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Growth and Development of Meadow Plants as Affected by Environmental Variables[1]

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ABSTRACT

The low production of seasonally flooded meadows is a problem in many locations throughout the world. An understanding of the effects of environmental factors on the growth and production of the meadow species will aid in developing practices to increase forage production. Controlled studies were undertaken to determine the effect of soil moisture, temperature, irradiance, and soil fertility on the phenological development and growth of slender sedge (*Carex praegracilis* W. Boott), beardless wildrye (*Elymus triticoides* Buckl.), Nevada bluegrass (*Poa nevadensis* Vasey ex Scribn.), and reed canarygrass (*Phalaris arundinacea* L.). Potted plants were grown in growth rooms under various environmental conditions: temperatures of 15 and 30 C, irradiances of 4.2 and 42.0 W/m^2; soil moisture levels with amounts of moisture added approximating the volume of water that the soil would retain at 0, 0.3, and 10 bars; fertilizer-N at rates equivalent to 0, 110, 220. and 440 kg/ha. Plant responses were evaluated by number of leaves per stem, number of stems per plant, leaf area per plant, plant height, and herbage yield at the end of three growth periods. In the controlled-study conditions, mortality of bluegrass plants was high when grown with 4.2 W/m^2. Phenological development progressed faster and plant growth-rate increased when the irradiance received was increased to 42.0 W/m^2. Canarygrass, however, continued in a vegetative stage regardless of temperature or light treatments. Increasing temperature from 15 to 30 C increased the rate of growth for plants receiving 42.0 W/m^2, but the increased temperature also increased the mortality of all species receiving 4.2 W/m^2. Fertilizer rates and soil-moisture levels generally had no significant effect on plant-growth parameters when plants, except for canarygrass, were grown at 15 C or with 4.2 W/m^2. The greatest rate of growth was produced when plants were grown at 30 C with 42.0 W/m^2. Under these conditions, yields tended to increase with fertilizer, and yields from canarygrass increased as fertilizer rates and soil-moisture levels increased.

Additional index words: **Slender sedge (*Carex praegracilis* W. Boott), Beardless wildrye (*Elymus triticoides* Buckl.), Nevada bluegrass (*Poa nevadensis* Vasey ex Scribn.), Reed Canarygrass (*Phalaris arundinacea* L.), Leaf area, Yield, Phenology, Irradiance, Soil moisture, Temperature, Fertilization.**

THE complex and interacting effects of environmental variables on growth and development of native meadow plants are not well known. Hay production from native meadows varies considerably from year-to-year and differs among locations. Production of seasonally flooded meadows is notably low throughout the temperate zones of the world, averaging 1.5 to 2.5 metric tons/ha (3, 8, 9, 12, 15, 16, 20, 21).

Several authors have reported the effects of environmental factors on the production of meadow plants. Keefe (7) and Bernard (1) reported decreased production as altitude and latitude increased, and Gorham (6) showed a positive correlation between the temperature of the warmest month and production of sedge meadows. Mornsjo (10), Rumburg and Sawyer (14), and Walker and Wehrhahn (17) found that water depth and duration of flooding determine the productivity of meadows and the dominant species. Rumburg and Sawyer (14) observed that the density of rushes (*Juncus* spp) increased but density of sedges (*Carex* spp) and grasses decreased with increased depth of flooding and increased length of the flooding period. When rushes and sedges were the major species, hay yields increased with length of flooding at flooding depths less than 12 cm. Flooding depths over 12 cm for longer than 50 days decreased production.

Fertilization of meadows with N has proven effective in increasing forage production on flood meadows. The efficiency of the N depends on the botanical composition of the sward and the rates of fertilization applied (3, 9, 13).

The objective of this study was to determine the effect of the major environmental factors: soil moisture, temperature, irradiance, and soil fertility on the phenological development and growth of four major species: slender sedge (*Carex praegracilis* W. Boott), beardless wildrye (*Elymus triticoides* Buckl.), Nevada bluegrass (*Poa nevadensis* (Vasey ex Scribn.), and reed canarygrass (*Phalaris arundinacea* L.).

MATERIALS AND METHODS

The study was conducted in a growth room where irradiance, temperature, and soil moisture were controlled.

Plant plugs (6 cm diam. × 6 cm long) of slender sedge, beardless wildrye, Nevada bluegrass, and reed canarygrass were cut from the meadow in October, 1971 and refrigerated at 2 C until placed in pots to commence growth. One plant plug was placed in each pot (15 × 15 × 15 cm) and filled with 2.5 kg of coarse sand. Irradiance was controlled with banks of flourescent and incandescent lights programmed for 16 hours of light per day. Temperature was controlled by heat from lights, auxilary heat source, fans to circulate the air, and ventilation. Soil-moisture levels were maintained by adding water to approximate the desired moisture regime. Water was applied by pouring 100 cc of water every 2nd day into pots of the medium moist regime and 100 cc of water every 4th to 6th day in pots of the dry regime. Water was added to water-tight containers as necessary to keep the soil of the saturated regime thoroughly saturated for the duration of the study.

The following levels of control were imposed:

1. Air and soil temperatures of 15 C±3 and 30 C±9. Temperatures of air and soil were similar. Fluctuations were associated with dark and light periods of night and day changes.
2. Irradiance of 4.2 and 42.0 W/m^2. The lower light treatment was shaded from direct lighting. Irradiance was determined by converting photometric flux in the 400-700 nm waveband by the factor W/m^2/ Klux = 3.9 as determined from conversion factors for incandescent (4.57) and cool white fluorescent (3.38) light sources.
3. Nitrogen fertilier at 0, 180, 360, and 720 mg N/pot. These rates were equivalent to 0, 110, 220, and 440 kg N/ha determined for surface area.
4. Soil moisture of low moisture (approximately 10 bars), medium moist (approximately 0.3 bar), and saturated (0 bar). Moisture tensions were approximated from pressure-chamber values and water content of soil samples selected from moisture treatments. The exact moisture tension

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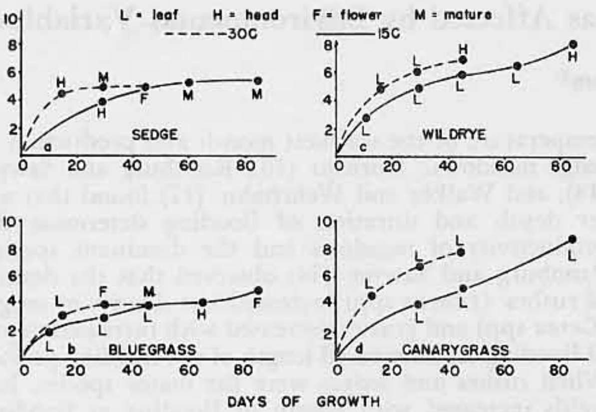

Fig. 1. Growth rate and phenology of meadow plants grown with 42.0 W/m² as affected by temperature. Each value is a mean of three soil moisture levels, four rates of fertilizer-N, and three replications.

experienced by the plant was not known because the soil of the intact plug was finer textured than was the surrounding potted soil.

Plant responses determined at the end of growth periods were:

1. Phenological stage at 15, 30, and 45 days when grown at 30 C; and at 45, 65, and 85 days when grown at 15 C.
2. Rate of growth as determined by leaf-surface area, plant height, number of leaves per stem, and number of stems per plant.
3. Oven-dry weight yield of herbage.

Pots were arranged as incomplete blocks with three replications per treatment. Treatments were stratified for temperature by time as the major whole-block and for irradiation by location within the growth room as first-order treatment. Moisture treatments were stratified within irradiance treatments. Species were arranged randomly within moisture treatments and fertilizer treatments were randomly allotted within species. Yield data were analyzed in accordance with the split-split-split plot design. Because of missing data due to mortality of bluegrass and wildrye, statistical analyses of other plant data consisted of t-tests and calculation of standard errors of means.

RESULTS AND DISCUSSION

Phenological Development. New growth was observed on plants 3 days after being placed in the growth room when they received 42.0 W/m², but those receiving 4.2 W/m² did not show new growth until the 4th day. Plants receiving 4.2 W/m² continued to grow at a reduced rate but none developed beyond the vegetative stage.

When native meadow plants were grown at 15 C, growth rate and phenological development were retarded. In most respects, plant development at 15 C for 45 days and 85 days was similar to that of plants grown at 30 C for 15 and 45 days, respectively (Fig. 1). Slender sedge, Nevada bluegrass, and beardless wildrye, grown at 15 C developed most of their leaves in the first 45 days, and reed canarygrass continued to add leaves after that date. Phenological development of all species progressed when they received 42.0 W/m². Sedge matured seed within 60 days, whereas bluegrass flowered and wildrye headed in 85 days. Canarygrass did not head by the end of the study. The number of leaves produced per stem by a species was statistically similar at the two temperatures regimes, but all species produced more leaves with 42.0 W/m² than they did with 4.2 W/m², regardless of temperature (data not shown). Bluegrass was the species least tolerant of low irradiance, and many plants died. Mortality was more severe with 4.2 W/m² when plants were grown at 30 C than when grown at 15 C. Neither soil moisture level nor fertilizer rate affected phenological development of any species (data not shown).

Apparently, the physiological processes which bring about cell differentiation were accelerated at the higher temperature, but dry matter production lagged behind phenological development. When yields were compared at 45 days of growth, plants grown at 30 C generally yielded more than those grown at 15 C. This was especially the case with reed canarygrass but not with slender sedge. This correlation of temperature with the increased production of dry matter in grasses is consistent with the findings of Weihing (18).

The complexity of the interrelations of temperature and light was shown by Went (19) who concluded that weak light and high temperature affect plant growth similarly, resulting in stem elongation and pale green leaf color. The reduced growth or death of plants when they were grown with 4.2 W/m² was apparently the result of light deficiencies. Without the necessary irradiance to drive photosynthesis, carbohydrate production would have been minimal. Under this low irradiance level, high temperature would be expected to increase the respiration rate, and much of the carbohydrate reserve would be lost through respiration. Chlorohpyll formation also would be reduced as was evidenced by the pale green color. As a result, many plants died. The mortality of these plants was assumed to be the result of an unbalanced photosynthesis-respiration (P-R) ratio. This conclusion is compatible with the work of Deinum (4, 5) and Murata (11). They found that when the P-R balance was disrupted by shade or a low irradiance level, carbohydrate production was decreased and respiration reduced the carbohydrate reserve. As a result, shade decreased yield, protein-N, and water-soluble carbohydrates.

Bickford and Dunn (2) suggested that the upper temperature limit for growth of most plants is about 35 to 40 C, and within the growth limits of a plant, photosynthesis will usually increase with rise in temperature. In this experiment, plants growing with 42.0 W/m² at 15 C probably were fully utilizing the light, but at 30 C many plants of bluegrass, wildrye, and canarygrass could have been light-deficient for photosynthesis. Undoubtedly, the respiration rate at 30 C was greater than that at 15 C, and more of the photosynthesized carbohydrates were utilized in respiration.

It appears that under the temperature and irradiance conditions of this experiment, sedge and bluegrass have definite limitations of the number of leaves that will be produced per stem. When grown at 15 C, they approached their limit at about 45 days. At 30 C, phenological development progressed more rapidly. Sedge reached its limitations of leaf numbers at about 15 days, and bluegrass reached it at about 30 days. In contrast, wildrye and canarygrass may not be as strictly limited to leaf numbers. At 15 C, with 4.2 W/m², phenological development of these plants progressed so slowly that the leaf development was inadequate to initiate those physiological processes required for formation of the seed head. When wildrye was grown with 42.0 W/m², phenological development

Table 1. Developmental response of meadow plants growing in medium moist soil at two temperature regimes and two irradiance levels.†

		Developmental responses at two levels of irradiance (W/m^2)							
		Tiller-stem		Plant height		Leaf area		Yield	
Species	Temperature regime	4.2	42.0	4.2	42.0	4.2	42.0	4.2	42.0
	C	No./plant		cm		cm^2		g/plant	
Slender sedge	15	7.3	9.4	27.6	38.6	0.97	2.09	0.17	0.86
	30	3.7	5.0	19.8	23.1	0.53	0.80	0.13	0.21
Nevada bluegrass	15	3.6	8.8	12.4	34.9	0.16	1.51	0.04	0.56
	30	4.0	8.9	16.0	24.2	0.22	0.63	0.22	0.27
Beardless wildrye	15	4.5	6.4	24.5	57.3	0.53	4.68	0.07	1.09
	30	2.2	3.5	22.7	35.5	0.49	0.99	0.08	0.33
Reed canarygrass	15	3.6	4.7	39.6	61.0	2.99	6.11	0.18	1.53
	30	2.8	4.1	25.5	39.3	0.92	3.75	0.16	0.59

† Each value is a mean of four fertilizer rates, three growth periods, and three replications.

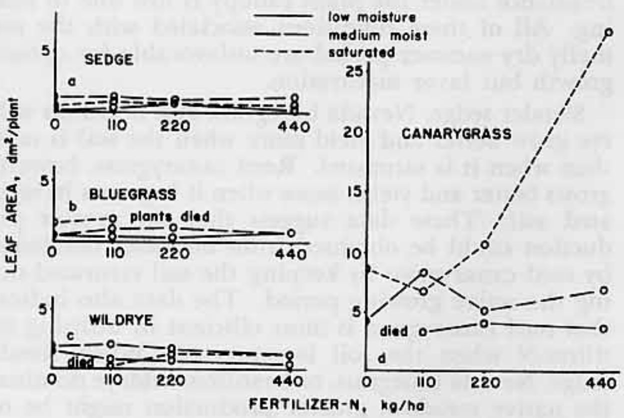

Fig. 2. Leaf area of meadow plants as affected by soil moisture and fertilizer rate after 45 days of growth at 30 C with 42.0 W/m^2. Each value is a mean of three replications.

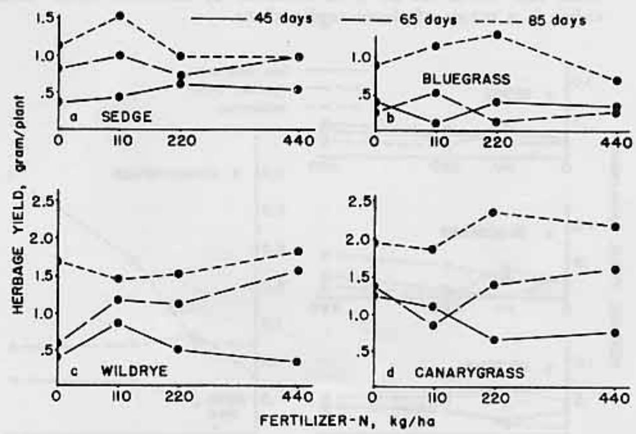

Fig. 3. Yield of meadow plants grown in medium moist soil with 42.0 W/m^2 at 15 C as affected by fertilizer rate. Each value is a mean of three replications.

advanced to the seed-head-formation stage. Since canarygrass remained vegetative and continued to produce more leaves, this species apparently had light and photoperiod requirements not met in this study.

Number of Stems. More stems were produced when plants in medium-moist soil were grown with 4.2 W/m^2 at 15 C than at 30 C ($P<0.01$), and the greatest numbers of stems were produced when plants were grown with 42.0 W/m^2 at 15 C ($P<0.01$). Canarygrass, however, was less responsive to variations in temperature and irradiance than the other species (Table 1).

Generally, fertilizer rates and soil-moisture levels had little effect on the number of stems each plant produced, except when grown at 30 C with 42.0 W/m^2 (data not shown). Under these high temperature and irradiance conditions, more tillers were produced in saturated than in unsaturated soils.

Plant Height. All species were taller when grown with 42.0 W/m^2 than with 4.2 W/m^2 (Table 1). Plants were also taller when grown with 42.0 W/m^2 at 15 C than at 30 C ($P<0.01$).

Most plants grown at 30 C attained 60-80% of their maximum elongation within the first 15 days of growth (data not shown). Wildrye and canarygrass were also taller in 15 days with 42.0 W/m^2 than they were in 45 days with 4.2 W/m^2. Sedge was the least responsive to differences in temperature and irradiation.

Generally, fertilizer did not affect the height of plants when they were grown in low-moisture soils. However, when grown in saturated soil, canarygrass increased in height with the 220 and 440 kg/ha rates of N (data not shown).

Leaf Area. The surface area of leaves of plants grown at 15 C with 42.0 W/m^2 was twice as great as that of plants grown under the lower irradiance (Table 1). When grown at 30 C, the leaf-surface area increased with the higher irradiance, but except for canarygrass, the difference was not as pronounced.

Soil moisture and fertilizer levels appeared to have little effect on leaf area of plants grown at 15 C (data not shown), but when canarygrass was grown in saturated soil at 30 C with 42.0 W/m^2, its leaf area increased sharply at rates of N above 110 kg/ha (Fig. 2).

Herbage Yield. Herbage yields reflect the combined effects of environmental factors as they influenced other growth characteristics. Statistical analyses of yield data indicate the highly significant influence of irradiance and stage of development. They also indicate the significant, interactive influence of temperature and irradiance.

When plants were grown in medium moist soil, canarygrass had the greatest yield (Fig. 3). Bluegrass and sedge yielded the least. As a group, the meadow plants grown at 15 C and 42.0 W/m^2 yielded more at 85 days of growth than they did at less mature stages.

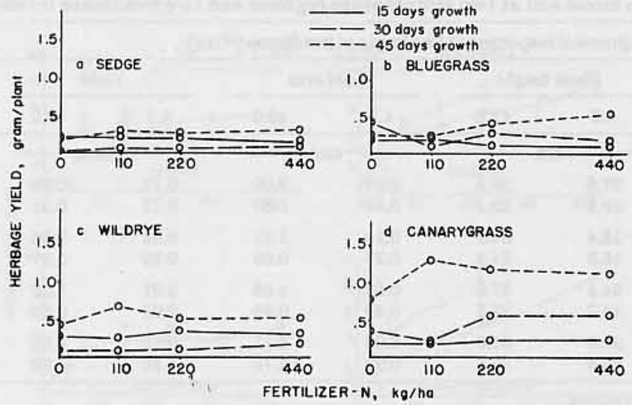

Fig. 4. Yield of meadow plants grown in medium moist soil with 42.0 W/m² at 30 C as affected by fertilizer rate. Each value is a mean of three replications.

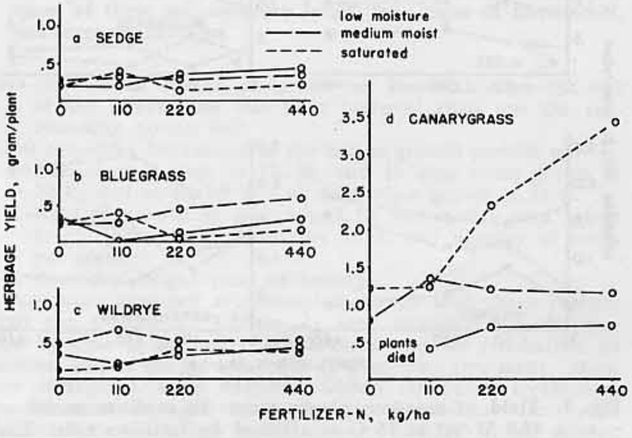

Fig. 5. Yield of meadow plants at 45 days of growth as affected by soil moisture and fertilizer rate when grown with 42.0 W/m² at 30 C. Each value is a means of three replications.

To the contrary, plants grown with 4.2 W/m² yielded more at 45 days of growth, and yields decreased at more mature stages (data not shown). Because of the slow or poor growth of plants at 15 C and 4.2 W/m², yield differences due to fertilizer rates and soil moisture were not significant.

Plants grown at 30 C in medium-moist soil yielded more at the end of the study than at less mature stages (Fig. 4), and they yielded more when grown with 42.0 W/m² than with 4.2 W/m² (average yields are shown in Table 1). Yields tended to increase with fertilization levels, but except for canarygrass, the magnitude of the increase was small and only statistically significant between fertilized and unfertilized treatments (Fig. 5). Yield differences among species were also significant, mainly because of the greater growth of canarygrass. Herbage yields of canarygrass increased as fertilizer rate and soil-moisture level increased, and plants grown with the 440 kg/ha rate of N in saturated soils yielded the greatest amount.

CONCLUSIONS

The lower temperature (15 C) regime of the controlled study relates to early-spring field conditions experienced in the temperate zones world-wide. In early spring, flood-meadow soils generally contain sufficient moisture to support plant growth and irradiance is high. Because temperature is relatively low, however, one would expect plant growth to be retarded. As the season progresses and the air and soil temperatures increase, plant growth and development progress more rapidly. Long, cold spring periods, however, would delay phenological development.

The most rapid rate of growth of these cool-season plants occurs in mid-spring when the soil is moist or saturated and before the temperature rises to the upper threshold for meadow species. High temperature, even when soil moisture and fertility are adequate, appears to be detrimental to their growth and production. Most of the plant growth in the North Temperate Zone occurs by early July before air and soil temperatures are high, soil moisture is depleted, and irradiance under the plant canopy is low due to shading. All of these conditions associated with the normally dry summer period are unfavorable for optimal growth but favor maturation.

Slender sedge, Nevada bluegrass, and beardless wildrye grow better and yield more when the soil is moist than when it is saturated. Reed canarygrass, however, grows better and yields more when it is grown in saturated soil. These data suggest that the greater production could be obtained from meadows dominated by reed canarygrass by keeping the soil saturated during the active growing period. The data also indicate that reed canarygrass is most efficient in utilizing fertilizer-N when the soil is saturated. When slender sedge, Nevada bluegrass, or beardless wildrye dominate the native meadow, greater production might be obtained if the water is controlled sufficiently to prevent long-time saturation periods. The data also suggest that production response from fertilizer-N may be small and relatively inefficient, especially when large amounts of N are applied.

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