by date and habitat for 1972. Like lower case letters denote statistically equivalent (.01) mean values.

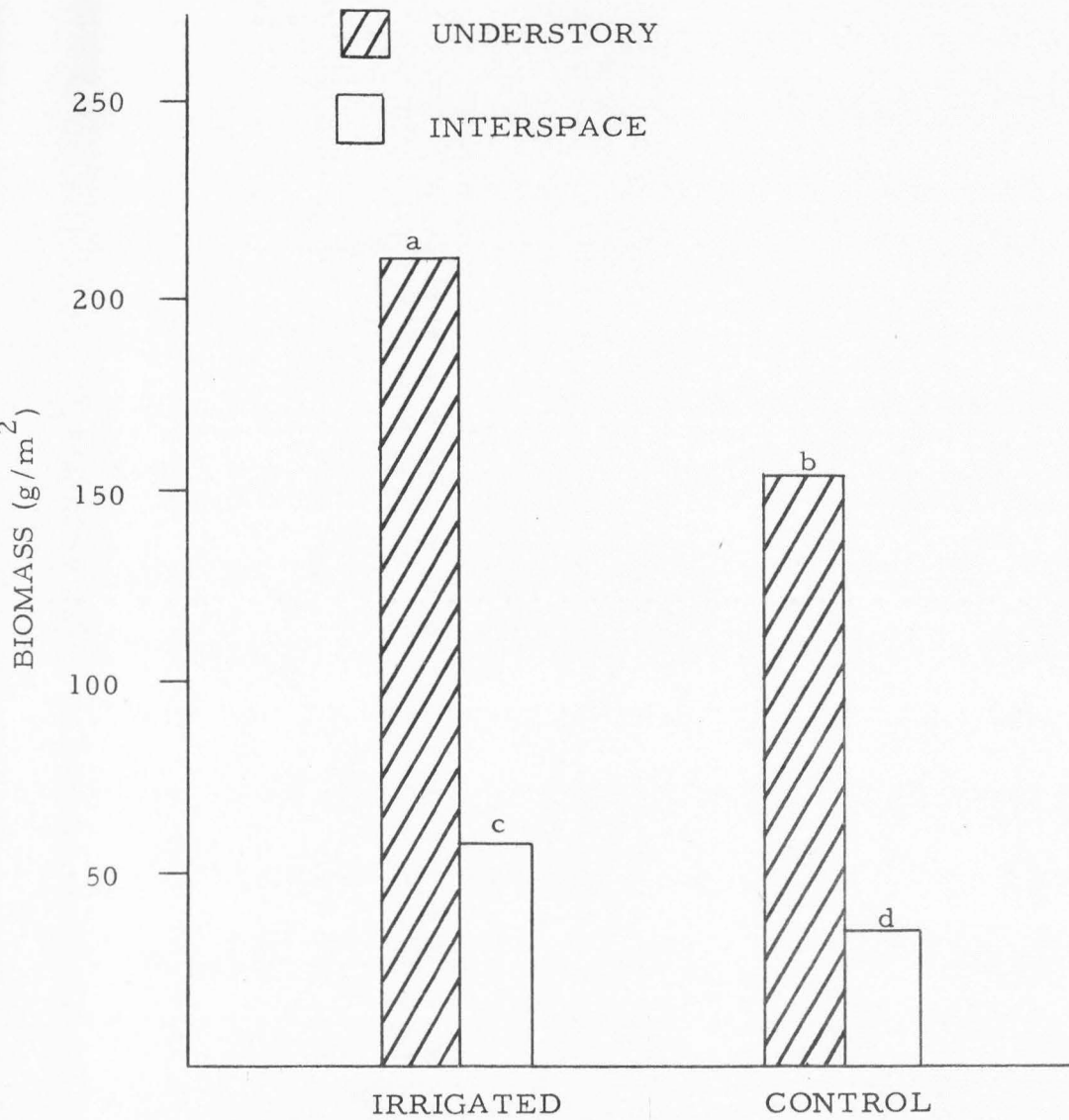


Figure 5. Bromegrass biomass compared by treatment and habitat for 1972. Like lower case letters denote statistically equivalent (.01) mean values.

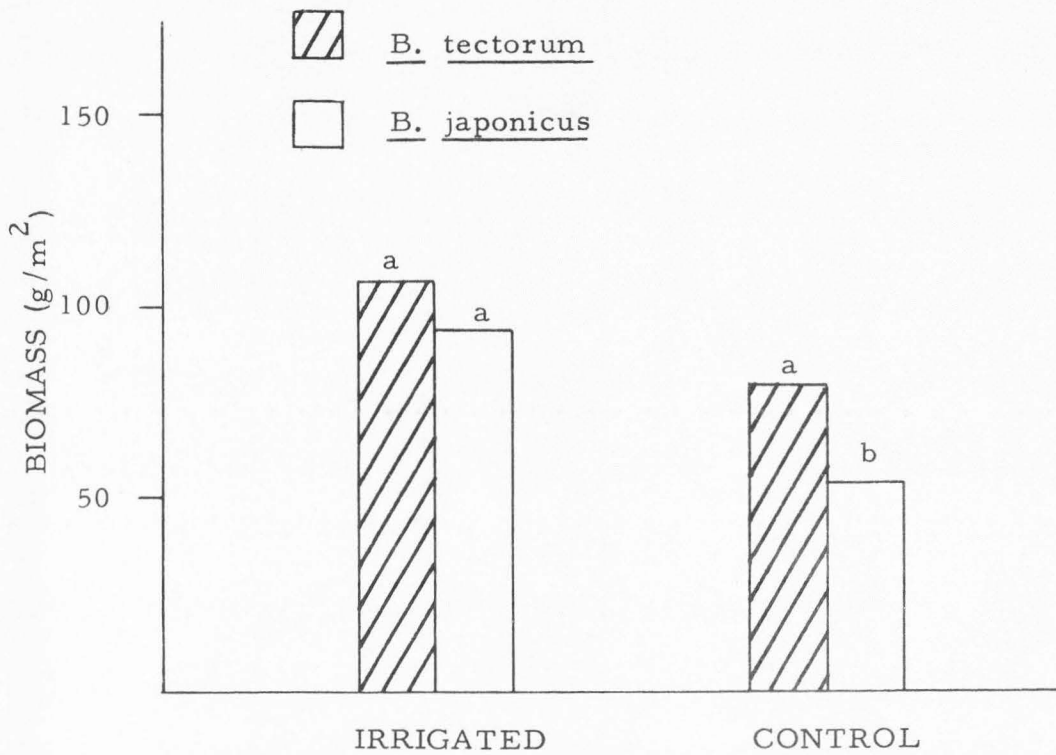


Figure 6. Bromegrass biomass compared by treatment and species for June 1972. Like lower case letters denote statistically equivalent (.01) mean values.

B. japonicus did significantly better (.01) in irrigated than control plots (93 versus 54 g/m²) when species differences within each treatment are compared without regard to habitat.

Species differences in June biomass (Figure 7) show that both B. tectorum and B. japonicus grew more abundantly in the shrub understory (154 and 109 g/m² respectively) than in the interspace (32 and 40 g/m² respectively). The data also show that B. tectorum had a significantly greater (.01) productivity in the understory habitat than did B. japonicus, while no species differences in biomass were noted in the interspace. The interaction between species and habitat was significant. It indicated that regardless of treatment B. tectorum grew significantly better (.01) than B. japonicus in the understory while interspace habitat productivity of both species was not dominated by either species.

Forb Biomass

Ranunculus testiculatus exhibited a significant preference (.01) for the interspace habitat on the April 1972 sampling date. Forb biomass in control plots was 45.2 g/m² in the interspace and only 2.3 g/m² in the understory (Table 1). A significant (.05) treatment difference existed in forb biomass values obtained in both the interspace (52.8 g/m²) and understory (9.2 g/m²) of irrigated plots.

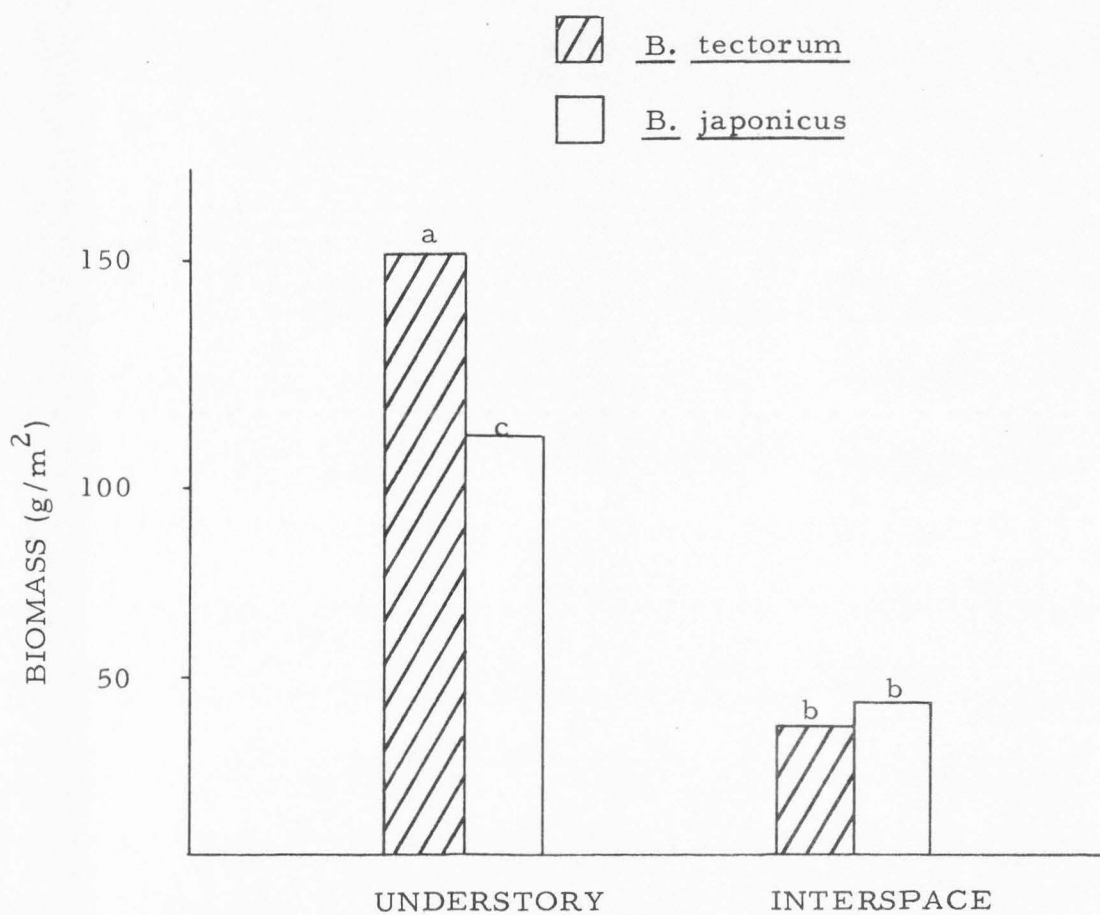


Figure 7. Bromegrass biomass compared by habitat and species for June 1972. Like lower case letters denote statistically equivalent (.01) mean values.

Table 1. Ranunculus testiculatus biomass and percent total nitrogen content for April 1972 compared by treatment and habitat. Like lower case letters in parentheses denote statistically equivalent (.01) mean values.

	<u>IRRIGATED</u>		<u>CONTROL</u>	
	Understory	Interspace	Understory	Interspace
BIOMASS (g/m ²)	9.2 (a)	52.8 (b)	2.3 (c)	45.2 (d)
TOTAL NITROGEN (%)	1.37 (e)	0.86 (e)	1.18 (e)	1.21 (e)

Forb Nitrogen

Total nitrogen content values for R. testiculatus (Table 1) revealed no significant difference due to treatment or habitat. Forbs in control plots showed a 1.18 percent nitrogen content in the understory versus 1.21 percent in the interspace.

Soil Moisture

Soil moisture content was measured gravimetrically and expressed as a percentage by weight. Soil moisture content was significantly greater (.01) in irrigated plots (12.2 percent) than in control plots (8.3 percent) regardless of date, habitat or depth. Soil moisture content was significantly greater (.01) in the understory (10.7 percent) than in the interspace (9.7 percent) regardless of date, treatment or depth.

Soil moisture content was significantly greater (.01) at the 15-cm depth (11.6 percent) than the 1-cm depth (8.9 percent) regardless of date, treatment or habitat.

The above comparisons of soil moisture content reflect the gross effects of irrigation, habitat and depth. Soil moisture comparisons between date and treatment (Figure 8) show significant differences (.01) due to treatment regardless of habitat or depth. The spring irrigation treatment increased the soil moisture content on treated plots during the treatment period. During the two sampling periods in the exceptionally dry period of May, control plots exhibited 7 and 4 percent soil moisture contents (respectively) while corresponding soil moisture contents of 17 and 13 percent were maintained in irrigated plots. The soil moisture content in treated and control plots was identical from July through September due to lack of irrigation treatment. The significant (.01) interaction between date and treatment soil moisture content values indicates that the irrigation treatment increased the soil moisture content above that experienced in control plots only during the spring growth period.

Mean comparisons of soil moisture content by date and habitat (Figure 9) showed that the understory soil moisture content was significantly greater (.01) than that of the interspace during the spring irrigation period and again in the fall when rains initiated bromegrass germination. These soil moisture differences amounted to no more than two percentage points and there is considerable overlap

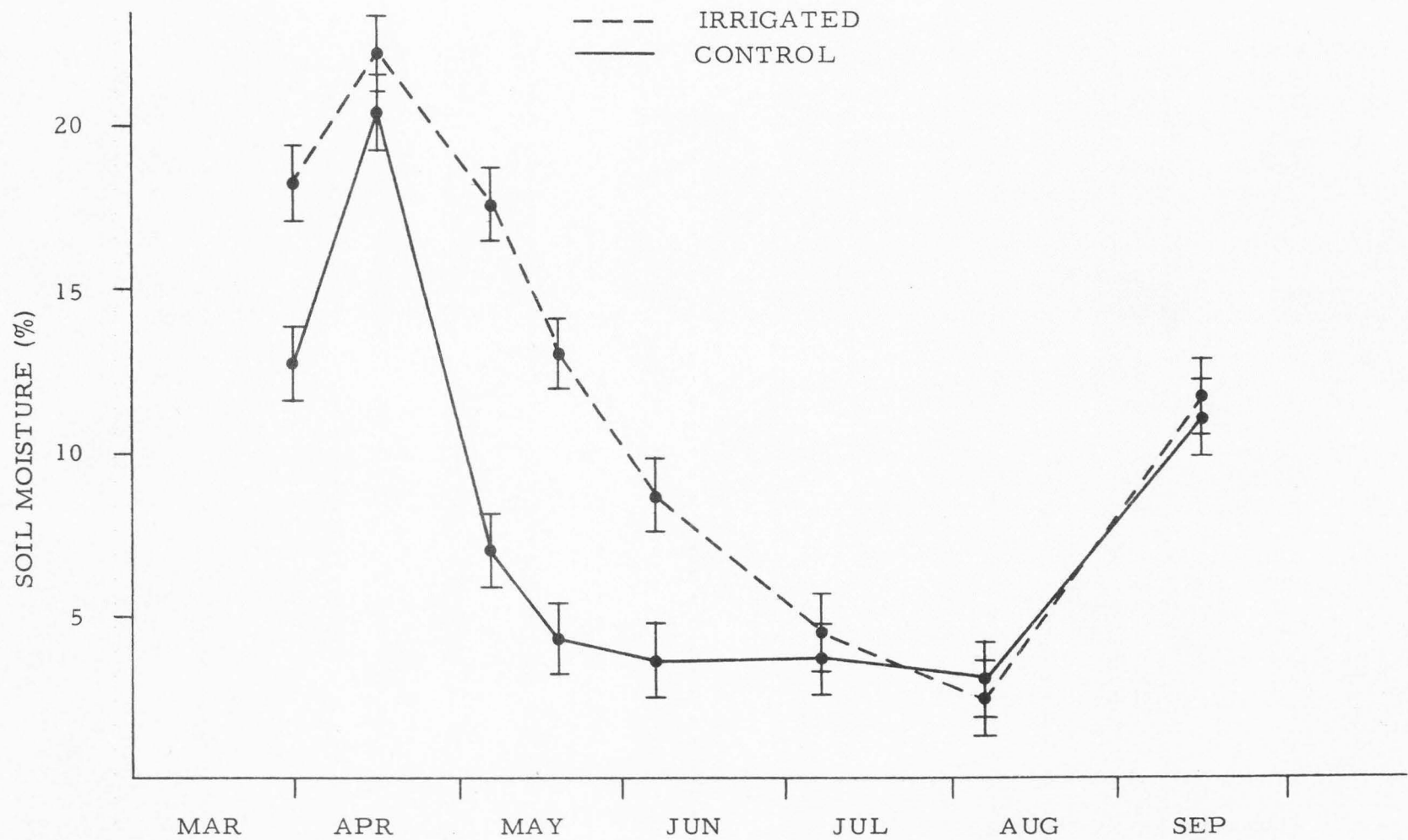


Figure 8. Percent soil moisture content compared by date and treatment for 1972. Ninety nine percent confidence limits are shown.

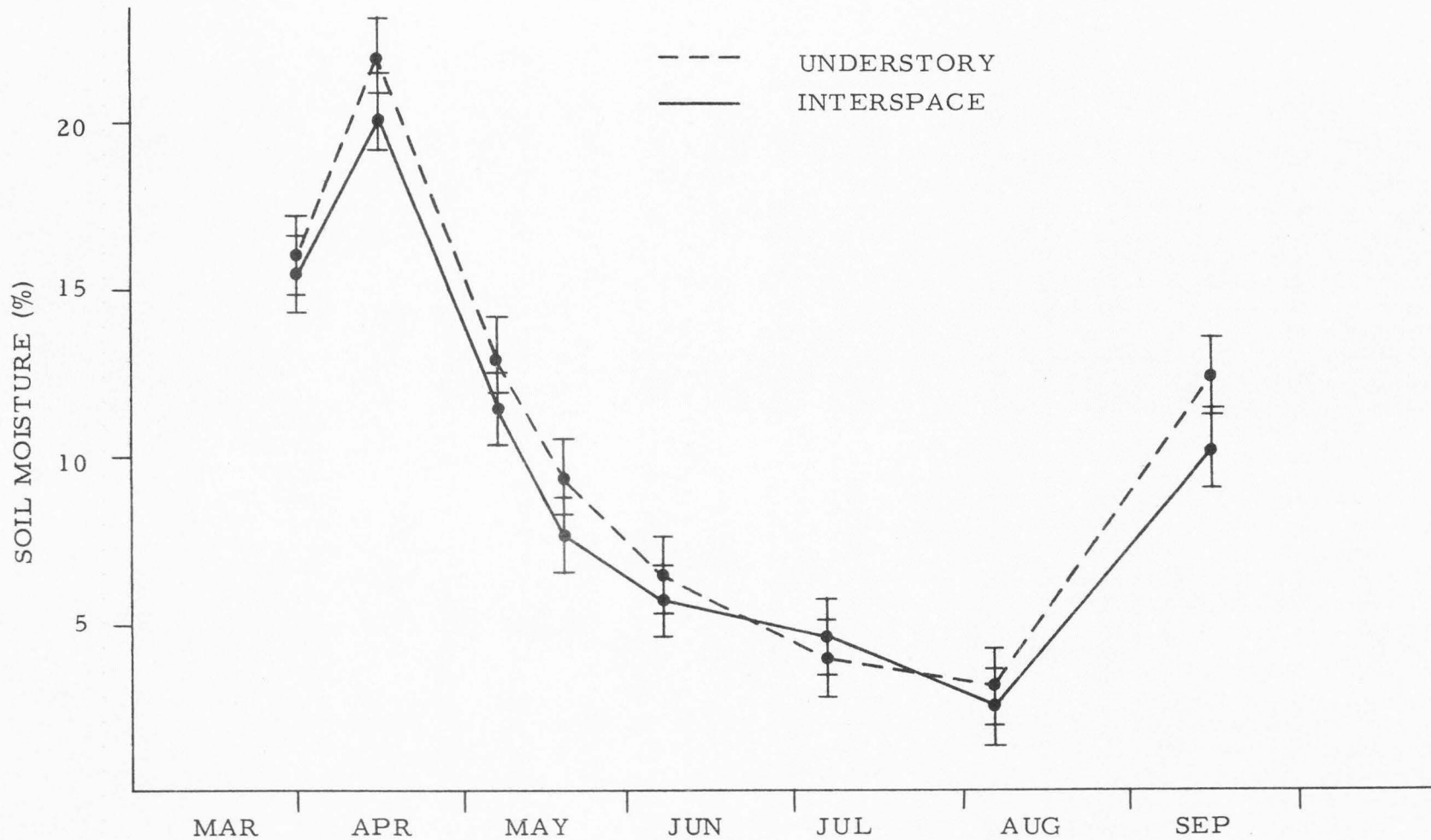


Figure 9. Percent soil moisture content compared by date and habitat for 1972. Ninety nine percent confidence limits are shown.

in the confidence limits (99 percent) of the mean values. No habitat differences existed during the summer months. The significant (.01) interaction between date and habitat soil moisture content values indicates that the understory was able to maintain a microclimate more amenable to plant growth only during the normal spring and fall wet periods.

When compared by treatment and habitat (Figure 10) soil moisture content was significantly greater (.01) in the irrigated understory (12.9 percent) than in the irrigated interspace (11.5 percent). No such difference was noted in control plots; however, control plots had a lower soil moisture content (8 percent) than irrigated plots.

Soil Nitrogen

The understory had a significantly (.01) greater total nitrogen content (0.149 versus 0.128 percent) than the interspace regardless of date, depth or treatment. Analysis with respect to depth indicated that the 1-cm depth had a greater total nitrogen content than the 15-cm depth (0.156 versus 0.121 percent) regardless of date, treatment or habitat.

Comparisons of the percent total soil nitrogen content with respect to date and treatment (Figure 11) showed a significant (.05) treatment difference. In addition, a seasonal trend was evident in irrigated plots. This trend corresponded well with bromegrass phenology. Soil nitrogen levels were high in spring (0.150 percent) when bromegrasses were vegetative; levels decreased with bromegrass maturity (0.136 percent); and then increased as litter decay released nitrogen into the soil.

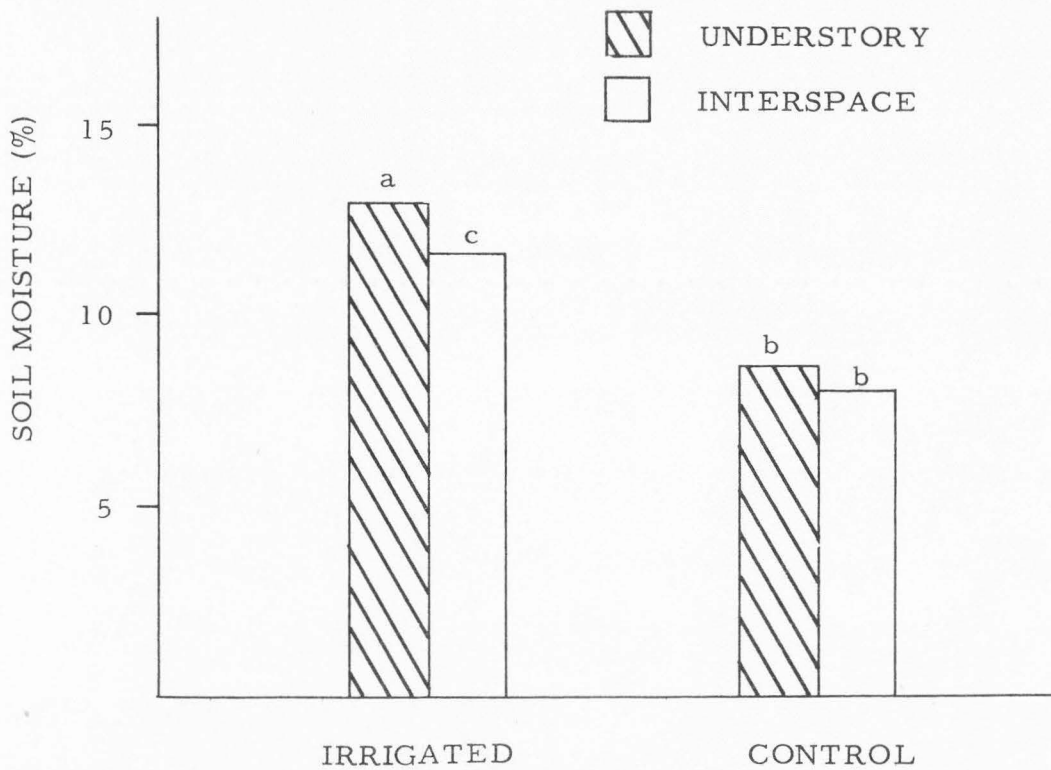


Figure 10. Percent soil moisture content compared by treatment and habitat in 1972. Like lower case letters denote statistically equivalent (.01) mean values.

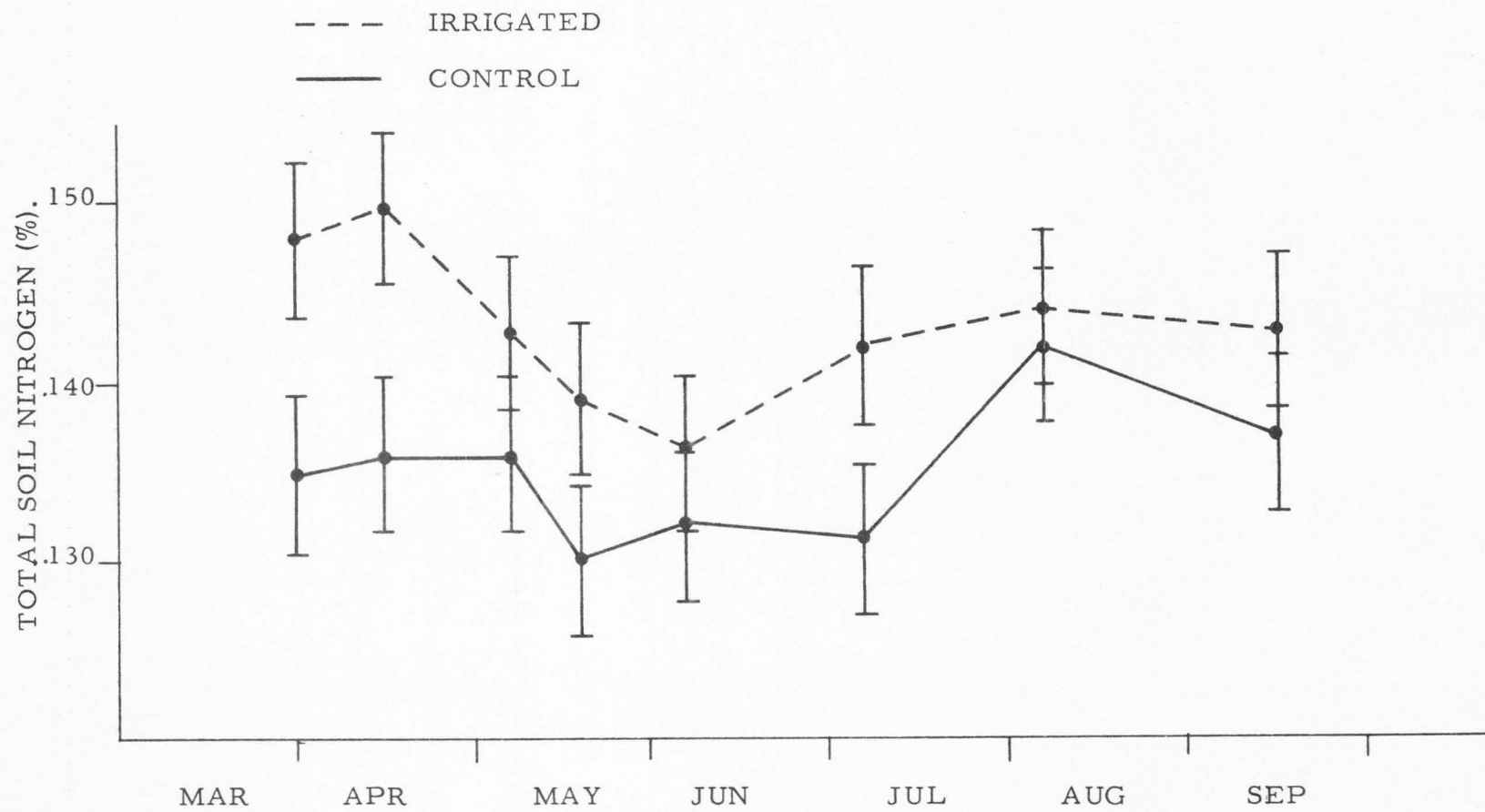


Figure 11. Percent total soil nitrogen content compared by date and treatment for 1972. Ninety five percent confidence limits are shown.

Percent total soil nitrogen content by date and habitat (Figure 12) was significantly greater (.05) in the understory than in the interspace. Total nitrogen content in the interspace soil did not differ during the entire study period while the understory exhibited a considerable variation in conjunction with bromegrass phenology regardless of treatment, date or depth.

Percent total soil nitrogen content mean comparisons by treatment and habitat (Figure 13) showed significantly greater (.01) values in treated plots and in the understory habitat. Understory nitrogen content was 0.154 percent in treated plots and 0.145 percent in controls regardless of depth or date. Interspace values were 0.131 percent in treated plots and 0.124 percent in controls regardless of depth or date.

Bromegrass Nitrogen

Bromegrass total nitrogen content decreased threefold from April to September (1.56 versus 0.59 percent). A negative irrigation effect was clearly established by the June maturity date and was maintained throughout the summer (Figure 14). This nitrogen "dilution effect" is due to increased bromegrass biomass production on irrigated plots and is evidenced by the fact that the nitrogen content in June was significantly (.01) lower (0.81 versus 0.96 percent) in bromegrass from treated than control plots regardless of species or habitat when expressed as a percentage by weight. The significant (.01) interaction between date and treatment values for bromegrass percent nitrogen

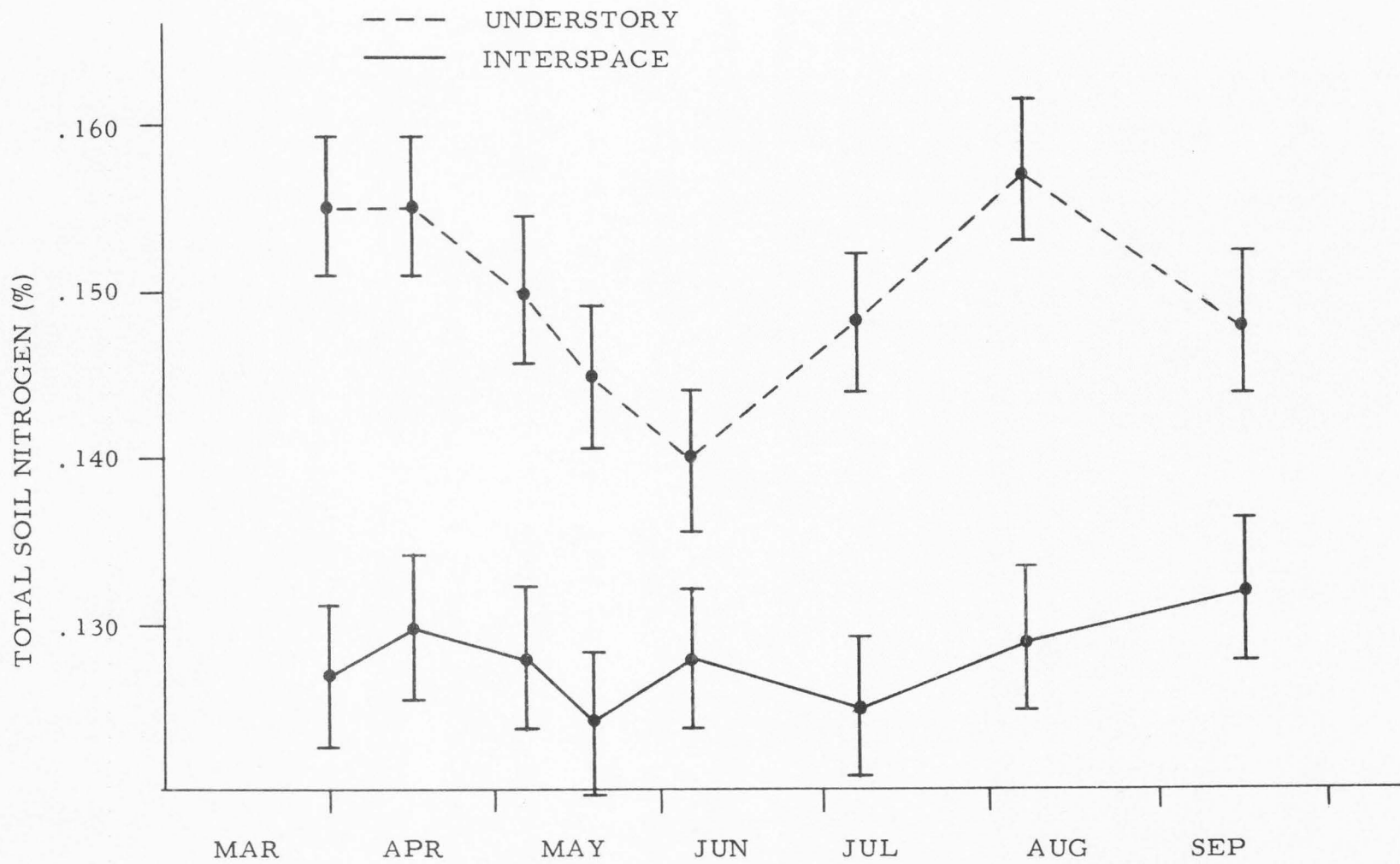


Figure 12. Percent total soil nitrogen content compared by date and habitat for 1972. Ninety five percent confidence limits are shown.

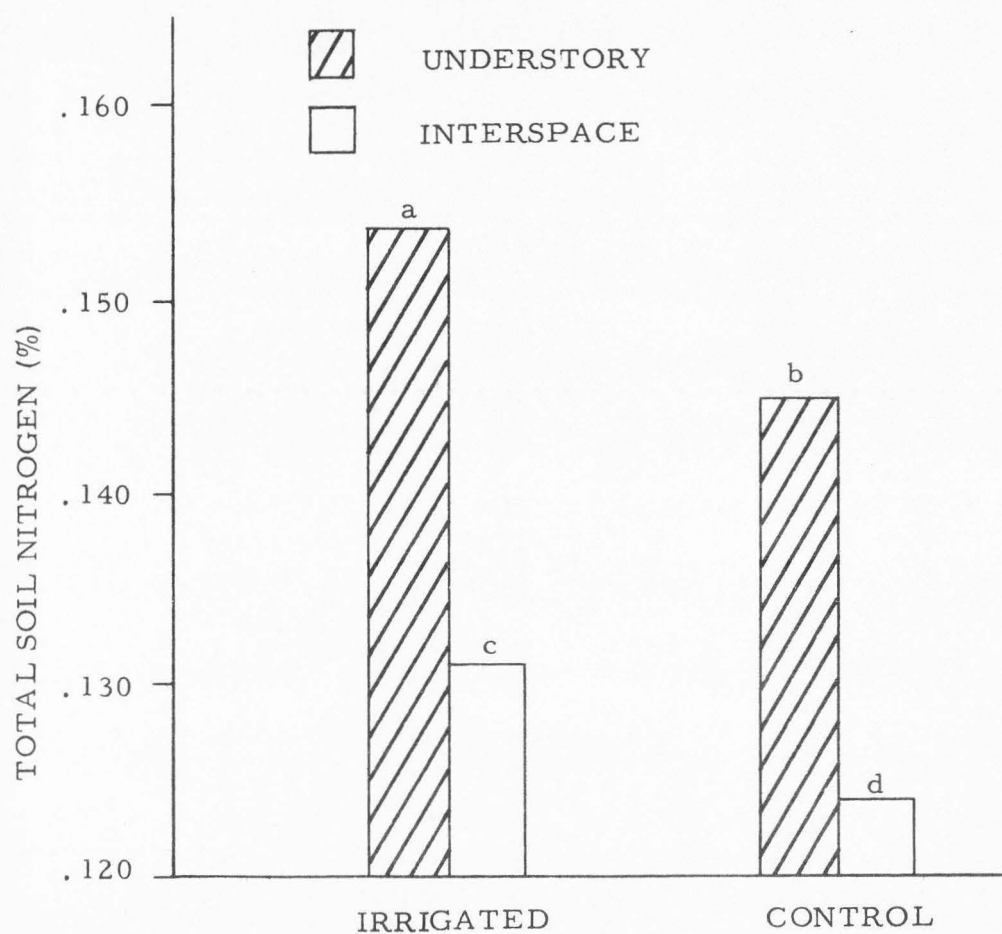


Figure 13. Percent total soil nitrogen content compared by treatment and habitat for 1972. Like lower case letters denote statistically equivalent (.01) mean values.

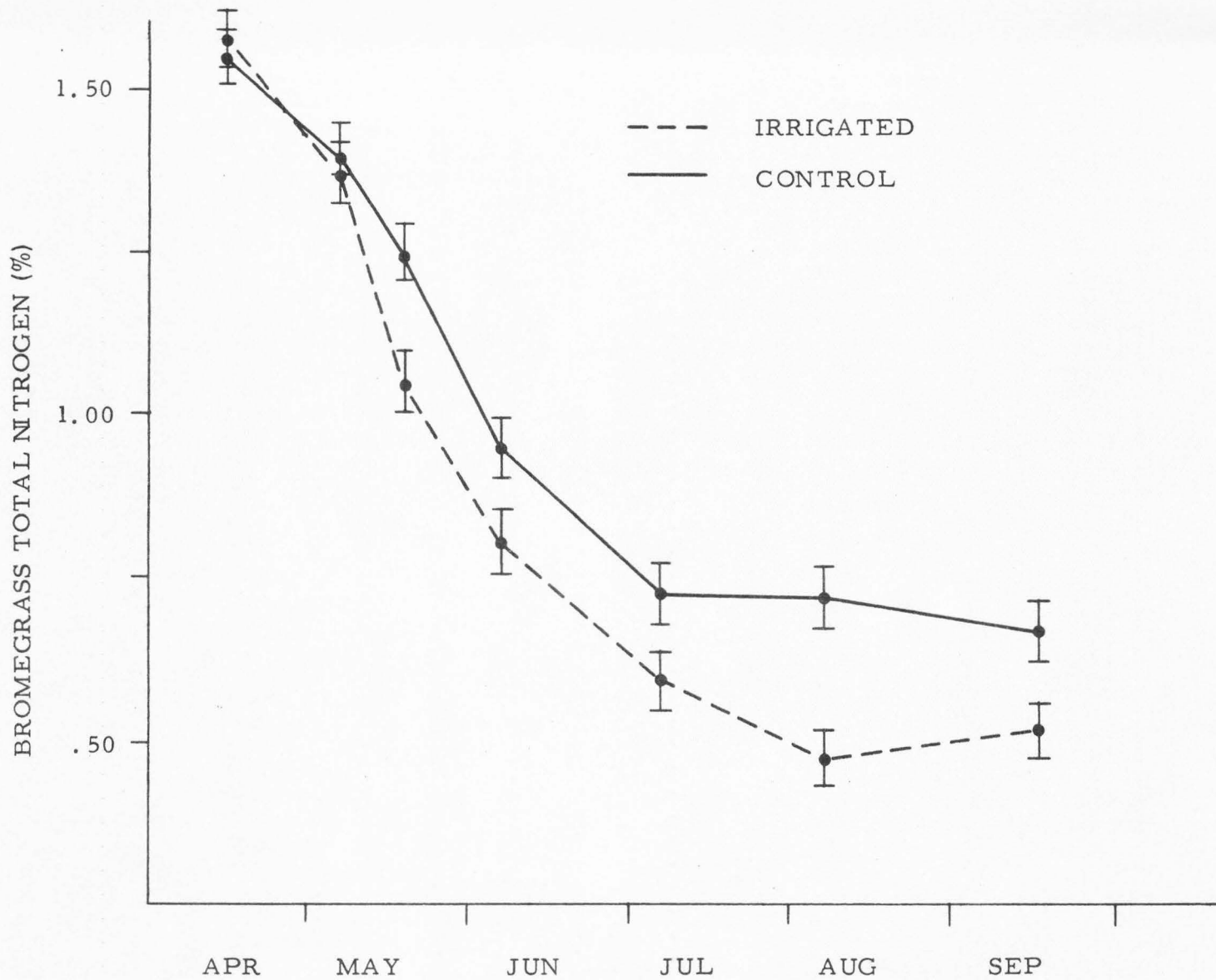


Figure 14. Bromegrass percent total nitrogen content compared by date and treatment for 1972. Ninety nine percent confidence limits are shown.

content also indicates that spring irrigation treatment produced a significant decrease in bromegrass nitrogen content only during the spring growth period and not in the following summer months.

The nitrogen content dilution effect due to differences in biomass production is also evident when habitat differences are compared over time (Figure 15). The abundant spring understory growth resulted in a significantly (.05) lower nitrogen content in that habitat (1.42 percent) compared to the interspace (1.69 percent) in April 1972. This habitat difference was maintained through the bromegrass June maturity date; however, litter decay during the summer rapidly reduced the bromegrass nitrogen content in control plots to levels found in irrigated plots (0.65 percent). The interaction (.01) between date and habitat also indicates that understory bromegrass nitrogen content is less than that in the interspace during the spring growth period but not during the summer decay period.

Bromus tectorum had a significantly higher (.01) nitrogen value in June than B. japonicus (1.03 versus 0.74 percent) regardless of treatment or habitat. This difference is most probably a species characteristic. If differences in maturity date or productivity were the cause, then B. japonicus (late maturing specie) would have had the higher percent nitrogen content in June since the common case is for the percent nitrogen content to decrease (Figure 14) with maturity (Bovey et al, 1961).

Nitrogen uptake by bromegrass was determined for the June sampling period by multiplying each biomass data point by the mean

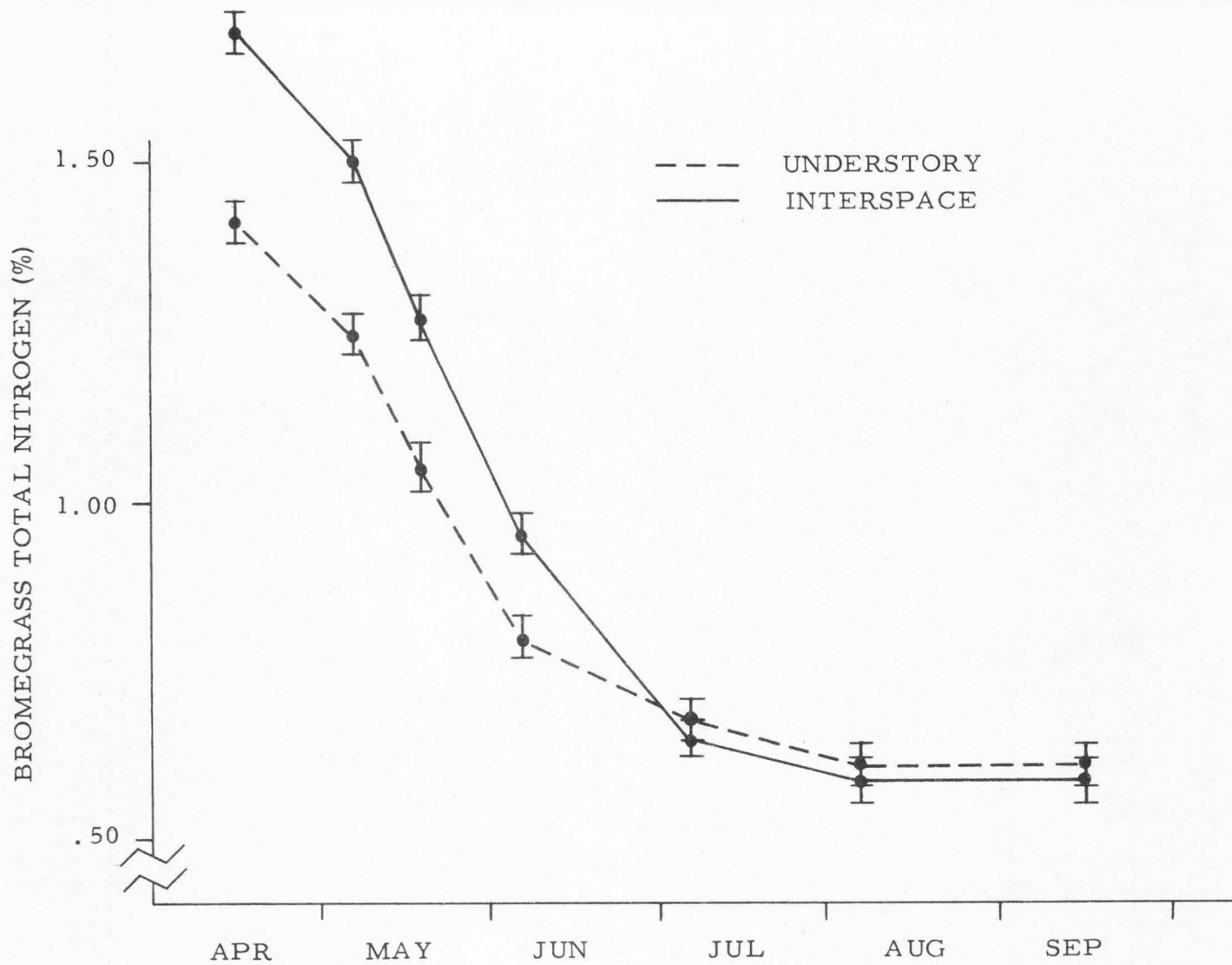


Figure 15. Bromegrass percent total nitrogen content compared by date and habitat for 1972. Ninety five percent confidence limits are shown.

bromegrass percent nitrogen content corresponding to the treatment and habitat from which the biomass sample was obtained. A similar bromegrass litter nitrogen retention value was calculated for the September sampling period. The values obtained express the bromegrass nitrogen content in grams of nitrogen per unit area.

June nitrogen assimilation values for species did not differ regardless of treatment or habitat. Bromus tectorum assimilated 66 gN/m^2 while B. japonicus assimilated 72 gN/m^2 . June nitrogen assimilation and September nitrogen retention values compared by treatment (Figure 16) show that irrigated plots exhibited a significantly higher (.01) bromegrass nitrogen content on both dates (78 and 65 gN/m^2 respectively) than did the control bromegrass (60 and 47 gN/m^2 respectively) regardless of habitat. Comparison of nitrogen assimilation and retention by habitat on the same dates (Figure 17) shows that the understory plants contained significantly (.01) more nitrogen (105 and 90 gN/m^2 on respective dates) than did the interspace plants (33 and 22 gN/m^2 on respective dates).

The effect of irrigation on bromegrass percent nitrogen content was in a negative direction (Figure 14) while total nitrogen assimilation measured in grams of nitrogen per unit area was positive (Figure 16). The reason for this difference in nitrogen content is the increased bromegrass productivity noted in both the understory habitat and in treated plots (Figures 3 and 4). Thus, when expressed both as a percent nitrogen content and as total nitrogen assimilation by bromegrass, the

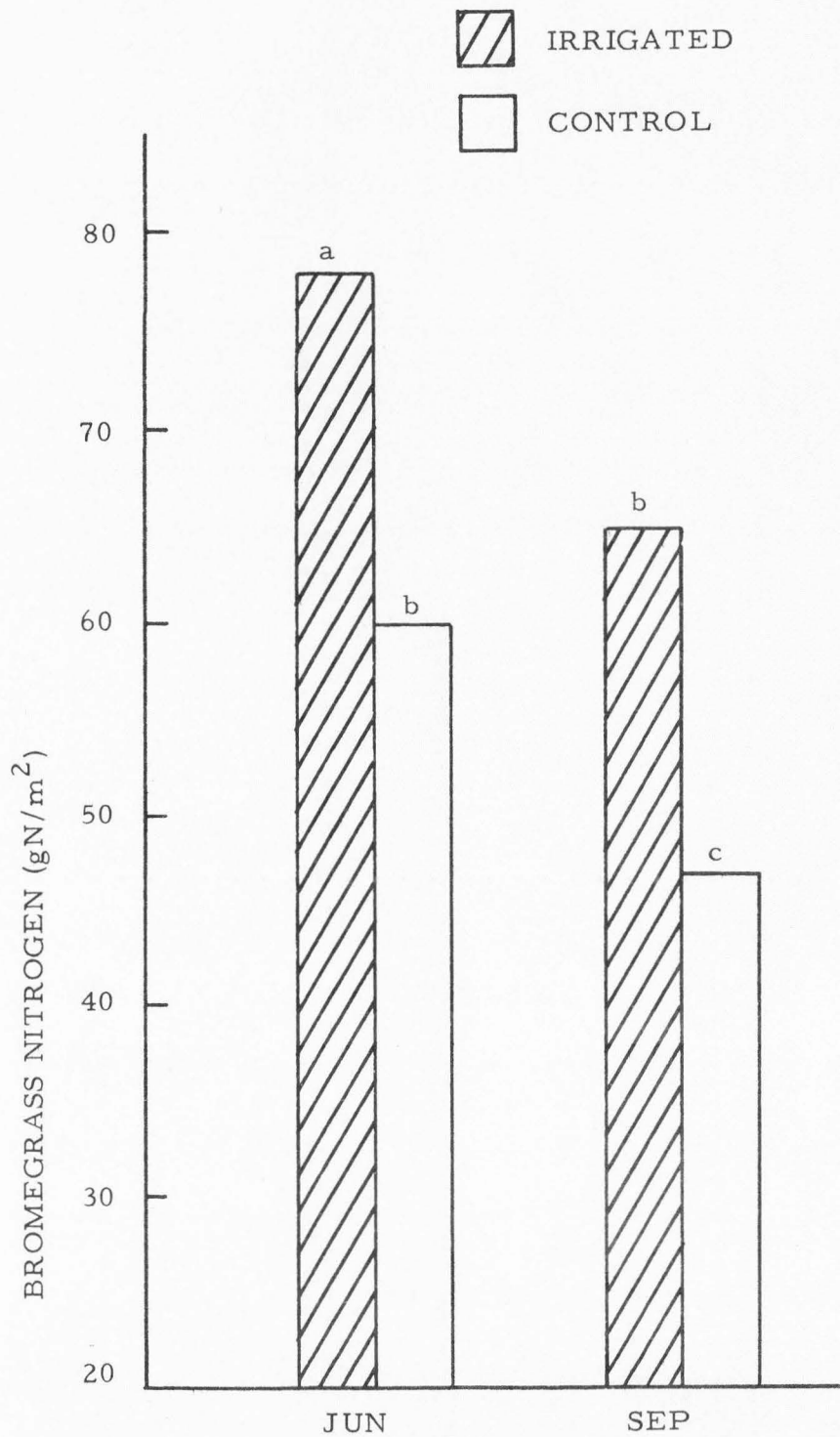


Figure 16. Bromegrass nitrogen assimilation (June) and retention (September) compared by date and treatment for 1972. Like lower case letters denote statistically equivalent (.01) mean values.

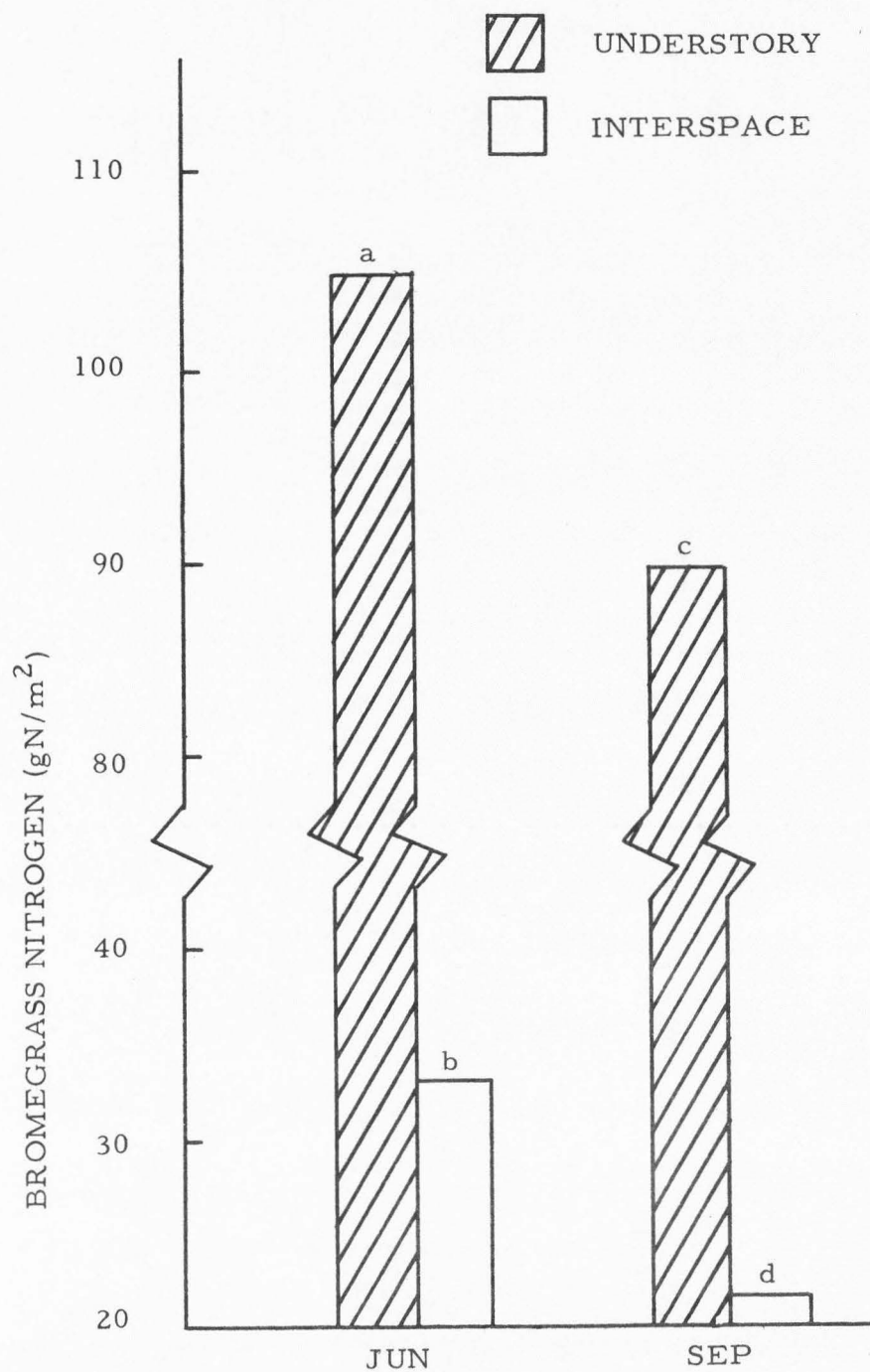


Figure 17. Bromegrass nitrogen assimilation (June) and retention (September) compared by date and habitat for 1972. Like lower case letters denote statistically equivalent (.01) mean values.

spring irrigation treatment had produced an effect at the June maturity date which was carried through the summer and into the germination period of the subsequent annual growth cycle. This irrigation effect was manifest as a tie up of a significant amount of nitrogen in the bromegrass litter.

Computation of a nitrogen utilization ratio proved useful in examining the ability of bromegrass to assimilate nitrogen under favorable environmental conditions (Cline and Rickert, 1973). June bromegrass biomass (g/m^2) and nitrogen assimilation (gN/m^2) values for each treatment and habitat combination are given in Table 2. The nitrogen utilization ratio is calculated by dividing the biomass by the nitrogen assimilation value and is expressed as grams of biomass produced per gram of nitrogen assimilated. While no statistical comparisons are possible, it is apparent that bromegrass in the irrigated understory was the most efficient user of nitrogen compared to the other treatment and habitat combinations (2.69 versus 2.00 to 2.29 g/gN).

Table 2. Bromegrass nitrogen utilization ratio based on June 1972 biomass and nitrogen assimilation data for both treatments and habitats.

	<u>IRRIGATED</u>		<u>CONTROL</u>	
	Understory	Interspace	Understory	Interspace
BIOMASS (g/m^2)	307	94	218	50
NITROGEN ASSIMILATION (gN/m^2)	114	41	95	25

Table 2 Continued

	<u>IRRIGATED</u>		<u>CONTROL</u>	
	Understory	Interspace	Understory	Interspace
UTILIZATION RATIO ($\frac{\text{g/m}^2}{\text{gN/m}^2} = \text{g/gN}$)	2.69	2.29	2.29	2.00

Shrub Growth Rate

A significant difference in stem relative growth rate (.01) was experienced due to date with the month of June experiencing the greatest stem growth rate regardless of treatment. Mean comparisons by date and treatment (Figure 18) show that stem growth proceeded rapidly in the spring and declined in the summer. In May the stem growth rate was 0.007 cm/cm/day; it increased to an average of 0.018 cm/cm/day in June and then declined to values of 0.003 to 0.001 cm/cm/day in July and August respectively. No statistical difference (.05) was noted due to spring irrigation treatment.

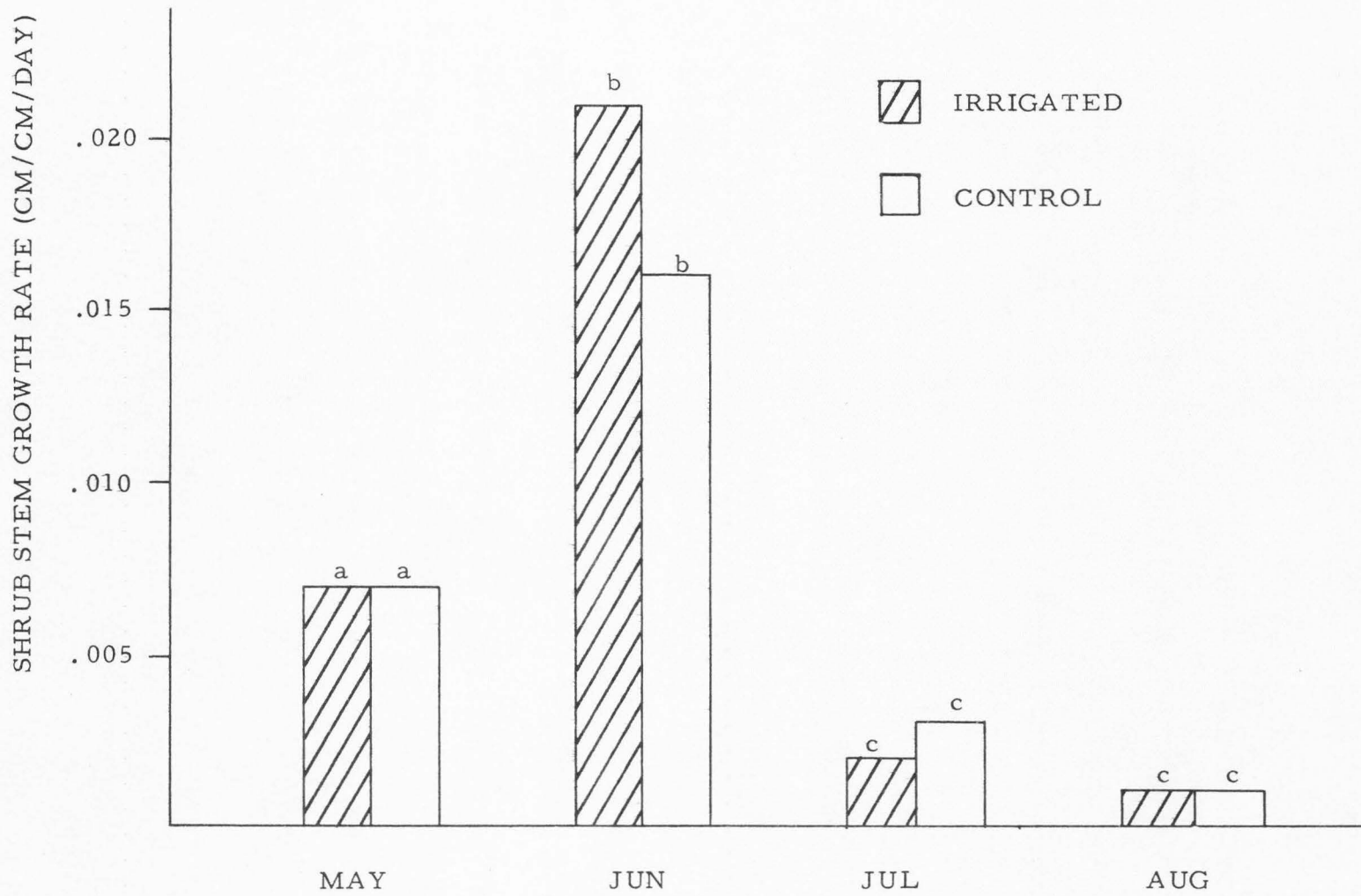


Figure 18. Shrub stem growth rate compared by date and treatment for 1972. Like lower case letters denote statistically equivalent (.05) mean values.

DISCUSSION

The central concern of this research was to determine the effect of spring precipitation distribution on annual growth cycles. Six 10 x 10 meter study plots were established in an A. tridentata-mixed annual brome-grass plant community in northern Utah. Three of these six plots were sprinkler irrigated during April and May of 1972 at the rate of 12-15 mm/plot/week. Bromegrass, shrub, forb and soil samples were collected throughout the study period for analysis of nitrogen content and other parametric values.

The natural precipitation distribution 1971-72 proved ideal for the study according to Hull and Pechanec (1947) who reported that B. tectorum seedling establishment required about 50 mm of concentrated rainfall. The bromegrass population was well established during September and October 1971 following the abundant precipitation (140 mm) received in that period (Figure 2). The natural precipitation from January to August 1972 was below normal except for April. Weekly irrigations in March, April and May were timed to simulate a season of abundant and frequent rainfall. Irrigation proved to be a critical factor in May when only 2 mm of natural precipitation were received at the study site.

The irrigation treatment stimulated a significant increase in bromegrass productivity from April to June (Figure 3). This effect was established in the last six weeks of the irrigation period but the major effect was probably established in May when natural precipitation was severely limiting. Irrigation maintained the soil moisture in treated plots well above that in control plots throughout the spring growth period. Control plots reached their driest soil moisture content a full month before treated plots (Figure 8).

The effect of irrigation on bromegrass productivity appears to be of a secondary nature. Figure 11 shows that irrigation resulted in

increased total soil nitrogen levels during the spring treatment period only. Irrigation apparently allowed the soil microflora to increase their mineralization and nitrification activities on the more resistant humic soil fraction not included in normal Kjeldahl analysis (Bremner, 1965) and thus release nitrates for plant use. Charley (1971) notes that alternate drying and wetting promotes accelerated mineralization of organic matter in soils of tropical, temperate and desert regions. The amount of nitrogen mineralized is a function of the humus content of the soil; less nitrate is produced from soils low in organic nitrogen and carbon (Birch, 1960). The ability of soil microorganisms to carry out these bursts of nitrification declines as the pool of organic nitrogen is reduced to a more resistant humic fraction by previous biological activity. It is possible that the soil nitrogen data by treatment interaction is a reflection of this decline in nitrogen mineralization and nitrification potential. That is, high soil nitrogen levels in the early spring are associated with microbial activity on the less resistant organic nitrogen fraction but later irrigation does not enable the microflora to attack the more resistant humic fraction. As this study dealt with total nitrogen, further studies should deal with available forms of soil nitrogen to verify this explanation for the increased nitrogen levels noted in treated plots.

The biological importance of the small habitat differences in soil moisture content (Figure 9) are probably insignificant with regard to bromegrass productivity since the soil moisture treatment by habitat

interaction is not significant. That is, irrigation increased the understory soil moisture content (Figure 10) to a greater extent than in the interspace but not so great that it became the single major factor responsible for increased brome grass productivity.

The understory soil always had a higher total nitrogen content than the interspace (Figure 12). The fact that shrubs act as "islands of fertility" (Garcia-Moya and McKell, 1970) is strongly supported in this regard because the soil surface understory possessed a more suitable nitrogen environment for plant germination and growth than the interspace. With a large pool of organic nitrogen to draw from, the soil microflora were able to mineralize and nitrify this pool into greater quantities of inorganic nitrogen. With irrigation being applied over a period of weeks the annual plant population was able to respond to these flushes of bacterial activity. This response was notably greater in the understory especially in irrigated plots (Table 2).

These results suggest that the shrub interspace is a rather austere habitat for plant growth. For one, Robertson (1947) noted that the higher temperature regime under an A. tridentata canopy permitted B. tectorum in the understory to begin spring growth two weeks earlier than in the interspace due to snowmelt difference. Observations at our study site indicated that other factors are also involved. Adjacent to the study site there existed A. tridentata-brome grass stands with shrub canopy cover of less than 40 percent and the interspace in these stands supported as vigorous a stand of annuals as did the understory. While this study

does not purport to explain these differences, it does describe some of the effects of the shrub canopy dominance.

In a study of the perennial Bromus inermis, Power (1971) suggested that the percentage stress (reduction in growth rates) due to nitrogen deficiency was greatest where available nitrogen was lowest; this stress also increased with maturity. Percentage stress due to water deficiency was greatest where nitrogen availability was lowest. Examination of total soil nitrogen (Figure 12) and soil moisture content values (Figure 9) indicate that both factors were lower in the interspace habitat during the spring growth period. Evans' (1960) greenhouse study of competition between the two annual grasses Bromus mollis and Festuca megalura and the annual forb Erodium botrys led to the conclusion that shading and differential ability for nitrogen uptake were primary factors in annual grass-forb interactions. The grasses were able to utilize nitrogen when applied at low rates while the forb responded only at the highest rates (455 kg/hectare). Under the field conditions of this study much the same response was noted. Irrigation apparently stimulated soil microorganisms to convert nitrogen to available forms. Bromegrasses responded to the favorable moisture and nutrient conditions but the perennial shrub A. tridentata, exhibited no such response.

Another factor which limits interspace productivity is that of litter accumulation. Evans and Young (1970) found that B. tectorum failed to germinate in sites with a small litter component. This finding was consistent with the "safe site" germination concept espoused by

Harper, et al (1965). This concept states that plant populations are regulated by frequency of germination safe sites rather than number of seeds produced. Evans and Young (1970) stated that the relatively large but lightweight B. tectorum caryopses required a rough microrelief for burial and germination. The presence of abundant litter (as in the understory) acts as an insulating layer which moderates temperature and moisture fluctuations and thus provides favorable microsites ("safe sites") for seed germination.

A final factor related to increased understory productivity is that of continuous germination potential. Young, et al (1969) noted the annual carryover of viable caryopses by B. tectorum and suggested that continuous germination potential was exhibited by this specie. The continuous germination phenomenon is consistent with the "safe site" concept especially when temperature and water are limiting. That is to say, the fall germination characteristics of fresh caryopses can be environmentally conditioned to continuous germination. With "safe sites" being more frequent in the understory habitat it is conceivable that continuous germination could account for the productivity advantage the bromegrasses maintained in this particular habitat.

With the environmental conditions of low soil nitrogen and moisture levels found in the interspace, it is not surprising that when these competitive factors were removed by irrigation (Figures 10 and 13) the interspace vegetation showed a threefold productivity increase compared to the twofold increase noted in the understory. A high growth potential

exists in the interspace habitat but it is restrained by the depressive effects of soil moisture stress and low nitrogen levels.

The lack of bromegrass productivity in the interspace was partly compensated for by an abundance of R. testiculatus in that habitat (Table 1). Its cespitose growth habit was apparently better suited to the open interspace habitat whereas competition for light and nutrients due to the decidedly greater biomass of understory bromegrass provided a less amenable habitat. The extent to which R. testiculatus is a factor in the low bromegrass productivity of the interspace is not clear especially since plant nitrogen content was the same in all treatments and habitats.

Low summer precipitation and the reduction of habitat soil moisture differences during the summer would suggest that litter decay by soil microflora was limited equally in both habitats; however, the brief wetting periods during summer thundershowers and the presence of large amounts of litter in the understory argue that environmental conditions there are more favorable to litter decay than in the interspace. However, both understory and interspace habitats (Figure 4) lost 40 percent of their litter biomass from June to September (262 versus 154 g/m² and 72 versus 41 g/m² respectively). Nonetheless, the greater absolute abundance of litter in the understory required a significantly greater microbial decay rate than the sparsely vegetated interspace if both habitats were to exhibit the same proportional degradation of litter.

The stimulating effect of drying and re-wetting on nitrogen mineralization is known to be greatest when repeated. Birch and Friend (1961) showed that, for organic soils, 46.4 percent of the nitrogen was mineralized after 204 such cycles. By September 85 percent of the nitrogen uptake (90 versus 105 gN/m² in June) was retained in the understory bromegrass litter while only 67 percent (22 versus 33 gN/m² in June) was retained in the interspace plant litter. Although the proportional losses vary by 15 percent, the absolute losses are about 50 percent greater in the understory (15 gN/m²) than in the interspace (11 gN/m²). From these observations one can conclude that rates of biomass loss and nitrogen mineralization are greatest in the understory.

The June sampling period at bromegrass maturity permitted a close look at species differences in biomass and nitrogen content. Under the severe environmental conditions of the interspace neither species was able to grow well while in the understory both species did better with B. tectorum maintaining a competitive advantage with regard to biomass over B. japonicus only in control plots (Figure 6).

Hulbert (1955) reported that B. tectorum had given way to B. japonicus in Kansas over a period of several years. He attributed this phenomenon to the change of precipitation distribution maximum from spring to early summer. This shift in rainfall pattern favored B. japonicus because of its more extensive root system and later maturity date. An early spring precipitation maximum was exemplified in control plots due to their lack of irrigation. Under control plot conditions B. tectorum possessed the competitive advantage over B. japonicus due

to its early growth initiation ability. Irrigation effectively simulated a precipitation cycle more favorable to B. japonicus. Statistical mean comparisons show that B. tectorum productivity was not affected by irrigation while B. japonicus productivity in treated plots increased to the point where no species biomass differences were evident. Thus, early spring precipitation favors B. tectorum growth and early summer precipitation favors B. japonicus. Shifts in seasonal precipitation patterns is a major influence in this interspecific competition. Presumably with rainfall pattern changes over a period of years the species composition of the annual brome grass population would shift in the same manner as Hulbert observed.

The possibility exists that the continuous germination phenomenon could account for these anticipated changes in species composition but several investigations indicate otherwise. Newman (1961) noted that for winter annuals in Great Britain the later the germination date the smaller the plant and the lower the seed productivity. In fact, Hulbert (1955) noted that B. tectorum must be subjected to cold temperatures for normal flowering to occur; if not, spring germination usually resulted in vegetative plants. A greenhouse study by Finnerty and Klingman (1962) demonstrated that B. tectorum required an inductive vernalization (cool, short days) period for panicle production. Flowering was then initiated by long day length. Thus, if spring germination is a major factor in biomass increases in irrigated plots, it is doubtful that this could lead to species composition changes since production of

new seed would not be a major result of these flushes of spring growth. In fact, Young, et al (1969) found that in years of high plant densities B. tectorum seed production was reduced while in low density sites seed production was increased.

The present study demonstrated that irrigation increased annual grass productivity due to favorable soil moisture and soil nitrogen conditions especially in the shrub understory. To determine whether this annual productivity fluctuation could affect subsequent annual growth, one must examine the nitrogen tie up in both plant litter and soil. Bromegrass percent nitrogen content (Figure 14) shows that the irrigation dilution effect was well established in June and carried through the summer. Capiel, et al (1972) noted this same effect on high yield stands of Napiergrass (Pennisetum purpurem). Doss and Scarsbrook (1969) also noted the decreased percent nitrogen content in irrigated cotton stands but concluded that the greater yield due to irrigation increased the total nitrogen uptake.

Analysis of the bromegrass nitrogen uptake confirms the observations of Doss and Scarsbrook. At maturity irrigated plots of bromegrass tied up more nitrogen than plants in control plots (78 versus 60 gN/m²). Nitrogen tie up was also higher in the understory than the interspace habitat (105 versus 33 gN/m²), but there were no such species differences. These nitrogen tie up differences were carried over to the September germination period of the following annual bromegrass cycle. Thus, productivity fluctuations in bromegrass species might

have a constraining effect on subsequent annual growth cycles. A further indication that increased productivity could affect subsequent annual cycles is the maintenance of the irrigation dilution effect on bromegrass litter percent nitrogen content throughout the summer. With the low percent nitrogen content and the high productivity of bromegrass evidenced in irrigated plots, it is possible that a higher bromegrass litter C/N ratio existed in the irrigated plots than in the controls. If so, the soil microflora could be seriously delayed in reducing the C/N ratio to a level which would permit the accumulation of nitrates in the soil.

Whether this difference in C/N ratio actually exists and whether it is a significant factor in nitrogen availability for seedlings is open to discussion. Indications are that a possible C/N ratio difference between treatments has no effect on subsequent annual growth cycles. Bromegrass litter in both irrigated and control plots experienced a 40 percent loss in weight from June to September (200 versus 123 g/m² in irrigated plots and 134 versus 72 g/m² in control plots). Nonetheless, the absolute magnitudes of litter biomass loss (77 and 62 g/m² in irrigated and control plots respectively) may overshadow these proportional equalities. A more definitive statement can be made with respect to nitrogen mineralization losses during this same time period. In September 83 percent of the June nitrogen uptake (65/78 gN/m²) was retained in bromegrass litter from irrigated plots while 78 percent (47/60 gN/m²) was retained in litter from control plots.

Thus equivalent percentages as well as equal absolute values (13 gN/m^2) of litter nitrogen were mineralized in both treatments.

Even more conclusive is the fact that while a treatment difference in total soil nitrogen content existed in the spring, no treatment difference was evident during the summer or fall bromegrass germination period (Figure 11). It appears that from the standpoint of litter nitrogen mineralization and total soil nitrogen content, no constraining effects on subsequent annual growth cycles can be attributed to the spring irrigation treatment. Further analysis with regard to available forms of nitrogen are needed to confirm this conclusion.

Mean comparisons of treatment differences for shrub stem relative growth rate showed no significant differences. The irrigation period was selected primarily for its impact on the annual species' spring growth and as a result there was no effect on shrub stem relative growth rate. The soil moisture data show that no treatment differences (Figure 8) existed after the spring irrigation period when the perennial species was completing its flowering phenological stage. It is also noteworthy that no treatment effect on stem relative growth rate was detected at early shrub growth periods when irrigation was in progress. A later irrigation period would probably have been more amenable for shrub response.

These results are somewhat surprising in view of the following findings. Tabler (1964) found that an extensive lateral root system developed from the thick portion of the A. tridentata tap root. A

noticeably heavy concentration of short fine roots occupied the top 15 cm of soil under the shrub crown. He concluded that the root configuration permitted utilization of both surface and subsurface moisture and nutrients. Robertson (1943) studied the root growth timing of A. tridentata and found that active root growth occurred between May and August. Moreover, he found that it coincided with or preceded the most active shoot growth period. The results obtained from our stem growth rate study indicate that vegetative stem length increased rapidly in May and June and then decreased in the summer months. If root growth precedes shoot growth then it is difficult to imagine why the shrub did not respond to the spring irrigation treatment.

CONCLUSIONS

An A. tridentata-mixed brome grass plant community was irrigated during the spring of 1972 to simulate a spring growth period of abundant precipitation and thus extremely amenable to annual brome grass productivity. Biomass and nitrogen content parameters were monitored throughout the spring and summer to evaluate the short and potential long term effects of this seasonal increase in "precipitation".

Irrigation increased annual brome grass productivity almost 50 percent. This increase was a result of the combined factors of increased soil moisture content and increased nitrogen availability due, apparently, to increased soil microfloral nitrification activity under low water stress conditions.

Understory habitat productivity was four times that of the interspace habitat given a 40 percent shrub canopy cover. The following are suggested as factors responsible for this difference: 1) total soil nitrogen and soil moisture content were greater in the understory, and 2) understory litter accumulation provided more germination safe sites than the interspace. When released from competition for moisture and nitrogen by irrigation treatment, the understory exhibited a greater biomass increase than did the interspace indicating a high productivity potential given the proper environmental conditions.

Irrigation produced significant differences in biomass between annual brome grass species. Bromus tectorum had a greater productivity in control plots than B. japonicus; however, B. japonicus was able to

eliminate this difference in irrigated plots. In essence, a shift in precipitation pattern from early to late spring resulted in a productivity change similar to that observed by other investigators. The possibility that the continuous germination potential could account for a subsequent species composition change was discussed.

A potential exists for nitrogen carryover effects on subsequent annual brome grass cycles. Irrigation produced abundant annual growth which resulted in a greater nitrogen uptake despite an observed decrease in irrigated brome grass percent nitrogen values. Both the tie up and irrigation effect were maintained throughout the summer and into the subsequent annual germination period. However, total soil nitrogen levels and brome grass nitrogen mineralization rates strongly suggest that soil nutrient conditions for subsequently germinating brome grass seedlings do not differ because of previous spring irrigation treatment. It may be that levels of available forms of nitrogen are such as to effect subsequent germination.

The shrub growth rate did not respond to the spring irrigation treatment. While such early watering would be expected to stimulate root and subsequent shoot growth, the naturally occurring low levels of available nitrogen were apparently more efficiently utilized by the brome grass.

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