73-4957

NICKELL, Gaylin Lee, 1945-
THE PHYSIOLOGICAL ECOLOGY OF UPLAND AND LOWLAND PANICUM VIRGATUM.

The University of Oklahoma, Ph.D., 1972
Botany

University Microfilms, A XEROX Company, Ann Arbor, Michigan

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

THE PHYSIOLOGICAL ECOLOGY OF UPLAND AND LOWLAND *PANICUM VIRGATUM*

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

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Norman, Oklahoma

1972

THE PHYSIOLOGICAL ECOLOGY OF

UPLAND AND LOWLAND PANICUM VIRGATUM

A DISSERTATION

APPROVED FOR THE DEPARTMENT OF BOTANY AND MICROBIOLOGY

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ACKNOWLEDGMENTS

The author wishes to express his appreciation to the members of his advisory committee: Dr. Paul G. Risser, Dr. James Estes, Dr. Norman Boke, Dr. Elroy Rice, and Dr. Simon Wender for assistance and advice during the research and in preparation of the manuscript.

Also, appreciation is extended to Dr. M. A. K. Lodhi and Anthony Dvorak for assisting in portions of the research and for suggestions during the preparation of the manuscript.

Lastly, special thanks goes to my wife, Linda, for her patience and support throughout this endeavour.

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THE PHYSIOLOGICAL ECOLOGY OF

UPLAND AND LOWLAND PANICUM VIRGATUM

CHAPTER I

INTRODUCTION

Panicum virgatum[1], switchgrass, in central Oklahoma consists of two distinct races which have been designated upland and lowland (Potts, 1951; Archer and Bunch, 1953; Okla. Agr. Exp. Sta., 1954; Porter, 1966, Brunken, 1971). These races differ with respect to morphology (Means, 1959; Porter, 1966; Brunken, 1971), chromosome number (Church, 1940; Carver, 1957; Reeves, 1962; Bragg, 1964; Porter, 1966; Barnett and Carver, 1967; Brunken, 1971), physiology (Porter, 1966), and ecological specificity (Porter, 1966; Brunken, 1971).

The upland race occurs in upland tall-grass prairie ecosystems, whereas the lowland race occurs along river bottoms and in moist disturbed localities such as roadside ditches. The lowland race has been reported to be larger in size, to form more distinct bunch-like clones, to have a lower nitrogen requirement, and to be more flood tolerant than the upland race (Porter, 1966). Barnett and Carver (1967), Porter (1966, and

[1]Nomenclature after Waterfall, 1966.

Brunken (1971) agree that the lowland race is tetraploid (2N=36), whereas the upland race is basically octoploid (2N=72). The upland race was found to have a larger pollen diameter than the lowland (Brunken, 1971). Reeves (1962) failed to produce artificial hybrids between these races and Brunken (1971) found no morphological or cytological evidence of naturally occurring hybrids.

The apparent environmental specificity of these switchgrass races indicated their ecological amplitudes were controlled by differential physiology. The upland and lowland habitats provided numerous environmental differences through which differential physiology could affect distributional control. To determine physiologically based explanations for the ecological amplitudes of upland and lowland switchgrass, these races were compared regarding their physiological reactions to environmental stresses of flooding, drought, salinity, and mineral limitation. The physiological processes examined were photosynthesis, respiration, growth rate, water relations, comparison of leaf organic constituents, and mineral content. Carbon dioxide exchange rates have previously been used to demonstrate ecologically distinct races (Björkman, 1966, 1968; Björkman et al., 1970; Mooney and Billings, 1961; Zavitkorski and Ferrel, 1968). Growth and carbon dioxide exchange rates have been shown to be affected by plant water status (Boyer, 1965, 1970a, 1970b; Boyer and Bowen, 1970; Brix, 1962; Pallas et al., 1967; Troughton, 1969) as have biochemical reactions (Barnett and Naylor, 1966; Stutte and Todd, 1967, 1969; Stewart et al., 1966; Vassiliev and Vassiliev, 1936; Vieira-da-Silva, 1968; Naidu et al., 1967; Protsenko et al., 1968) and mineral content (Rahman et al., 1971; Kozlowski, 1968). Salinity has been shown to affect carbon dioxide exchange rates (Gale et al., 1967; Maksimova and Matuhkin, 1965; Nieman, 1962; Schröder, 1966), ionic content (Solověv, 1969; Meiri and Poljakoff-Mayber, 1969; Greenway et al., 1966; Gates et al., 1970), water status (Gale et al., 1967; Kirkham et al., 1969; Meiri and Poljakoff-Mayber, 1970) and organic constituents (Saakyan and Petrosyan, 1964; Rakova et al., 1969; Porath and Poljakoff-Mayber, 1968).

CHAPTER II

DESCRIPTION OF STUDY SITES

Two sites in McClain County near Norman, Oklahoma, were selected for field studies of upland and lowland races of switchgrass. The upland site, the University of Oklahoma Grassland Investigations Plot, was in Sec. 12, T8N, R4W. This site supported typical tall grass prairie dominated by *Andropogon scoparius* and *A. gerardi* with *Panicum virgatum*, and *Sorghastrum nutans* as important secondary species (E. L. Rice, personal communication). Since the area has been protected from disturbances such as grazing, mowing, and fire since 1949, there has been some invasion by woody species represented by *Quercus*, *Ulmus*, *Populus*, *Celtis*, *Rhus*, *Prunus*, and *Diospyros*. The lowland site was located on the South Canadian River floodplain in Sec. 2, T8N, R3W, approximately 7 miles to the east of the upland site. This site was never inundated for long periods of time during the investigative period of 1970-1972, although Porter (1966) reported flooding to be common. Switchgrass was definitely a dominant community component and was associated with *Tamarix gallica*, *Populus deltoides* seedlings, *Xanthium strumarium*, *Aristida oligantha*, and *Cassia fasciculata*.

CHAPTER III

METHODS AND MATERIALS

Soil Analysis

Soil samples from six widely spaced points were collected from the 0-15, 15-30, 30-45, and 45-60 cm level of each study area, subsequently composited according to depth and analyzed for soil texture, pH, nitrogen, phosphorus, and potassium. Soil texture was determined by a method modified from Bouyoucos (1936) and Piper (1942). Percent nitrogen, pounds per acre of phosphorus and potassium, and pH were determined by the Oklahoma State University Extension Service, utilizing the following techniques: pH was determined on a soil:H_2O paste with a pH meter, active organic matter (nitrogen) was determined with a Klett-Summerson colorimeter following a wet oxidation procedure using sulfuric acid and potassium dichromate, potassium was determined colorimetrically, the amount of phosphorus soluble in dilute acid was also determined colorimetrically. These techniques are described in a manual for county soil testing laboratories in Oklahoma as prepared by W. E. Baumann, extension agronomist.

In addition, soil saturation extracts (Bower and Wilcox,

1965) were made of the 0-30 and 30-60 cm depth samples from each study area. Water potential measurements of these extracts by thermocouple psychrometry were taken to provide an indication of the soil water status as affected by readily water soluble ions. Measurements of Mg, Ca, Fe, Zn, Cu, Mn, and K were made on these water extracts with a model 303 Perkin-Elmer Atomic Absorption Spectrophotometer, using procedures given in the analytical manual supplied with the instrument (Perkin-Elmer Corp., 1966). P was determined by a vanadomolybdate colorimetric technique. The determined mineral content of the saturation extract is not total soil mineral content but is an estimate of the mineral concentration in the soil water.

Plant Material

All plants grown under controlled conditions were propagated from rhizomes. This reduced genetic variation inherent in seeds and was necessary to circumvent breaking seed dormancy which was prevalent in both switchgrass races. The possibility existed that rhizome sprouts would be less sensitive to the environmental stresses applied than would seedlings but this was determined to be beneficial because differential responses could be interpreted more definitely. Upland and lowland switchgrass rhizomes were collected from large established clones in their respective sites and only rhizomes from one clone were utilized per experiment. These were then washed, trimmed, and planted in appropriately labelled flats of sand. Only those which were producing shoots were later individually planted in labelled black plastic vials with drainage holes containing 105 g of white quartz sand. The plants were grown in a controlled environment chamber under a 16-hr photoperiod of 1000 ft-c light intensity, 27 C, and 40% relative humidity with an alternate 8-hr dark period at 21 C and 50% relative humidity, unless indicated otherwise.

Field Studies

Field studies in 1971 involved periodic height measurements in both study areas (Chapter II), making monthly leaf collections for organic compound analyses, and water content determination with concomitant soil collections for soil water measurements. Reciprocal transplants were also made and growth rates were followed throughout the summer. These were then harvested for analyses of minerals, organic compounds, and water content. Voucher specimens were preserved and deposited in The Bebb Herbarium, University of Oklahoma.

Six widely separated naturally occurring clones of switchgrass were selected in each of the study sites. These clones were marked and periodic height measurements were made throughout the 1971 growing season. Leaves were periodically collected, sealed in labelled plastic bags, and transported to the laboratory in an ice chest. Leaf samples (2 g fr wt) were subsequently fixed in boiling 80% ethanol for organic compound analyses and subsamples of known fresh weight were oven-dried for water content determination, and mineral analyses were made on leaves dried at 45 C. In conjunction with these monthly leaf samples, 6 soil samples at 0-15, 15-30, 30-45, and 45-60 cm deep from each site were collected for soil moisture measurements.

Transplants were made on May 1-2, 1971. In each study site (Chapter II) a rectangular plot approximately 4 m x 2 m was staked out. Sprouted rhizome material was collected and 20 individuals of each race were planted in both transplant plots. Individual sprouts were planted at least 15 cm deep and 25 - 30 cm apart in four rows, two alternating rows of each race per plot. The plants were initially watered with cistern water and no further waterings were made. Natural vegetation in the plots was undisturbed except where the actual hole was made. Recreational use is made of the river bottom, so this plot was fenced. The upland transplant plot was not fenced. Culm height measurements were made periodically throughout the growing season of 1971. At termination of growth measurements, the shoots were harvested, sealed into labelled plastic bags, and transported to the laboratory in an ice chest. Two grams fresh weight of leaf tissue, in duplicate, were fixed in boiling 80% ethanol for sugar, starch, amino acid, and protein analyses; moisture content of another 2 g fr wt leaf sample was determined along with water potential measurements of those from the river transplant site; mineral analyses were made on leaves dried at 45 C; and voucher specimens were again preserved.

Leaf water potential was determined by thermocouple psychrometry. Leaf discs were made with a paper punch avoiding the midrib and procedures given in the manual supplied with the model C-51 sample chamber psychrometer (Wescor, Inc., 1971) were followed. A 3 minute equilibration time and 10 second thermocouple cooling time were used.

Leaf and soil water content was determined gravimetrically by obtaining fresh and oven dry weights. The water content was expressed either as per cent dry or fresh weight.

Mineral analyses of plant material included N, P, Fe, Ca, K, Mg, Zn, Cu and Mn. Nitrogen was quantified by a semi-micro Kjeldahl procedure (Hiller et al., 1948), phosphorus by a vanadomolybdate colorimetric technique (Jackson, 1958) on an extract made by a 60% nitric and 10% perchloric acid digestion of the plant material. The remaining seven minerals were quantified from the above acid digest using Atomic Absorption Spectrophotometry as above.

Organic compounds quantified from leaf material were sugars, starch, amino acids and protein. A qualitative comparison of phenolic compounds was also conducted. The procedures used in extracting and quantifying the sugars, starch, amino acids and protein are outlined in the accompanying flow sheet (Figure 1). Sugars and digested starch, amino acids, and protein were quantified colorimetrically using an anthrone test

FIGURE 1.

Flow diagram of extraction procedure.

Leaf Sample

- 2 g fr wt
  ↓
  Boil in 80% EtOH
  ↓
  Grind in Virtis grinder
  ↓
  Centrifuge (15,000 g-10 min)
  Decant supernatant
  Wash pellet in 80% EtOH
  Recentrifuge
  Decant supernatant
  - Combined supernatants
    (Soluble Amino acids & sugars)
    - Aliquot for sugar determination (Anthrone test)
    - Aliquot for amino acid determination (Ninhydrin test)
  - Pellet
    (Protein & Starch)
    ↓
    Starch digestion
    (10 ml 60% $HClO_4$ at 0 C-20 min)
    ↓
    Increase volume with 50% $HClO_4$
    Centrifuge
    Decant supernatant
    Re-digest pellet as above
    Recentrifuge
    Decant supernatant
    - Combined supernatants
      (Digested starch)
      ↓
      Glucose content of Aliquot determined
      (Anthrone test)
    - Pellet
      Protein precipitated
      (5% TCA wash)
      ↓
      Protein extracted
      (1.0 N NaOH)
      ↓
      Extract diluted to 0.1 N NaOH
      Centrifuge, Decant
      ↓
      Protein quantified
      (Folin phenol reagent)
- 2 g fr wt
  ↓
  Determine water content

(Yemm and Willis, 1954), the ninhydrin reaction (Yemm and Cocking, 1955) and Folin phenol (Lowry et al., 1951) respectively.

Phenolic compounds were extracted and isolated by techniques described by Rice (1965). Water extracts of 15 g fresh weight leaf tissue were adjusted to pH 2.5 with HCl and extracted with two half-volumes of diethyl ether. Both fractions (water and ether) were taken to dryness by flash evaporation and taken up in 10 ml of 50% ethanol and 5 ml of 95% ethanol, respectively. Two-dimensional paper chromatograms were ran using 100 λ of each extract on Whatman No. 1 paper previously washed with butanol: methanol: acetic acid: H_2O (2:9:1:6 v/v). The solvent used in the first dimension was butanol: acetic acid: H_2O (BAW) (63:10:27 v/v) followed in the second dimension with 6% aqueous acetic acid as solvent. The chromatograms were analyzed with short (2537 Å) and long (3360 Å) ultraviolet light. The compounds were marked under UV light and R_f values were subsequently determined.

Drought Tolerance

Experimentation was designed to determine the effect of drought on net photosynthetic and respiratory rates of these races of switchgrass. Upland and lowland switchgrass plants were cultured from rhizomes as indicated above and after a period of 15 days in the growth chamber, watered three times per day (Hoagland nutrient solution was applied in equal amounts to all plants), gas exchange of six plants of each race was monitored in the light and dark after each of 0-, 12-, and 36-hr desiccation periods.

Carbon dioxide exchange rates (photosynthetic and dark respiratory) were determined with a Beckman 215A infrared gas analyzer in a closed gas circulation system described previously (Brown, 1970). The entire plant and vial of sand in which it grew were placed in the sample chamber when measurements were taken. Plants were allowed to equilibrate to the sample chamber environment (2000 ft-c of light at 24 C, unless otherwise indicated) for at least 15 minutes before beginning measurements, which were taken at CO_2 concentrations ranging from 320 to 380 ppm. Net photosynthetic rate was determined first and respiratory CO_2 production was monitored immediately upon turning off the light. Thirty to forty-five minutes per plant were required to obtain these two rates. All CO_2 changes were related to dry weight of the shoot.

Growth, Water, and Mineral Content

To determine relationships between drought and plant mineral concentration, these races of switchgrass were grown from seed under conditions of relatively constant stress or no stress in the greenhouse. Seeds were planted in plastic pots (12.5 cm diameter X 13 cm deep) containing a soil: sand (3:2) mixture, 10 pots per switchgrass race. The pots were watered equally for 15 days at which time seedlings were thinned to yield densities of 10 equal-sized seedlings per pot and the pots were divided making 2 groups of 5 pots each for both races. One group of 5 pots of each race was thereafter watered every other day for 4 weeks and the other groups were left unwatered until the plants became wilted at which time 40 ml distilled water was added, this sequence of watering with a constant volume when the plants wilted was continued throughout a 4 week experimental period. The time required for wilting to occur varied with greenhouse conditions, but all plants reached the wilting stage before water was applied so they were under approximately the same relatively constant plant water stress. The small quantity of water applied to stressed plants did not result in any water draining out of the pots. Possible mineral leaching from control pots was eliminated by adding water to saucers in which the pots sat. After 4 weeks under these conditions, the plants were harvested, separated into shoot and root categories, fresh and dry weights of shoots and dry weights of roots were determined, and shoot minerals were quantified as described previously.

Drought and Nutrient Concentration

In effort to determine the relationships between leaf water content, leaf ψ, and leaf diffusive resistance of switchgrass when under drought stress, upland and lowland plants grown 2 months in the growth chamber in individual vials watered with one of each 0, 0.0625, 0.125, 0.25, and 0.5 strength

Hoagland nutrient solution were subjected to drought by not watering. Four plants of each race at each nutrient concentration were measured for leaf diffusive resistance initially and periodically throughout the experimental periods. After 84 hours (upland) or 72 hours (lowland) of drought, leaf ψ and leaf water content were also determined as previously described.

Leaf diffusive resistance was measured with a LI-60 diffusive resistance meter and LI-15S horizontal sensor (Lambda Instruments Co., Inc., 1972). Instrument calibration was performed at 25 C as were all leaf measurements. Leaf measurements were conducted on leaves approximately the same width (0.5 cm ± 0.1) and age (third leaf from the apex) from plants pre-illuminated at 2500 ft-c light intensity at 25 C for 45 minutes. Since none of the leaves monitored was 1 cm wide, the sensor aperture (2 cm^2), was not filled by leaf tissue and thus the values obtained were likely underestimates. Attempts to correlate leaf width with diffusive resistance in order to correct the obtained values were unsuccessful due probably to lower diffusive resistance of smaller and younger leaf segments.

Flood Tolerance

Determination of the physiological effects of flooding on these switchgrass races which correlated to their reported differential flood tolerance (Porter, 1966) was attempted through the following experiments: The effects of flooding on these races with sand or soil as substrate and in conjunction with various mineral nutrient concentrations were observed. Plants were cultured from rhizomes as previously described. Flooding was accomplished by placing the vials in deep porcelain pans in which the water level was maintained at 2 cm above the surface of the vial substrate. The flood control vials had free water drainage. Observations of effects of these experiments included growth, net photosynthesis, dark respiration, shoot water content, and leaf ψ. Before CO_2 exchange rates of plants grown in soil were determined, the soil surface was covered with paraffin which was found to eliminate CO_2 produced within the soil.

Salinity Tolerance

Evidence existed which indicated the river site contained a relatively high soil salt content and it was thus theorized that salinity might be involved, along with other factors, in excluding upland switchgrass from this site. Experimentation was designed to test the relative responses of upland and lowland switchgrass to salinity.

Experimentation was designed to determine the effects of 0, 0.05, and 0.1 molal (m) NaCl solutions on leaf diffusive resistance, CO_2 exchange rates, leaf ψ, and leaf water content. Upland and lowland switchgrass plants were cultured from rhizomes and grown in sand as previously described. At 3 weeks of age, 4 plants of each race were subjected to one of each NaCl concentration by placing the vials into beakers containing

50 ml of the solutions. The solution level in all cases was approximately 1/4 the vial height so all roots were not completely inundated, but in sand with water content equivalent to field capacity. The solutions were changed regularly to prevent salt concentration changes. Leaf diffusive resistance of these plants was measured prior to and periodically for 16 days after solution treatments were initiated. CO_2 exchange rates, leaf ψ, and leaf water content of all plants were measured after the 16 day experimental period.

CHAPTER IV

RESULTS AND DISCUSSION

Soil Analysis

The upland soil contained more silt and clay and less sand than the lowland at all depths (Table 1). Lowland soil reaction (approximately pH 9) was more alkaline than the upland soil. The upland soil exhibited a gradual increase in pH with an increase in depth from pH 6.8 at the 0-15 cm level to pH 7.9 at the 45-60 cm level. At all depths the latter soil was higher in both nitrogen and potassium but lower in phosphorus than the lowland soil. Soil samples from the upland site contained highest nitrogen concentration (2.65%) at the 0-15 cm level and the lowest (1.2%) at the 45-60 cm level. Lowland soil contained the highest nitrogen concentration (0-15%) at both the 0-15 and 15-30 cm level and the lowest (0.10%) at both the 30-45 and 45-60 cm level. Phosphorus in the upland soil did not show any trend related to depth, and lowland soil contained the highest amount of phosphorus (22.6 pounds per acre) at the 0-15 cm level. Upland soil contained the highest concentration of potassium (255 pounds per acre) at the 0-15 cm level, with decreasing amounts corresponding to increasing depth down to the 30-45 and 45-60 cm levels, which contained 109 pounds per acre K.

Table 1. Soil analysis of upland and lowland environments.

Soil Origin	Depth (cm)	Nitrogen[1]	Phosphorus[2]	Potassium[2]	pH	% Sand	% Silt	% Clay
Upland	0-15	2.65	11.0	255.0	6.8	83.7	3.4	12.9
Lowland	0-15	0.15	22.6	97.0	9.0	94.7	1.2	4.1
Upland	15-30	1.55	7.9	115.0	7.0	81.1	2.2	16.7
Lowland	15-30	0.15	14.3	85.0	9.2	96.6	0.1	3.3
Upland	30-45	1.65	10.8	109.0	7.4	76.2	5.1	18.7
Lowland	30-45	0.10	14.5	67.0	9.1	96.4	0.4	3.2
Upland	45-60	1.20	11.4	109.0	7.9	77.2	4.7	18.1
Lowland	45-60	0.10	15.8	67.0	8.9	96.4	0.5	3.1

[1]% of organic material.

[2]pounds per acre.

Lowland soil contained 97 pounds K per acre at the 0-15 cm level and demonstrated the same trend as did the upland soil regarding K concentration and depth. Potassium content decreased with increasing depth to the 30-45 cm level after which the content of K, 67 pounds per acre, showed no change with increased depth.

The soil analyses demonstrated a number of microenvironmental differences between the upland and lowland sites, which might have been instrumental in controlling the distribution of upland and lowland races of switchgrass. These differences included texture, the lowland soil was much more sandy; pH, the lowland soil was more alkaline; nitrogen, the lowland soil contained considerably less at all depths tested; potassium, the lowland soil contained less at all depths examined; and phosphorus, the lowland soil contained more at all four depths.

Porter (1966) found essentially the same differences between the upland site used here and another lowland site on the same river. He ascribed the differences in soil reaction between upland and lowland soils to lower amounts of organic carbon and clay as well as to the river's deposition of alkali on the lowland soils. The fact that alkali is deposited on these soils is evident in the salt encrustations observable on the surface of the lowland soil. This indicated that salinity might have a role in controlling plant distribution in this instance. Further evidence that the salt concentration in the river site may have been important was reflected in the water potential values obtained from soil saturation extracts (Table 2). The water potential of the river soil saturation extract at the 0-30 cm depth (-3.6 bars) was considerably lower than this value of either the 0-30 or 30-60 cm depth prairie soil. This indicated that a higher solute concentration existed in the upper level of the river soil than in prairie soil. This was substantiated by the solutes measured since the saturated extract of river soil had a considerably higher total solute content, and of these, calcium accounted for most of the difference. The river soil extract at the 0-30 cm depth also contained higher quantities of magnesium, zinc, and copper than did either level of prairie soil extract. The prairie soil extract contained more manganese and phosphorus at both depths than did the river soil extract. There were generally much lower amounts of ions at the 30-60 cm depth than the 0-30 cm depth in the river soil. This is due to the nature of the shallow water table which rises and then evaporates, leaving a high salt concentration in the upper soil layer.

Field Studies

Growth of naturally occurring upland switchgrass was shown to follow a typical growth curve with an initial rapid rate followed by a slower rate toward maturity (Figure 2). The maximum average height attained was approximately 120 cm. Flowering was first noted on the August sampling date, and some nonflowering

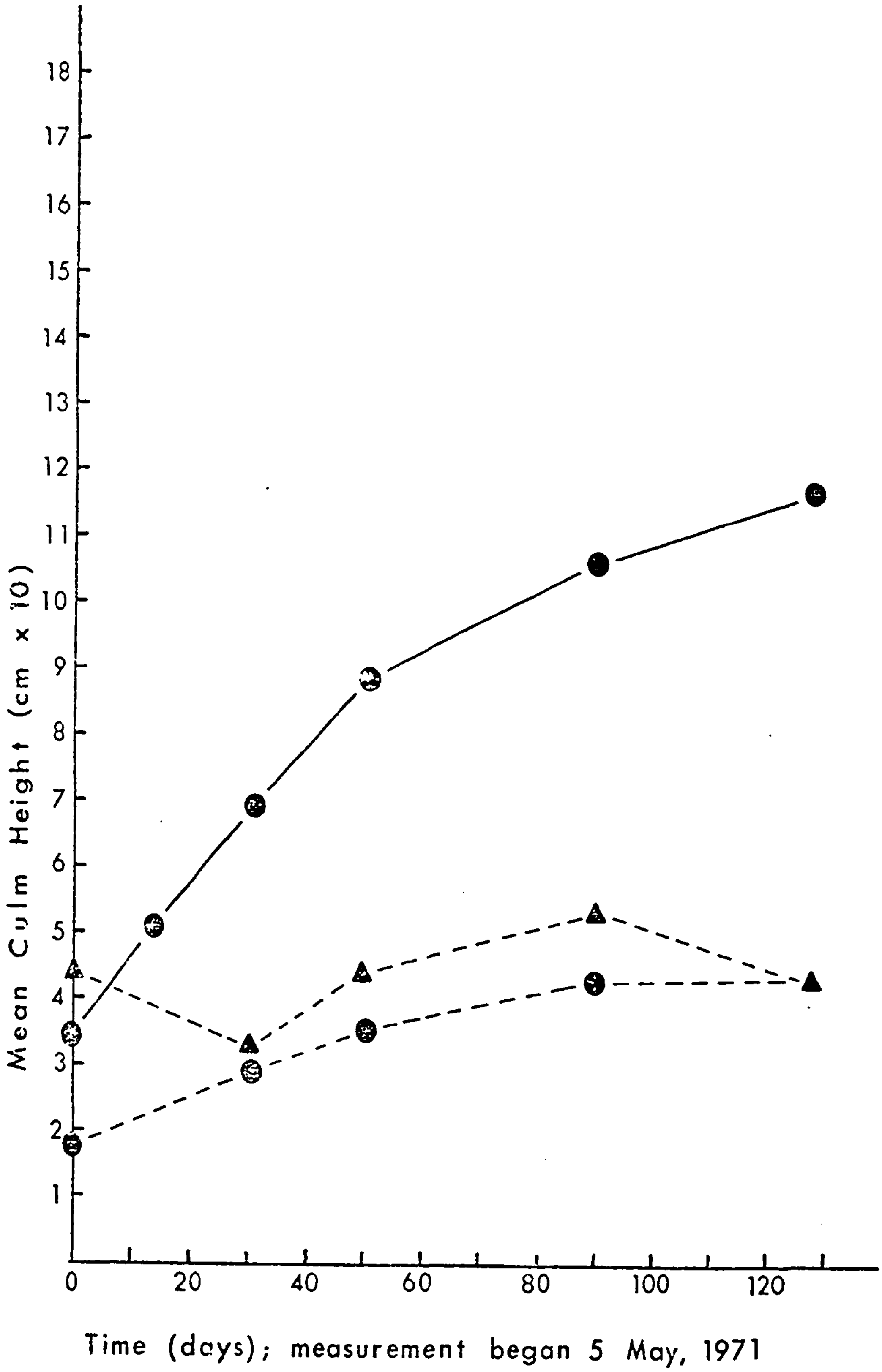
Table 2. Mineral analysis and water potential of prairie and river soil saturation extracts[1].

	Prairie soil		River soil	
	0-30 cm	30-60 cm	0-30 cm	30-60 cm
Mg	1.21	1.30	1.59	1.13
Ca	115.84	116.51	178.58	36.17
Fe	0.0	0.0	0.0	0.0
Zn	0.03	0.03	0.04	0.01
Cu	0.0	0.0	0.06	0.0
Mn	3.74	1.09	0.87	0.05
P	0.08	0.08	0.04	0.04
K	0.89	0.39	0.89	0.56
Total solutes measured	121.79	119.39	182.08	38.97
Ψ (bars)	-2.4	-2.4	-3.6	-2.0

[1]Mineral values are single measurements expressed in ppm.

FIGURE 2.

Growth of naturally occurring and transplanted switchgrass in the upland site. (●, upland plants; ▲, lowland plants; dashed lines, transplants; solid line, naturally occurring).



18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
Mean Culm Height (cm x 10)
0
20
40
60
80
100
120
Time (days); measurement began 5 May, 1971

plants were measured on that date but not subsequently.

Upland switchgrass transplanted in the upland site also exhibited the typical growth curve, but a maximum average height of only about 43 cm (35% of naturally occurring plants) was attained. The decreased growth of these transplanted rhizomes as compared to naturally occurring plants may have been due to the effects of severing roots and rhizomes when transplanting. Root growth may have occurred at the expense of shoot growth. Mortality rate was zero, the average number of culms produced per surviving rhizome was 1.65, and the total number of flowering culms, including secondary tillers, was eleven (Table 3). Flowering occurred in 45% of the surviving transplanted rhizomes. Lowland switchgrass transplanted in the upland site exhibited a deviant growth pattern (Figure 2). During the first month there was a decrease in height followed by a gradual increase until the maximum height was attained (53 cm) in August. There was another decrease in the last month resulting in final growth equivalent to that of the upland switchgrass transplants. Lowland switchgrass was initially taller than upland plants and a greater size was maintained throughout the summer until the last measurements. The decrease in height of lowland plants was due to their becoming brittle and being broken by the wind. Mortality rate of these rhizomes was 20%, the average number of culms produced per surviving rhizome was 1.73, and none of the lowland transplants in the upland site flowered.

Table 3. Summary of growth responses of transplanted upland and lowland switchgrass.

	PRAIRIE SITE		RIVERBOTTOM SITE	
Race	Upland	Lowland	Upland	Lowland
# Surviving rhizomes	20	15	17	19
Mean maximum ht (cm)	43	53	40	71
Mean # culms/ramet	1.65	1.73	2.47	3.63
Total # flowering culms	11	0	17	36
% Surviving rhizomes that flowered	45	0	64.7	84.2

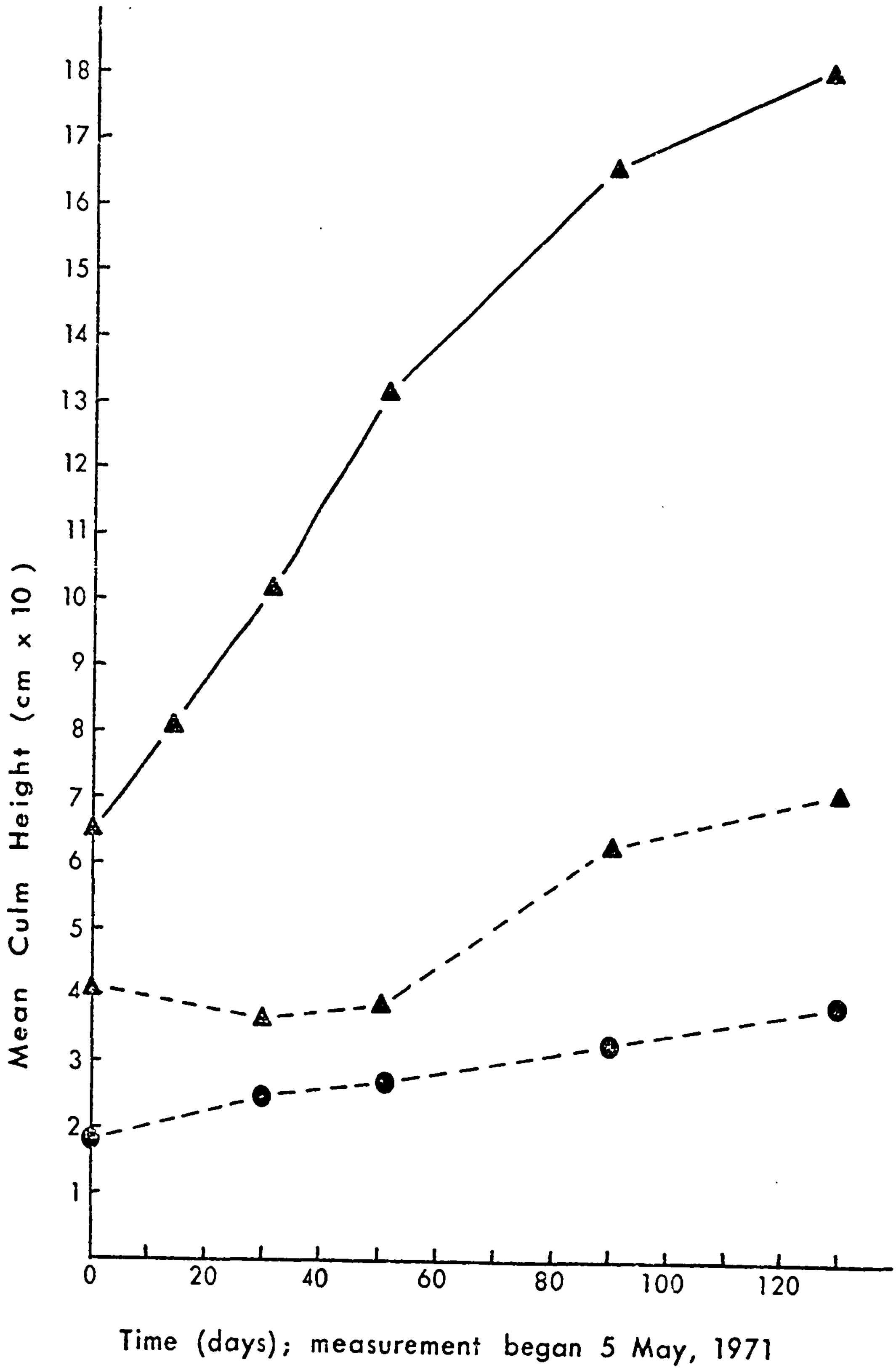
Growth of naturally occurring lowland switchgrass also exhibited a typical pattern (Figure 3) when compared with the growth of natural populations of upland switchgrass (Figure 2). The initial rapid growth rate of lowland switchgrass, although similar to that of upland switchgrass, lasted longer, resulting in a greater maximum average height (180 cm). Flowering of lowland switchgrass was first noted on the August sampling date, and at this and subsequent times only flowering culms were measured.

Lowland switchgrass transplanted in the lowland site exhibited a deviant growth pattern (Figure 3) similar to that of transplants in the upland site (Figure 2), in that an initial decrease in height was followed by a gradual increase, but no final decrease. The maximum average height attained was 71 cm (39.5% of naturally occurring plants). This was an average of 18 cm greater than lowland transplants in the upland site. Again, as in the transplanted upland plants, transplanting resulted in decreased growth of culms. The mortality rate was 5% and this one death was the result of vandalism, an average of 3.63 shoots were produced from each surviving rhizome, and a total of 36 culms flowered including all secondary shoots produced (Table 3). Flowering occurred in eighty-four percent of the surviving rhizomes.

Upland switchgrass transplanted in the lowland site increased in height slowly throughout the growth period and reached a maximum of 40 cm (33% of naturally occurring plants).

FIGURE 3.

Growth of naturally occurring and transplanted switchgrass in the lowland site. (●, upland plants; ▲, lowland plants; dashed lines, transplants; solid line, naturally occurring).


Mean Culm Height (cm x 10)
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
20
40
60
80
100
120
Time (days); measurement began 5 May, 1971

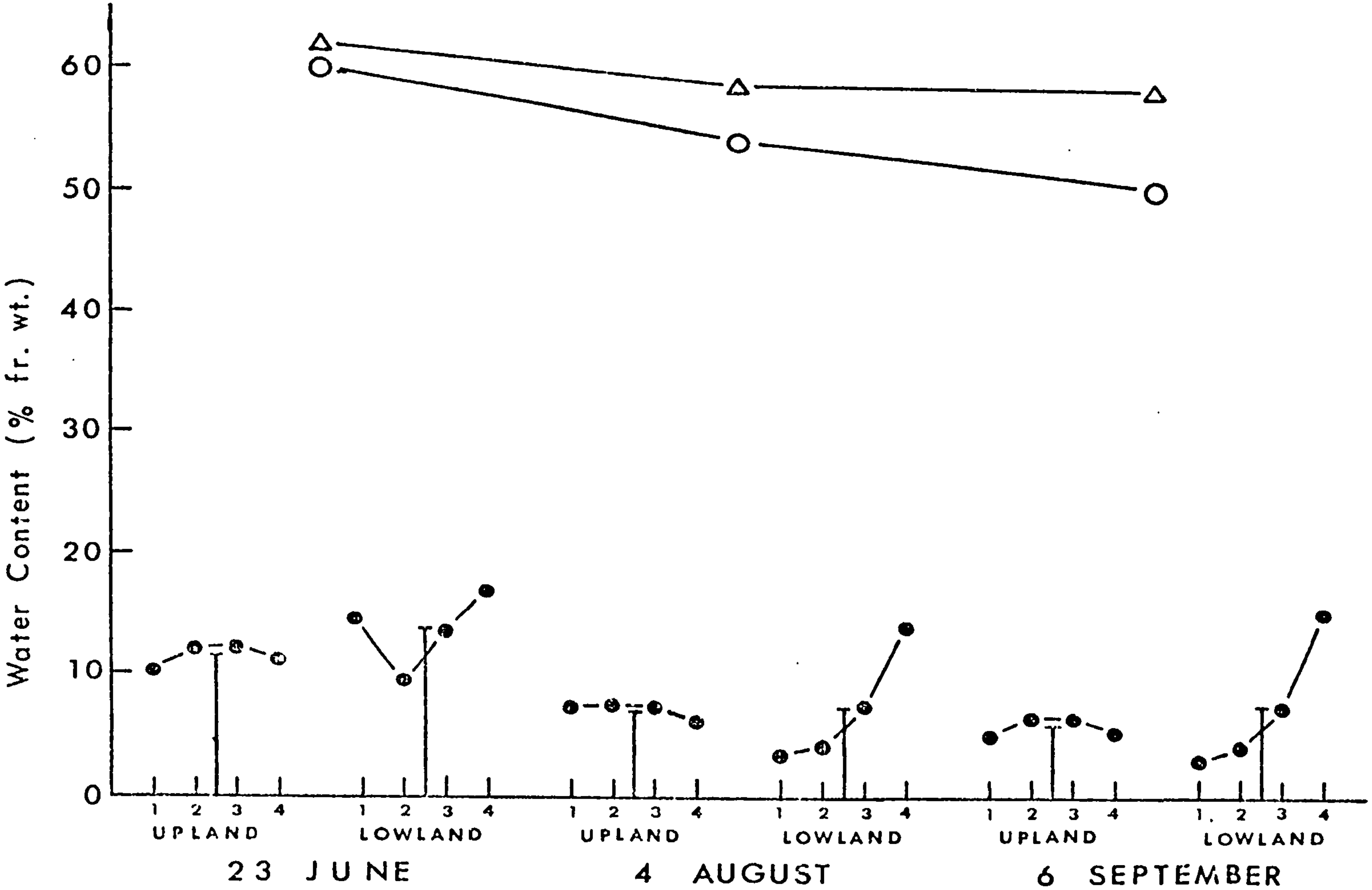
This was an average decrease of 3 cm compared with those transplanted in the upland site. The mortality rate was 15%, but 10% was due to vandalism, the average number of tillers produced per surviving rhizome was 2.47, and approximately 65% of the surviving rhizomes flowered, a total of 17 including secondary tillers.

These data indicated that transplanting in itself decreased growth of both upland and lowland switchgrass races. Because of this, comparison of the reciprocal transplants of each race provides the only indication of relative effects of the foreign environment on growth. Upland switchgrass transplanted into the river site reached a maximum average height of 40 cm as compared with 43 cm when transplanted into its site of origin, whereas lowland switchgrass transplanted into the prairie site reached a maximum height of 53 cm which subsequently decreased to 42 cm as compared to 71 cm maximum height when transplanted into its site of origin. The foreign environments decreased growth of both switchgrass races, but the upland environment had a more deleterious effect on lowland plant growth than did the lowland environment on upland plants under existing conditions.

Soil and plant water content values taken at three of the measurement dates (Figure 4) provide some indication of the water environment and its effect on plant water status. On the first sampling date (28 June) lowland switchgrass leaves contained 61.8% water and the average water content of the

FIGURE 4.

Water content of soils at 4 depths and corresponding values of leaf material samples at three dates in 1971 (0, upland leaf; △, lowland leaf; ●, soil : 1, 0-15 cm; 2, 15-30 cm; 3, 30-45 cm; 4, 45-60 cm; T-bar, mean soil water content of the 4 depths).


Water Content (% fr. wt.)
60
50
40
30
20
10
0
1 2 3 4
UPLAND
1 2 3 4
LOWLAND
23 JUNE
1 2 3 4
UPLAND
1 2 3 4
LOWLAND
4 AUGUST
1 2 3 4
UPLAND
1 2 3 4
LOWLAND
6 SEPTEMBER

lowland soil was 13.7%. The lowest soil water content (9.6%) was at the 15-30 cm depth and the highest (17%) at the 45-60 cm depth. At the same time, upland switchgrass leaves contained 60.2% water and the average upland soil water content was 10.3%, the highest (12.3%) and lowest (10.3%) soil water content being in the 30-45 and 0-15 cm levels, respectively. On the two subsequent sampling dates leaf water content of both races of switchgrass declined, the upland race declining from 60.2 to 50.4%, a decrease of 9.8% and the lowland race declining from 61.8 to 57.9%, a decrease of only 3.9%. Since the 45-60 cm soil depth in the lowland site was the only one which did not decrease substantially in water content, this zone was probably critical in supplying water to these plants, allowing them to maintain a relatively constant high water content throughout the measurement period. This plus the low clay content of this soil, (Table 1) resulting in a higher proportion of the water being available to the plant, created conditions of high water availability. The upland soil on the other hand exhibited a steady decrease in water content at all depths over the period examined, and this in conjunction with a high clay content minimized water availability.

Leaf water potential data from field studies are sketchy due to late arrival of the instrumentation; however, that obtained is given in Table 4. Measurements were conducted as described previously, using a leaf disk from 10 plants under each condition. The mean leaf water potential of lowland

Table 4. Leaf water potential of naturally occurring and transplanted switchgrass.

Date	Leaf Material	Origin	Leaf[1]
6 Sept. '71	Upland	Upland Natural	-33.54 bars
6 Sept. '71	Lowland	Lowland Natural	-17.17 bars
15 Sept. '71	Upland	Lowland trans.	-30.53 bars
15 Sept. '71	Lowland	Lowland trans.	-28.50 bars

[1]Values are the means of 10 measurements.

switchgrass on Sept. 6 was -17.17 bars, approximately double that of upland switchgrass on the same date. This large difference in water potential was associated with leaf % water content values of 57.9 and 50.4 in lowland and upland switchgrass, respectively (Figure 4), illustrating the very large effect a few percentage points in water content can have on the actual water energy in the leaf. Upland switchgrass leaves had a lower mean water potential (-30.53 bars) than did lowland when transplanted to the lowland site, but this difference was not statistically significant. This slight difference in water status between upland and lowland races of switchgrass may have been due to differential sensitivity to salinity in the lowland site.

Analysis of organic constituents of these switchgrass races was conducted to determine possible biochemical differences. Phenolic compounds were found to be more abundant in the lowland race than in the upland (Table 5). Of 31 phenolic compounds isolated, only four were determined to be common to both races. These four compounds were suspected to be chlorogenic acid, scopoletin, ferulic acid, and isochlorogenic acid. Of the remaining 27 compounds, 20 were restricted to lowland switchgrass and seven to upland switchgrass. Lowland switchgrass then contained a total of 24 phenolic compounds as compared to only 11 isolated from the upland race. Because it is rare to find such a diversity in phenolic compounds, even between different species, these results were interpreted to indicate a difference in

Table 5. Phenolic compounds isolated from switchgrass.

Suspected Compound[c]	R_f's on Whatman No. 1[a]					
	Lowland		Upland		UV Fluorescence[b]	
	BAW	6% A.A.	BAW	6% A.A.	Short	Long
Chlorogenic acid	.60	.65,.80	.60	.63	bl	bl
Scopoletin	.71	.46	.68	.43	bl	bl
Ferulic acid	.76	.37	.70	.32	bl	bl
Isochlorogenic acid	.68	.07,.18	.66	.14,.32	bl	bl
Neochlorogenic acid	.44	.62,.77	--	--	bl	bl
Caffeic acid	.73	.32	--	--	bl	bl
Quercetin or Myricetin	.45	.01	--	--	yel	yel
?	.47	.20	--	--	d abs	f abs
?	.55	.32	--	--	d abs	f abs
?	.40	.39	--	--	d abs	f abs
?	.23	.11	--	--	d abs	f abs
?	.65	.36	--	--	d abs	f abs
?	.18	.90	--	--	bl	bl
?	.09	.90	--	--	bl	bl
?	.17	.40	--	--	bl	bl
?	.36	.90	--	--	bl	bl

Table 5.--(Continued)

Suspected Compound[c]	Rf's on Whatman No. 1[a]					
	Lowland		Upland		UV Fluorescence[b]	
	BAW	6% A.A.	BAW	6% A.A.	Short	Long
?	.23	.01	--	--	bl	bl
?	.41	.87	--	--	bl	bl
?	.66	.07	--	--	bl	bl
?	.68	.18	--	--	bl	bl
?	.53	.14	--	--	l bl	l bl
?	.31	.54	--	--	w bl	w bl
?	.78	.56	--	--	lav bl	lav bl
?	.79	.68	--	--	lav bl	lav bl
?	--	--	.25	.21	dk abs	f abs
?	--	--	.23	.39	dk abs	f abs
?	--	--	.68	.46	bl	bl
?	--	--	.70	.67	bl	bl
?	--	--	.22	.56	b bl	b bl
?	--	--	.22	.69	b bl	b bl
?	--	--	.21	.27	l bl	l bl

[a]see text for solvent systems; [b]abs = absorption, b = bright, bl = blue, dk = dark, l = light, lav = lavender, w = whitish, yel = yellow; [c]based on comparison with published R_f's and colors.

metabolic by-products and thus in biochemical systems. The possibility remained that this variation in phenolic compound content was environmentally induced since a number of environmental stresses have been demonstrated to increase the quantity of these compounds in plant tissues (Armstrong et al., 1970, 1971; Koeppe et al., 1969, 1970; Lehman and Rice, 1972) and the riverine and prairie environments differ in stress-type potential. Analysis of these compounds from plants grown under identical conditions should establish whether the observed difference was genetically or environmentally controlled.

Collection of leaf samples from the field for sugar, starch, amino acid, and protein analysis was initiated on 28 June, 1971 and continued periodically through 17 October, 1971.

There was significantly more starch in lowland switchgrass leaves than in upland leaves on all sampling dates (Table 6). Both races exhibited a continual decrease in leaf starch content with increasing age. Leaf sugar concentrations of both races increased after the initial sampling date, but subsequently decreased. This decrease occurred at different times in the two races. Upland leaves began decreasing in sugar content after 4 August, whereas lowland leaf sugar was increasing. The amount of sugar in lowland leaves did not decrease until after 6 September. On the last two sampling dates, lowland leaves contained significantly more sugar than upland leaves. Leaf amino acid content of naturally occurring upland and lowland switchgrass was found to differ in quantity and in changes throughout most

Table 6. Biochemical analysis of naturally occurring upland and lowland switchgrass[1].

Biochemical Assayed	Race	28 June	4 August	6 September	17 October
Sugar (mg/g)	Upland	111.23±1.00	133.00±0.00*	123.08±0.00*	113.02±0.00*
	Lowland	108.68±13.67	111.36±0.9	141.22±1.05	132.87±2.07
Starch (mg/g)	Upland	69.05±1.70*	60.94±0.87*	53.28±0.00*	33.72±0.00*
	Lowland	100.87±1.67	6[illegible].29±0.00	60.74±0.86	35.33±0.00
Amino acid (mg/g)	Upland	0.21±0.00*	0.21±0.01*	0.12±0.00*	0.30±0.01
	Lowland	0.07±0.00	0.18±0.00	0.21±0.01	0.32±0.01
Protein (mg/g)	Upland	3.37±0.09	6.10±0.00*	5.69±0.04*	5.87±0.19
	Lowland	3.28±0.00	5.81±0.00	3.08±0.00	7.64±0.06

[1]Values are means of two measurements expressed as mg/g dry wt ± standard error.

*Significant difference between upland and lowland plants on that date at the 0.1 level or better.

of the sampling period. Upland leaf amino acid content was initially significantly higher than was lowland and did not change in quantity from 28 June to 4 August. A decrease in amino acid content was exhibited in these leaves on 6 September with a final increase on 17 October. Amounts of amino acid in lowland switchgrass leaves increased throughout the sampling period with the increase rate slowing between 4 August and 6 September. Protein content of upland leaves increased markedly between 28 June and 4 August and the content remained essentially unchanged through the remainder of the sampling period with a slight dip and subsequent slight rise. The slight dip in leaf protein content corresponded to a decrease in amino acids as did the slight rise in protein correspond to an increase in amino acid content. Lowland leaf protein increased between 28 June and 4 August at a rate similar to that of upland leaves, but a sharp decrease to below the initial content occurred between 4 August and 6 September. Subsequent to this decrease on 6 September, there occurred a marked increase in leaf protein content on 17 October. To determine environmental effects on the assayed biochemicals, it is necessary to compare this data of reciprocal transplants within each race. Lowland leaves had significantly less starch when transplanted into the prairie site as compared to transplants into the river site (Table 7). Upland switchgrass leaves, on the other hand, had significantly more starch when transplanted into the foreign environment as compared with transplants in its site of origin. It appeared

Table 7. Biochemical analysis of reciprocal transplants of upland and lowland switchgrass[1].

Transplant site	Race	Sugar	Starch	Amino acids	Protein
Prairie	Upland	139.99±4.06	40.12±1.92[c]	0.25±0.01[bc]	4.36±0.08[bc]
	Lowland	137.63±23.36	40.45±0.00[c]	0.19±0.00[bc]	2.81±0.07[bc]
Riverbottom	Upland	152.19±1.00[a]	85.86±0.00[a]	0.05±0.00[ac]	2.54±0.04[ac]
	Lowland	115.72±1.87	62.04±0.00	0.08±0.00[ac]	5.42±0.00[ac]

[1]Values are means of two measurements expressed as mg/g dry wt ± standard error.

[a]Significant difference between upland and lowland transplanted in riverbottom at the 0.1 level or better; [b]significant difference between upland and lowland transplanted in prairie at the 0.1 level or better; [c]significant difference between transplants in original site and in the foreign site at the 0.1 level or better.

that the lowland environment stimulated higher leaf starch quantities in transplants of both races than did the upland environment. Leaf sugar content, of upland and lowland switchgrass, was not significantly affected by these environments. Leaf amino acid content was significantly higher in both upland and lowland races when transplanted into the prairie as compared to transplants in the river site. Leaf protein content, on the other hand, was higher in both upland and lowland transplants when in the site of origin as compared to those grown in the foreign environment. It was apparent that decreased growth of these switchgrass races when grown in their respective foreign environments corresponded to decreased leaf protein content.

Analysis of leaf mineral content indicated that naturally occurring upland switchgrass contained significantly higher concentrations of Ca, Mg, and Mn than did naturally occurring lowland, whereas lowland leaves contained significantly higher concentrations of K, Fe, and Cu (Table 8). Of those minerals found to be significantly higher in upland switchgrass, Mn was also higher in the prairie soil saturation extract, whereas Ca was lower at the 0-30 cm depth but higher at the 30-60 cm depth (Table 2). Of those minerals which were significantly higher in lowland switchgrass, Cu and K was also higher in the river soil saturation extract. Soil mineral content as measured corresponded to plant tissue content regarding most minerals which were in significantly greater concentration in the plant

Table 8. Mineral analysis of naturally occurring and reciprocal transplants of upland and lowland switchgrass leaves[1].

	RIVERBOTTOM SITE		
	Lowland	Transplanted Upland	Transplanted Lowland
N	10.241±0.434[c]	7.308±0.028[a]	5.138±0.147
P	0.977±0.142	1.160±0.250	1.306±0.395
Ca	4.379±0.160[bc]	2.951±0.028[a]	4.623±0.662
K	0.762±0.016[bc]	1.086±0.028[a]	1.067±0.009
Mg	0.253±0.011[bc]	0.132±0.02[a]	0.172±0.007
Fe	0.132±0.005[bc]	0.154±0.0[a]	0.123±0.014
Zn	0.150±0.0[c]	0.1273±0.023	0.288±0.062
Cu	80.435±0.0[bc]	85.87±0.0[a]	90.218±0.0
Mn	26.416±1.056[b]	25.359±0.0[a]	40.416±3.434

[1]Mineral values are the means of two samples expressed as mg/g dry wt ± standard error with the exception of Cu and Mn which are expressed as µg/g dry wt.

[a]Significant difference between transplants into original habitat and transplants into the foreign habitat at the 0.1 level or better; [b]significant difference between naturally occurring upland and lowland races at the 0.1 level or better; [c]significant difference between naturally occurring plants and transplants into the original habitat at the 0.1 level or better.

Table 8.--(Continued)

	PRAIRIE SITE		
	Upland	Transplanted Upland	Transplanted Lowland
N	8.757±1.120	9.524±0.088[a]	9.758±0.119
P	0.942±0.108	1.015±0.104	1.195±0.145
Ca	6.401±0.0[c]	5.181±0.014	6.900±
K	0.653±0.003[c]	0.762±0.0[a]	0.820±0.002
Mg	0.301±0.002[c]	0.200±0.001[a]	0.199±0.008
Fe	0.092±0.008	0.095±0.012[a]	0.137±0.0
Zn	0.197±0.063	0.223±0.029	0.265±0.131
Cu	43.478±0.0[c]	66.304±0.0[a]	73.913±2.174
Mn	46.492±0.0[c]	93.776±2.378[a]	67.360±2.378

[a]Significant difference between transplants into original habitat and transplants into the foreign habitat at the 0.1 level or better; [c]significant difference between naturally occurring plants and transplants into the original habitat at the 0.1 level or better.

tissue.

Transplanting lowland switchgrass into the prairie site resulted in significantly increased N, Ca, Mg, and Mn, but significantly decreased K and Cu as compared to these concentrations in transplants in the site of origin. Transplanting upland switchgrass into the river site resulted in significantly increased K, Fe, and Cu, but significantly decreased N, Mg, and Mn as compared to these concentrations in transplants in the site of origin. Again plant tissue mineral content corresponded to soil mineral content. Since Ca was in all cases increased in the plants growing in the prairie site and the prairie soil saturation extract contained a higher quantity of Ca only at the 30-60 cm depth, it seemed likely that Ca was obtained from the deeper soil layers to the exclusion of the upper layer in both the prairie and river sites.

Considering minerals as possible environmental factors controlling distribution of these switchgrass races, it appeared the low quantities of accessible N and Mn in the river site was related to decreased growth of upland plants when growing there and the low quantities of K and Cu in the prairie soil might have been related to decreased growth of lowland plants when growing in this site. Lowland switchgrass was shown to have lower nitrogen requirement than upland plants (Porter, 1966). Requirements of these switchgrass races for the other elements indicated as related to growth can be shown only by controlled mineral deficiency experiments.

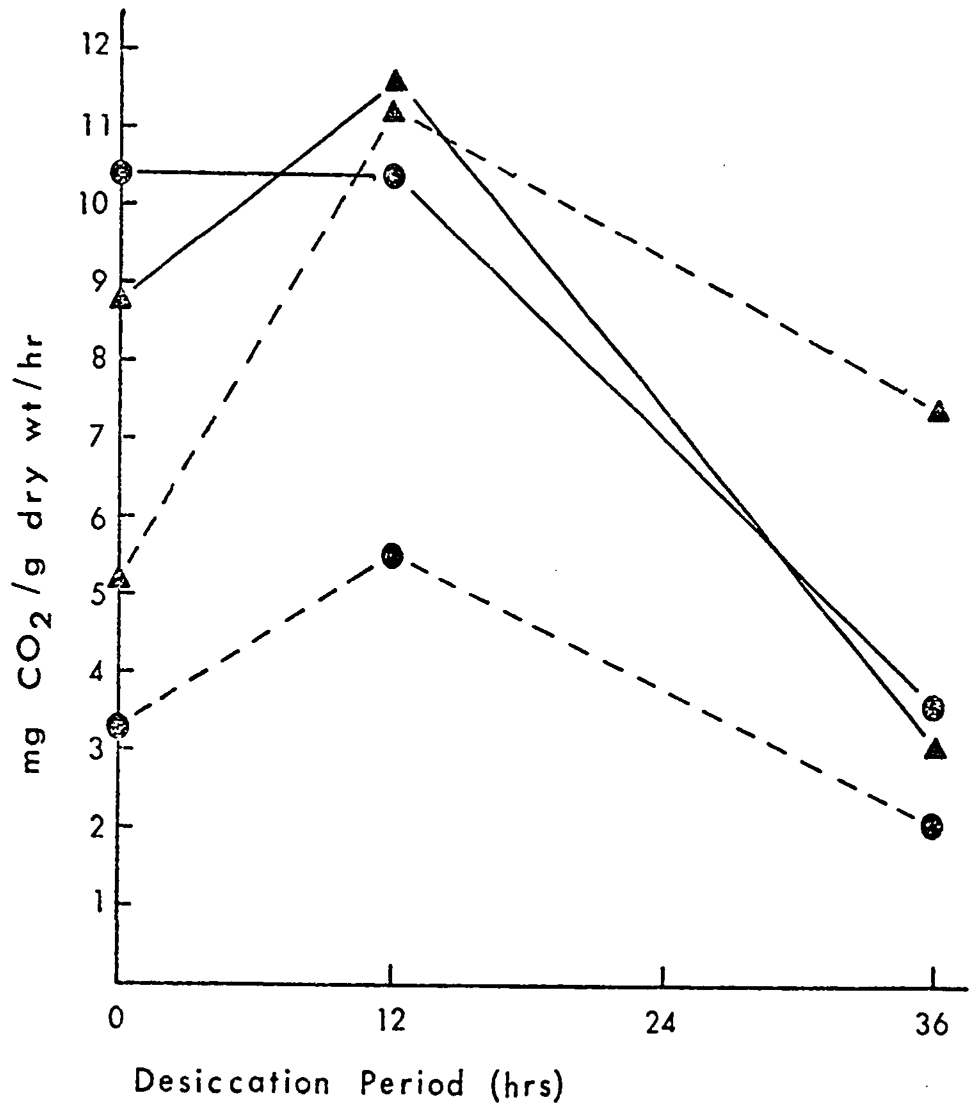
Drought Tolerance

After 12 hr of desiccation net photosynthetic rates of lowland switchgrass plants were increased significantly above initial rates, whereas this rate of upland plants was not changed significantly (Figure 5). Respiration rates of both upland and lowland switchgrass were significantly increased after 12 hours of desiccation, but the lowland plants exhibited an increase 5 times that of upland plants. The resultant photosynthesis/respiration (P/R) ratio of near 2 would accomodate growth, whereas the lowland plants had a P/R ratio of approximately 1 which would allow maintenance, but little growth could have been expected. The P/R ratio of these races of switchgrass was more striking after 36 hr desiccation. Both races of switchgrass demonstrated significantly decreased photosynthesis and respiration rates after 36 hr desiccation, but again the relative amounts of decreases and the resulting P/R ratio of the two races give evidence to their relative drought tolerance. The upland race maintained a P/R ratio of 1.7, whereas the lowland race, after 36 hr desiccation, had a P/R ratio of 0.4. The ability of upland switchgrass to maintain a P/R ratio conducive to maintenance and growth under moisture stress while the lowland race did not, demonstrates the superior drought tolerance of upland switchgrass.

The superior drought tolerance of upland switchgrass over lowland switchgrass was demonstrated above, but relative

FIGURE 5.

Effect of desiccation on net photosynthesis and respiration of upland and lowland switchgrass (●, upland; ▲, lowland; solid lines, photosynthesis; dashed lines, respiration).



12
11
10
9
8
7
6
5
4
3
2
1
mg CO_2/g dry wt/hr
0
12
24
36
Desiccation Period (hrs)

recoverability of these plants from drought stress might show further drought tolerance characteristics. A more rapid recovery from drought condition would confer a definite competitive advantage in a drought-prone site.

Relative ability of upland and lowland switchgrass to recover normal CO_2 exchange rates during a 24 hr recovery period following 36 hr desiccation is shown in Table 9. Upland switchgrass plants which had exhibited a 21.3% decrease in net photosynthetic rate after a 36 hr desiccation period, increased 33.3% following the 24 hr recovery period resulting in a net photosynthetic rate (16.33 mg CO_2/g/hr) greater than normal. On the other hand, lowland switchgrass decreased from a normal CO_2 fixation rate of 16.98 mg CO_2/g/hr to 7.89 (53.5%) after the 36 hr desiccation, the recovery photosynthetic rate was only 8.17 mg CO_2/g/hr, a 3.6% increase over desiccated rates and only 48% of the normal rate. Respiration rate of upland switchgrass decreased 26.4% from 10.55 mg CO_2/g/hr to 7.76, due to a 36 hr desiccation and increased 13.5% of the desiccated rate following recovery. Lowland switchgrass demonstrated a decrease in respiration rate of 21.4% when desiccated and a further 7.9% decrease after the 24 hr recovery period. Neither upland nor lowland switchgrass attained normal respiration rates during this recovery period, but upland respiration rate increased, whereas the rate of lowland plants decreased even more. The P/R ratio demonstrated further the relative drought recoverability of these races of switchgrass. Following the recovery

Table 9. Effect of desiccation and re-watering on the CO_2 exchange rates of upland and lowland switchgrass[1].

	PHOTOSYNTHESIS			RESPIRATION			P/R		
Race	Normal	Desiccated	Watered	Normal	Desiccated	Watered	Normal	Desiccated	Watered
Upland	15.53	12.22	16.33	10.55	7.76	8.81	1.57	1.57	1.85
Lowland	16.98	7.89*	8.17*	5.65	4.44	4.09	2.85	1.78	2.1

[1]Values are expressed in mg CO_2/g dry wt /hr and are the averages of 5 plants.

*Significant difference between this value and normal value at the 0.05 level or better.

periods, upland plants had a P/R ratio of 1.85 which was greater than that of normally watered plants. Re-watering increased the P/R ratio of lowland plants to a value of 2.0. Although this was an increase, the normal P/R ratio (2.85) was not reached.

Responses of upland and lowland switchgrass seedlings to drought stress varied mainly in degree (Table 10). Upland and lowland races both exhibited a decreased shoot and root mean dry weight per plant under drought stress as compared with controls, but these reductions were significant only in lowland plants. As expected, the water content of shoots was significantly reduced in both races, but it was evident that upland plants retained a higher water content at wilting (62% fresh wt) than did lowland plants (38% fresh wt). The shoot/root ratio of lowland plants significantly increased under drought stress as compared to controls, whereas that of upland plants did not significantly change. The increased shoot/root ratio of lowland plants under drought stress was due to root decrease exceeding shoot decrease.

Upland switchgrass exhibited significantly increased concentrations of Fe and Zn, but significantly decreased P, K, and Mn when stressed as compared to control plants. Lowland plants contained significantly higher concentrations of K, Mg, Ca, Zn, and Mn when under drought stress as compared with controls.

Comparison of mineral content as affected by drought with mineral content of transplants in the prairie (Table 8)

Table 10. Effect of drought stress on growth and water and mineral content of upland and lowland switchgrass seedlings[1].

	UPLAND RACE	
	Control	Test
Shoot Dry wt per plant (mg)	24.1±3.1	19.3±6.0
Shoot H_2O (% fresh wt)	74.67±1.25	62.48±4.2*
Root Dry wt per plant (mg)	24.4±4.5	22.0±8.8
Shoot/Root Ratio	0.9635±0.1104	0.8773±0.1817
N	9.924±1.543	11.958±0.473
P	4.796±0.143	1.531±0.187*
K	17.601±0.561	15.877±0.428*
Mg	2.045±0.218	1.778±0.043
Ca	0.113±0.016	0.098±0.010
Fe	0.196±0.005	0.205±0.004*
Zn	37.672±2.55	58.554±6.67*
Cu	22.217±0.810	22.217±2.423
Mn	52.196±3.196	38.057±3.78*

[1]Mineral values are the means of 5 samples ± standard error expressed in mg/g dry wt with the exception of Zn, Cu, and Mn which are expressed in µg/g dry wt.

*Significant difference between test and control at the 0.1 level or better.

Table 10.--(Continued)

	LOWLAND RACE	
	Control	Test
Shoot Dry wt per plant (mg)	11.2±0.9	6.8±0.6*
Shoot H_2O (% fresh wt)	72.18±0.46	38.36±1.34*
Root Dry wt per plant (mg)	10.8±1.6	5.3±0.8*
Shoot/Root Ratio	1.0653±0.0588	1.3262±0.0852*
N	8.605±0.553	9.121±0.4092
P	1.702±0.179	1.353±0.234
K	2.269±0.036	2.717±0.056*
Mg	0.212±0.005	0.288±0.010*
Ca	2.090±0.033	2.465±0.115*
Fe	0.137±0.037	0.120±0.022
Zn	78.35±1.926	89.082±4.801*
Cu	78.044±2.392	80.652±7.804
Mn	62.87±2.126	76.500±0.906*

*Significant difference between test and control at the 0.1 level or better.

illustrated that the increased concentration of Mn and Ca in lowland plants when grown in the prairie could have been enhanced by the relative dry conditions of the prairie in addition to their being present in higher amounts in the soil. Drought did not result in significantly decreased concentration of any minerals quantified, so the decrease of Cu, Fe, and K in lowland plants growing in the prairie was probably not due to water deficiency. On the other hand, drought stress of upland plants resulted in a response in only K that was similar to the response of upland transplants in the prairie. This indicated that the upland transplants did not receive as strong drought stress in the prairie as did lowland transplants.

In this study, the more drought tolerant race exhibited increased mineral concentration of relatively fewer minerals (Fe and Zn), but exhibited decreased mineral concentration of more minerals (P, K, and Mn) when stressed than did the drought susceptible race.

Initial leaf diffusive resistance values indicated that upland switchgrass was relatively intolerant of low nutrients as compared to lowland plants (Table 11). Upland leaf diffusive resistance when grown without nutrients or with very low nutrient concentrations was considerably higher than when grown with higher nutrient concentrations. This increased diffusive resistance may have decreased CO_2 diffusion into the leaf and resulted in decreased photosynthesis due to CO_2 limitation. Leaf diffusive resistance of lowland plants grown

Table 11. Effect of drought on leaf diffusive resistance of switchgrass previously grown at various nutrient concentrations[1].

Drought period	UPLAND RACE					LOWLAND RACE				
	0.0	0.0625	0.125	0.25	0.5	0.0	0.0625	0.125	0.25	0.5
Initial	11.25	6.15	2.66	1.89	3.6	6.44	6.12	8.22	9.90	2.06
24 hr	15.41	5.24	2.13	3.81*	4.51	10.34	8.19	20.39*	11.53	3.43
48 hr	16.13	5.64	23.45	24.10	9.30	14.10*	18.28*	58.14*	57.68*	70.0
60 hr	10.62	11.65	34.35*	43.52*	12.83	--	--	--	--	--
72 hr	--	--	--	--	--	10.82	93.80*	94.81*	79.60*	97.22*
84 hr	17.29*	23.03	43.96*	68.39*	22.97*	--	--	--	--	--

[1]Values are means of four measurements expressed as sec cm^{-1}.

*Value significantly different from the initial value at that nutrient concentration at the 0.1 level or better.

with no nutrients was actually less than these rates of plants grown with certain of the nutrient concentrations and thus would not have been expected to decrease CO_2 diffusion or photosynthesis.

Comparison of maximum leaf diffusive resistances between upland and lowland indicated lowland leaves acquired a much higher diffusive resistance under drought than did upland switchgrass and this correlated with the earlier experimentation demonstrating lowland plants to exhibit more marked decrease in photosynthesis when under drought stress then upland plants. These results indicated that upland switchgrass maintained a greater photosynthetic rate under drought than lowland plants due to less stomatal closure resulting in less diffusive resistance and thus less resistance to CO_2 diffusion into the leaf.

In general, leaf ψ and leaf water content of both upland and lowland switchgrass (Table 12) corresponded to leaf diffusive resistance (Table 11) of comparable plants. It was noted that leaf diffusive resistance of upland plants increased the least under drought when grown previously at either very low or very high nutrient concentration. However the low diffusive resistance of stressed upland leaves when previously at low nutrient levels, resulted in a high water loss from the tissue as compared with the water loss from plants with a low diffusive resistance previously in high nutrient levels.

Lowland leaf diffusive resistance at maximum drought

Table 12. Effect of drought stress on leaf ψ and leaf water content of upland and lowland switchgrass[1].

Nutrient concn.	UPLAND RACE[2]		LOWLAND RACE[3]	
	Leaf ψ	H_2O Content	Leaf ψ	H_2O Content
H_2O	-20.6	169.94	-18.1	198.54
0.0625	-20.2	185.39	-34.2	131.01
0.125	-31.6	176.06	-36.4	75.17
0.25	-37.1	83.02	-35.9	120.04
0.5	-26.5	259.37	-39.2	88.10

[1]Values are means of 4 samples expressed in bars (leaf ψ) and % Dry wt (H_2O content).

[2]These values after 84 hr drought.

[3]These values after 72 hr drought.

(72 hr) was lowest in plants from zero nutrient concentration, and all nutrient levels had an increasing effect on diffusive resistance. Again, although more water was expected to diffuse from plants with low diffusive resistance, this was not always the case. The lowland plants with the lowest diffusive resistance also had the highest shoot water content. Since upland and lowland switchgrass reacted oppositely in this instance, i.e., lowland plants from zero nutrient level had the lowest diffusive resistance but highest water content, whereas upland plants from the highest nutrient concentration had one of the lower diffusive resistance values and also highest water content. The apparent relationship between mineral concentration and water retention even when stomates are relatively open and the completely opposite nature of this relationship between upland and lowland switchgrass may be the key to their difference in mineral requirement.

Flood Tolerance

There was no significant effect of flooding on growth, net photosynthesis, or respiration of either upland or lowland switchgrass as compared to controls (Table 13). Inundation actually increased the mean net photosynthetic rate of upland switchgrass and decreased this mean value of lowland plants as compared to plants watered 3 times daily. Mean respiration rate of upland plants was slightly reduced by flooding and lowland plants demonstrated no alteration of the respiration

Table 13. Effect of inundation and watering 3x per day on CO_2 exchange rates and growth of upland and lowland switchgrass.

Plant Type	Photosynthesis[1] inundated	Photosynthesis[1] 3x/day	Respiration[1] inundated	Respiration[1] 3x/day	P/R inundated	P/R 3x/day	Increase in Height[2] inundated	Increase in Height[2] 3x/day
Upland	20.06	15.53	9.05	10.55	2.16	1.57	20.1	14.43
Lowland	11.34	16.98	5.65	5.65	2.01	2.85	19.7	20.01

[1]Values are expressed in mg CO_2/g dry wt /hr and are the averages of 5 plants.

[2]Values are expressed in cm and are the averages of 5 plants.

rate when flooded. As a result of the slight increase in mean net photosynthetic rate and slight decrease in the mean respiratory rate of upland plants when flooded, the P/R ratio was greater when flooded then when watered three times per day. This increase in P/R ratio was reflected in greater growth of upland plants when flooded as compared to the controls. Lowland plants demonstrated a slight net photosynthetic rate decrease and respiration was unaltered when flooded, resulting in a lower P/R ratio and parallel lessened growth under flooded condition when compared to controls.

This data indicated that flooding under these conditions was not harmful to upland plants. Instead of providing physiological data supporting previous reports, the data was contradictory. This response of upland plants to flooding may have been due to the use of sand as substrate. Thus, the experiment was repeated using prairie soil as substrate or using sand again and applying less nutrient solution than before.

With soil as the medium of growth, lowland switchgrass exhibited significantly stimulated shoot dry weight production when flooded (Table 14). Mean growth rate, water content, leaf water potential, photosynthesis and P/R ratio of lowland plants were slightly stimulated when flooded, but insignificantly as analyzed by a T-test, while respiration rate was slightly decreased when flooded when compared to controls. Upland switchgrass exhibited significantly enhanced growth

Table 14. Effect of flooding on upland and lowland switchgrass grown in soil[1].

Race	Condition	Growth[2]	Dry wt [3]	% Water[4]	Leaf H_2O Potential[5]	CO_2 Exchange Rate[6] Ps.	Resp.	P/R
Upland	Flooded	1.26*	0.1766*	256.02*	-21.54	6.69	2.75*	2.82
	Control	0.90	0.1030	310.42	-19.00	4.26	8.07	0.53
Lowland	Flooded	0.77	0.1956*	332.40	-27.13	4.61	6.11	0.92
	Control	0.32	.0689	329.18	-29.28	4.37	8.93	0.49

[1]All values are the means of 8 plants.

[2]cm per day height.

[3]grams

[4]% dry wt

[5]bars

[6]mg CO_2/g dry wt /hr

*Values are significantly different from controls at 0.1 level or better.

rate and dry weight production when flooded while water content and respiration rate were significantly decreased, and photosynthetic rate, and P/R ratio, while being slightly stimulated, were not significantly affected by flooding. Leaf water potential was decreased only slightly.

Upland and lowland plants were similar in reaction to flooding when grown in soil since both exhibited enhanced dry weight production, growth rate, photosynthetic rate and P/R ratio. The only noted difference in reaction was degree of significance in certain instances and the water content of upland plants decreased when flooded while that of lowland plants was not affected. Indications were that upland switchgrass was not significantly harmed by flooding under the test conditions.

Using sand as the culture medium and supplying low amounts of nutrients over a 10 day period, flooding had the effect of significantly decreasing growth rate, dry weight production, water content, photosynthesis and P/R ratio, while significantly increasing respiration rate and insignificantly reducing leaf water potential of upland plants (Table 15). Lowland switchgrass exhibited significantly decreased growth rate and water content while dry weight production, photosynthesis, respiration, leaf water potential and P/R ratio were slightly decreased, but not significantly.

These data indicated that flooding in combination with low nutrient content was harmful to both upland and lowland

Table 15. Effect of flooding with low nutrient content on upland and lowland switchgrass[1].

Race	Condition	Growth[2]	Dry wt[3]	% Water[4]	Leaf H_2O Potential[5]	CO_2 Exchange Rate[6]		
						Ps.	Resp.	P/R
Upland	Flooded	1.62*	0.1385*	277.97*	-12.60	4.36*	2.66*	1.65*
	Control	2.48	0.2029	333.05	-11.97	7.84	2.36	3.39
Lowland	Flooded	0.89**	0.1576	328.06*	-18.85	5.09	2.71	1.92
	Control	1.35	0.1602	382.44	-16.80	6.55	2.84	2.26

[1]Values are the means of 10 plants.

[2]cm per day height.

[3]grams

[4]% dry wt

[5]bars

[6]mg CO_2/g dry wt /hr

*Values are significantly different from the controls at the 0.05 level or better.

**Values are significantly different from the controls at the 0.1 level.

switchgrass, but the effect on upland plants was greater. Since similar plants were not grown flooded with high nutrient content, the possibility that these plants would have shown similar reactions to flooding with high nutrients existed. Therefore the same plants utilized above were set aside to allow regrowth of shoots to occur. After approximately two weeks the shoot regrowth was measured and both upland and lowland switchgrass plants were divided into two groups having approximately the same mean height. One group of each switchgrass race was subjected to flooding with no additional nutrients and the second group was flooded in 0.25 strength Hoagland nutrient solution for a period of 15 days.

Upland and lowland switchgrass both exhibited significantly increased growth rate, dry weight production, water content and photosynthetic rate when flooded with 0.25 strength nutrient solution when compared with plants flooded with no nutrients added (Table 16). Both switchgrass races also demonstrated enhanced respiration and P/R ratio when flooded with nutrient solution, but these increases were significant in only upland plants.

Although both upland and lowland plants demonstrated enhancement when flooded with nutrient solution compared to flooding without nutrients, the upland plants demonstrated a definite nutrient requirement under flooded conditons, whereas this was not true of lowland plants. This higher nutrient requirement of upland plants was demonstrated by their slow

Table 16. Effects of flooding in combination with 0.25 strength Hoagland nutrient solution or no nutrients on upland and lowland switchgrass[1].

					CO_2 Exchange Rate[5]		
Race	Nutrients	Growth[2]	Dry wt[3]	% water[4]	Photosyn.	Respiration	P/R
Upland	With	1.82*	0.08*	505.9*	12.15*	5.57*	2.20*
	Without	1.03	0.04	341.6	4.17	4.12	1.02
Lowland	With	1.77	0.196*	422.2*	14.08**	3.09	4.76
	Without	1.33	0.122	351.6	5.57	2.95	1.90

[1]Values are the means of 8 plants.

[2]cm per day height

[3]grams

[4]% dry wt

[5]mg CO_2/g dry wt/hr

*Values are significantly different from controls at 0.05 level or better as analyzed with T-test.

**Values are significantly different from controls at 0.1 level.

growth rate, low dry weight production, and near equality of photosynthesis and respiration, resulting in a P/R ratio of 1.0 when flooded with no nutrients.

These data show the lowland race of switchgrass to be much more tolerant of low nutrient conditions when flooded than the upland race, and was therefore better adapted to the low nutrient environment of the lowland site which is also flood-prone. Flooding alone could not be shown to be operative in controlling distribution of these switchgrass races but flooding in association with low nutrient content was demonstrated to be a very important factor.

The above experiment did not compare the effect of low nutrient concentration when flooded with this effect when not flooded so it remained questionable as to whether flooding in association with low nutrient concentration would be more or less deleterious to upland switchgrass than low nutrient concentration when not flooded. In effort to establish the answer to this question, 10 plants of both upland and lowland switchgrass were grown flooded in each of 0, 0.0625, 0.125, 0.25, and 0.5 strength Hoagland nutrient solutions and another 10 plants of each race were watered twice daily with one of each of the above nutrient solutions. The unflooded plants were watered every third day with distilled water to prevent nutrient concentration build-up due to evaporation. The plants were cultured as previously described and grown under these conditions for twenty days. At termination of the experimental period, increase in height of all plants, net photosynthesis and dark respiration, leaf water potential, and fresh and dry weights of 4 plants from each condition were measured.

Upland switchgrass exhibited significantly decreased growth rate, net photosynthesis, and P/R ratio when flooded with distilled water, whereas shoot dry weight, water content, leaf ψ, and respiration were not affected as compared with non-flooded plants with no nutrients (Table 17). These plants flooded with 0.0625 Hoagland nutrient solution exhibited significantly decreased water content, net photosynthesis, and P/R ratio, but significantly increased shoot dry weight and leaf ψ as compared to controls. When flooded with 0.125 nutrient solution, upland plants demonstrated significantly decreased water content and significantly increased shoot dry weight, while none of the other measurements were affected significantly. At the higher nutrient concentrations (0.25 and 0.5 Hoagland's) flooding did not significantly affect any of these measurements except for a reduction in respiration rate when flooded in 0.5 strength nutrient concentration as compared to controls.

Lowland switchgrass growth rate and shoot dry weight were significantly decreased whereas net photosynthesis and respiration were increased when flooded with distilled water as compared to controls (Table 18). Growth rate, shoot dry weight, water content, leaf ψ, and P/R ratio were significantly

Table 17. Effect of flooding in association with various Hoagland nutrient solution concentrations on upland switch-grass[1].

Nutrient concn.	Condition[2]	Growth Rate (cm/day)	Shoot Dry wt (mg)	H_2O content (% dry wt)
0.0	N.F.	1.06±.17	65.3±18.8	321.2±37.8
	F.	0.8±.13*	70.4±11.6	319.2±29.0
0.0625	N.F.	1.35±.14	51.7±8.2	508.0±19.0
	F.	1.42±.35	65.8±15.2*	420.0±50.9*
0.125	N.F.	1.42±.34	53.1±11.0	532.2±31.9
	F.	1.56±.7	78.5±25.3*	421.8±62.2*
0.25	N.F.	1.74±.41	63.5±22.6	554.0±47.4
	F.	1.42±.64	56.8±27.5	514.4±167.2
0.5	N.F.	1.3±.36	39.9±19.6	509.5±63.5
	F.	1.21±.72	50.8±34.7	486.5±142.36

[1]Values are means of 4.

[2]N.F. = not flooded, F. = flooded.

[3]mg CO_2/ g dry wt/hr

*Values significantly different from controls at the 0.1 level or better.

Table 17.--(Continued)

Leaf ψ (bars)	CO_2 Exchange Rate[3] Photosyn.	Respiration	P/R
-26.5±2.9	9.98±3.94	3.05±.93	3.22±.65
-26.2±2.7	5.25±1.46*	2.69±.15	1.95±.57*
-30.2±3.9	14.63±3.62	4.74±.74	3.10±.65
-26.8±1.8*	9.08±3.12*	4.31±1.25	2.12±.56*
-24.8±3.0	11.12±3.61	3.72±.95	3.0±.76
-24.8±3.3	8.72±4.88	3.39±1.28	2.48±.70
-23.9±2.2	18.21±3.89	4.25±.72	4.3±.68
-25.3±7.1	15.47±13.98	4.75±1.30	3.02±1.89
-25.4±8.4	17.36±9.55	5.13±.79	3.3±1.44
-25.7±2.8	13.34±2.77	3.16±.75*	4.5±1.73

[3]mg CO_2/g dry wt/hr

*Values significantly different from controls at the 0.1 level or better.

Table 18. Effect of flooding in association with various Hoagland nutrient solution concentrations on lowland switchgrass[1].

Nutrient concn.	Condition[2]	Growth Rate (cm/day)	Shoot dry wt (mg)	H_2O content (% dry wt)
0.0	N.F.	1.74±.18	230.0±20	372.2±16.0
	F.	1.30±.28*	140.0±60*	382.9±72.3
0.025	N.F.	1.99±.28	180.0±40	501.7±41.0
	F.	1.64±.39*	150.0±10*	436.5±22.4*
0.125	N.F.	1.64±.66	154.2±80	544.9±57.1
	F.	1.69±.27	138.9±40	509.1±26.4
0.25	N.F.	2.35±.24	200.9±50	601.5±43.9
	F.	1.47±.27*	105.4±20*	688.8±62.6
0.5	N.F.	0.96±.17	88.3±8.8	570.3±92.8
	F.	1.64±.68*	108.3±46.9	585.2±75.8

[1]Values are means of 4 ± standard deviation.

[2]N.F. = not flooded, F. = flooded.

*Values significantly different from controls at the 0.1 level or better.

Table 18.--(continued)

Leaf ψ (bars)	CO_2 Exchange Rate[3] Ps.	Resp.	P/R
-29.4±3.6	4.63±1.28	1.88±.19	2.50±.85
-28.3±3.5	7.24±1.92*	3.02±.58*	2.40±.4
-20.2±3.8	8.80±1.2	2.70±.43	3.32±.5
-24.2±2.3*	7.9±2.7	3.20±.52*	2.42±.42*
-19.9±3.8	13.4±5.4	2.88±.67	4.58±1.14
-22.4±4.8	31.12±25	3.24±.58	8.40±6.0
-21.9±3.4	10.26±2.0	2.91±.29	3.52±.61
-20.2±3.5	17.75±11.4	3.49±.44*	5.02±2.88
-27.6±3.4	10.88±2.31	3.02±.35	3.58±.57
-21.3±3.2*	10.07±2.12	3.69±.12*	2.72±.50*

[3]mg CO_2/g dry wt /hr

*Values significantly different from controls at the 0.1 level or better.

decreased while respiration of lowland plants was significantly increased when flooded with 0.0625 nutrient solution when compared with these controls. Flooding lowland plants with 0.25 strength nutrient solution resulted in significantly decreased growth rate and shoot dry weight, while respiration rate was significantly increased. These plants exhibited significantly increased growth rate, leaf ψ, and respiration rate, but decreased P/R ratio when flooded with 0.5 nutrient solution when compared to these controls.

In general, upland switchgrass possessed faster growth, increased water content, leaf ψ, photosynthesis, respiration, and P/R ratio at nutrient concentrations above zero with maximums of most of these measurements occurring at 0.25 Hoagland nutrient concentration. Lowland plants likewise demonstrated trends toward increases in most of these measurements with nutrient concentrations above zero, but these increases were not as consistent or marked as in upland switchgrass. Lowland plants exhibited a majority of maximum measured values at nutrient concentrations of 0.0625 or 0.125.

These results indicated that flooding associated with very low nutrient concentration was more deleterious to both upland and lowland switchgrass than was low nutrient concentration when not flooded and this was more marked in upland plants than lowland. In addition, lowland switchgrass was again demonstrated to be more tolerant to low nutrient concentration than was the upland race. The deleterious effects on upland switchgrass of low nutrient concentration plus the increased deleterious effects of low nutrients when flooded would indicate that upland plants would be severely restricted in the riverbottom site.

Salinity

Upland switchgrass leaves possessed an initially higher diffusive resistance (9.3 sec cm^{-1}) than lowland leaves (7.8 sec cm^{-1}) (Table 19). Upland leaf diffusive resistance was higher on all dates when exposed to NaCl solutions as compared to pure water, and 0.1 m NaCl increased the diffusive resistance much more than 0.05 m NaCl. The maximum upland leaf diffusive resistance (73.2 sec cm^{-1}) was associated with the 0.1 m NaCl solution on the sixteenth day.

Leaf diffusive resistance of lowland switchgrass exposed to 0.05 m NaCl was less than that of controls at all dates measured except the eleventh day after initiating the experimental conditions. Leaf diffusive resistance of these plants when in 0.1 m NaCl solution was increased on the sixth and subsequent days when compared with controls. Maximum diffusive resistance of lowland switchgrass (28.8 sec cm^{-1}) occurred when exposed to 0.1 m NaCl for eleven days.

Photosynthesis and respiration rates of upland plants on the sixteenth day of treatment decreased with increased NaCl concentration (Table 20) and thus correlated with increased diffusive resistance as NaCl concentration increased (Table 19).

Table 19. Effect of NaCl concentration on leaf diffusive resistance[1].

	UPLAND RACE			LOWLAND RACE		
	H_2O	0.05 m NaCl	0.1 m NaCl	H_2O	0.05 m NaCl	0.1 m NaCl
Initial	9.30	9.30	9.30	7.84	7.84	7.84
2 days	4.86	9.55*	9.79*	6.06	3.84*	5.19
6 days	6.22	8.82	15.34*	6.46	4.43	8.17
11 days	4.88	12.29*	61.75*	2.16	7.86*	28.80*
16 days	8.09	8.40	73.22*	6.93	5.47	23.81*

[1]Values are means of 4 measurements expressed as sec cm^{-1}.

*Value significantly different from the appropriate H_2O control at the 0.1 level or better.

Table 20. Effect of NaCl concentration on carbon dioxide exchange rates and plant water status[1].

	UPLAND RACE			LOWLAND RACE		
	H_2O	0.05 m NaCl	0.1 m NaCl	H_2O	0.05 m NaCl	0.1 m NaCl
Photosynthesis[2]	6.83	2.88*	0.03*	4.09	4.69	0.25*
Respiration[2]	1.80	1.04*	0.82*	1.23	1.75*	0.68
Leaf ψ[3]	-11.5	-29.3*	-40.3*	-14.8	-23.2*	-33.7*
H_2O Content[4]	292.6	222.2*	192.9*	273.6	238.8	150.0*

[1]Values are means of 4 measurements.

[2]mg CO_2/g dry wt/hr

[3]bars

[4] % dry wt

*Value significantly different from that of the control at the 0.1 level or better.

However, both leaf ψ and leaf water content also correlated with gas exchange rates since leaf ψ was highest when exposed to pure water and lowest when exposed to 0.1 m NaCl and shoot water content was lowest at the highest NaCl concentration.

Increased NaCl concentration resulted in decreased leaf water potential and water content of lowland switchgrass, but 0.05 m NaCl increased these plants' photosynthetic and respiratory rates while decreasing leaf diffusive resistance as compared to these values of plants in pure water. In this case, the only factor found to correlate exactly with gas exchange rates was leaf diffusive resistance.

Photosynthesis and respiration of upland switchgrass when subjected to saline conditions correlated with leaf diffusive resistance, leaf ψ, and leaf water content so it was impossible to differentiate between these factors in their effects of CO_2 exchange. Lowland plants however exhibited higher photosynthetic as well as respiration rate when subjected to 0.05 m NaCl as compared to pure water. Of the factors measured, only leaf diffusive resistance of lowland plants correlated with the increased CO_2 exchange rates. At least in this instance, it appeared CO_2 exchange rates were more closely related to leaf diffusive resistance than to either leaf ψ or water content. It seemed that not only photosynthetic CO_2 uptake but also respiratory CO_2 production was correlated with leaf diffusive resistance.

Sodium chloride appeared to affect these switchgrass races differentially. The 0.05 m NaCl solution actually stimulated gas exchange rates of lowland plants whereas both salt concentrations used decreased gas exchange of upland plants. These data suggest that salinity may be operative in controlling growth of these switchgrass races under natural conditions.

CHAPTER V

SUMMARY

The ecological segregation of *Panicum virgatum*, switchgrass, into upland and lowland races was investigated in an effort to determine physiological processes operative in controlling distribution of these switchgrass races.

Soil analysis of upland and lowland sites provided evidence of several environmental variations through which differential physiology could possibly affect distribution. The lowland soil was sandier, more alkaline and saline, contained less nitrogen, potassium, and manganese, but more phosphorus, magnesium, zinc, and copper than upland soil. In addition, the lowland soil possessed a higher water content, but this soil water had a lower water potential due to ion concentration.

Reciprocal transplants demonstrated that growth capacity was diminished in both races when grown in the foreign site as compared with transplants grown in the site of origin.

Analysis of organic constituents revealed varied biochemical systems in these switchgrass races since numbers of phenolic compounds were much higher in lowland leaves and both races demonstrated decreased protein when grown in the foreign environment.

Leaf mineral concentration of both naturally occurring and transplanted switchgrass corresponded to soil saturation extract and soil mineral content. Low amounts of N and Mn in the river site and low quantities of K and Cu in the prairie corresponded to decreased leaf concentration of these as well as growth of transplants from the foreign site as compared to transplants in the original site. Calcium, appeared to be taken from the 30-60 cm soil depth as indicated by plant content.

Carbon dioxide exchange rates of upland and lowland switchgrass under drought stress reflected the relative drought tolerance of upland switchgrass as compared to lowland plants and upland plants exhibited faster recovery from drought. Upland seedlings also exhibited greater growth, water retaining capacity, and different mineral concentrations under drought as compared to lowland seedlings. Since lowland plant concentrations of Mg, Mn, and Ca under drought was similar to that when transplanted in the prairie, the possibility that the dry conditions of the prairie affected concentration of these minerals was noted. Mineral concentration affected drought tolerance of both races. Upland switchgrass retained higher water content and water potential under drought at high nutrient levels even though leaf diffusive resistance was low allowing faster gas exchange rates, whereas lowland plants had higher water content and leaf water potential under drought at low nutrient levels and these values likewise corresponded to low leaf diffusive resistance.

Both races were tolerant of flooding when provided with sufficient nutrients, but lowland plants were better adapted to flooding in association with low nutrient concentration. These conditions occur in the riverbottom where upland plants are not found. In addition, upland plants had maximum physiological conditions at a higher nutrient level than lowland plants.

Based on carbon dioxide exchange rates, upland switchgrass was relatively intolerant of salinity as compared to lowland plants which maintained relatively open stomata and adequate carbon dioxide exchange rates under saline conditions although leaf water content and leaf ψ were seemingly adversely affected.

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