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A COMPARATIVE STUDY OF UPLAND AND
BOTTOMLAND TYPES OF PANICUM VIRGATUM
L. (SWITCHGRASS) IN THE VICINITY OF NORMAN,
OKLAHOMA.

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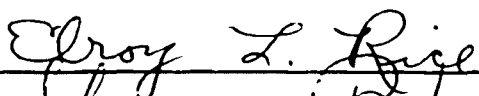
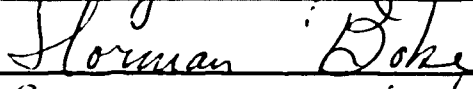
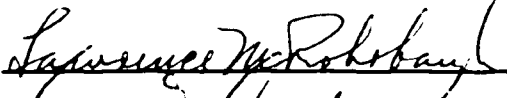
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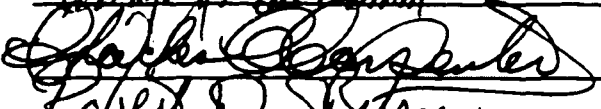
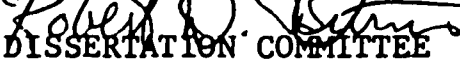
A DISSERTATION
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
DOCTOR OF PHILOSOPHY

BY
CLYDE LEHMAN PORTER, JR.
Norman, Oklahoma
1963

A COMPARATIVE STUDY OF UPLAND AND BOTTOMLAND TYPES OF
PANICUM VIRGATUM L. (SWITCHGRASS) IN THE VICINITY
OF NORMAN, OKLAHOMA

APPROVED BY



DISSERTATION COMMITTEE

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INTRODUCTION

The economic value of Panicum virgatum L. (switchgrass) in soil conservation and as a forage species has long been recognized. It is very widely distributed, ranging from Quebec and Maine to Montana, south to Florida, Nevada, Arizona, Mexico, and Central America and occupies habitats varying from dry uplands to wet lowlands (Hitchcock 1950).

Panicum virgatum is one of the dominants of the tall-grass prairie (Rice 1952) and of many floodplain grasslands (Hefley 1937, Turner 1933). Weaver and Fitzpatrick (1932) give the following interesting description: "In combination with Spartina and Carex vulpinoidea, etc. it covers many square miles of poorly drained bottomlands along the Missouri and its tributaries. Here it is found in clumps 3-4 ft in diameter. Moreover, the exclusive, dense sod becomes thinner

as the grass extends its area into drier lands, often a rod or two on the sides of a draw, until only scattered individual stems one to several inches apart occur. Height is often 3-3.5 ft in the uplands and 4.5-6 ft in the wet lowlands." Differences in size between upland and lowland forms have been noted by others.

According to Harlan (1954) the bottomland form may be 6-8 ft high and very coarse and stemmy whereas the upland form usually ranges from 3-5 ft in height. He comments further that the bottomland form is not recommended for reseeding the upland. Cornelius (1950) also found the bottomland form coarse, low in forage value, and not well adapted for reseeding on eroded upland sites. Phillips Petroleum Co. (1955) recognized upland and bottomland strains of switchgrass, the latter having a much coarser stem and being 1-3 ft taller than the former.

It seems unlikely that the same taxonomic entity would be dominant in the prairie, however moist, and in the wet lowlands particularly in view of the much better development reached in the latter habitat. The present work attempts to determine whether the same type or different switchgrass types occupy upland and lowland sites. It was begun in the autumn of 1959 and concluded in the spring of

1961.

Two sites, both in McClain County near Norman, Oklahoma, were selected for the study of upland and bottomland forms of switchgrass. The upland site, the University of Oklahoma Grassland Investigation Plot, is in section 12, township 8 north, range 4 west and covers an area of about five acres. This site supports typical tall-grass prairie which at one time extended throughout this area (Bruner 1931).

The bottomland site is in section 11, township 8 north, range 3 west and consists of approximately five acres of the second (late), third, and fourth successional levels of the South Canadian River floodplain.

METHODS AND MATERIALS

Measurement of Morphological Characters

Most of the subsequent studies are based upon the comparison of a series of morphological characters which were measured as follows. The height of the culm was measured from ground level to the tip of the panicle. The length of the panicle was measured from the lowermost branch of the panicle to the tip of the inflorescence and its width was measured at its widest point. The number of branches at the first, or lowermost, and second nodes of the panicle were recorded. Mature spikelets were measured from the base of the glumes to the tips of the lemmas and the average length of three spikelets per culm was recorded. The average length of three caryopses per culm was also determined and recorded. The length of the first internode was measured from the lowermost panicle branch to the first cauline node. The diameters of the first and fourth nodes below the panicle were determined. The lengths of the first and

fourth leaves below the panicle were measured from the ligule to the leaf tip, their widths were determined at a point one centimeter above the ligule, and the lengths of their ligules were measured. The total number of leaves, and in some cases, the total number of cauline branches per culm were also recorded. In addition to the foregoing measurements which were made in all comparative studies, the lengths of primary rhizomes, lengths of rhizome internodes, and diameters of rhizome nodes were also determined for the comparison of naturally occurring switchgrass types. The length of primary rhizomes was measured from the culm to the tip of the rhizome. The third, fourth, and fifth internodes from the culm were measured from one scale scar to the next and the mean value was recorded. The mean diameter of the third, fourth, and fifth nodes from the culm was also recorded.

Most measurements were made with a metric rule, some being facilitated by a binocular microscope. The levels of significance of the differences between means of the various measurements were determined by Student's "t" Test (Snedecor 1946).

Comparison of Naturally Occurring Types

Although differences between naturally occurring upland and bottomland switchgrass types were quite evident, it

seemed desirable to determine the extent of these differences. Therefore, 100 culms and rhizomes were collected at random from each study site during the fall of 1960 for the subsequent measurement and statistical comparison of a series of morphological characters (see preceding section for procedure).

Greenhouse Transplants

It was important to know the extent to which heredity and environmental conditions controlled the traits under consideration. If the differences observed in the field between the two types were entirely the result of different environmental conditions, then the two types might be expected to have the same gross morphology when grown under the same conditions in the greenhouse.

Four clones of each type were collected in December of 1960, washed free of soil, and potted in a 1:1:1 mixture of sand, soil, and manure. All were watered at the same time with equal amounts of cistern water. Following a growing period of 16 weeks, the five tallest culms in each pot were collected and most of the previously listed morphological characters were measured.

Development of Bottomland Switchgrass

Early in this investigation, extreme variation in size was observed between individual clones of the bottomland type whereas only minor differences were evident between clones in the upland. Before further comparisons could be executed between bottomland and upland types it was necessary to explain the diversity in size of the clones in the bottomland. Inasmuch as most graminoids reach full size in one growing season, these differences in size were thought at first to be due to environmental conditions.

At the same time as, and utilizing a procedure similar to that followed with the previous transplants, four small clones of the bottomland type, 70-80 cm in height, were transplanted to the greenhouse to compare their growth with that of somewhat larger clones of the same type utilized in the previous experiment.

Furthermore, the growth rates of clones of various size were determined in the field. A large number of clones of bottomland switchgrass were measured as to height and clone diameter during September of two consecutive years. Height was measured from ground level to the tip of the tallest culm and diameter was determined at ground level. Each clone was tagged with an identifying number during the

first year so it could later be identified. However, many were not relocated.

Soil Analyses

Soil samples were collected from each study area for subsequent analyses of organic carbon, mineral content, and soil texture. Four samples were taken from the 0-6 in. level and four from the 18-24 in. level in each area. Due to the nature of the soil of the bottomland site, four samples were also taken from the 30-36 in. level. Two augers, $1\frac{1}{2}$ and $1\frac{1}{4}$ in. in diameter, were used to obtain the samples. The samples were all air dried, rocks and undecayed organic matter were removed, and the soil was ground sufficiently with a mortar and pestle to pass through a 2 mm sieve. A portion of each sample was weighed before and after drying in a convection oven at 105 C to calculate the amount of water in the air dried soil. With the exception of 60 g required for pH and textural analyses, the soil samples were pulverized in a hammer mill containing a 0.5 mm sieve.

Soil texture was determined by the procedure outlined by Bouyoucos (1936). To determine the soil reaction, a suspension of 10 g of soil in 50 ml of aerated distilled water was prepared. The pH was read directly by means of a

Beckman glass electrode pH meter. Organic carbon was determined by a method modified slightly from Piper (1944), total nitrogen according to Noggle and Wynd (1941), and total phosphorus after Skelton and Harper (1941). The procedure for soil extraction used in the determination of exchangeable potassium was according to Peech and English (1944), and the measurement of exchangeable potassium was done with a Perkin-Elmer Flame Photometer, Model 146. Duplicate samples were run on all determinations. Analyses were made with air dried soil but calculations were based on the oven dry weight. The amounts of all elements were calculated on a percentage basis.

Reciprocal Transplants

To determine the effect of the upland environment on the gross morphology of the bottomland type and vice versa, reciprocal transplants were made in the field in March of 1960.

Fifteen clones of the bottomland type were randomly collected and each was divided into two pieces. Half of each clone was replanted in the bottomland within the environs of an exclosure (20 ft x 20 ft) and half was transplanted to another plot in the upland. Each clonal segment

was labeled for identification purposes. The same procedure was followed for the upland type. The two types were alternated within the two plots giving a total of 30 half-clones in each.

In September, 1960 the three tallest culms of each clonal segment were collected and morphological characters were measured according to the procedure given previously.

Seed Germination Studies

Seeds of both upland and bottomland switchgrass types were collected in the fall of 1959 and 1960 for use in subsequent experiments. Despite the large numbers of seeds used in preliminary germination experiments, none of the bottomland type and only a few of the upland type germinated. Dissection of a large number of seeds of each type showed that approximately 1% of the seeds of the bottomland type and 2.4% of those of the upland type contained embryos. In view of the large number of seeds available, the following procedure was initiated in an effort to break dormancy. Seeds of each type were soaked for 2 min. in various solutions, namely, 3% thiourea, 3% and 6% ethylene chlorhydrin, 3% and 6% ethylene glycol, gibberellic acid (4.5 mg/100 ml of water), and absolute ethyl alcohol, and then allowed to

stand in the vapor for 24 hours. The germination of seeds of the upland type was somewhat better after treatment with 3% and 6% ethylene chlorhydrin and 6% thiourea but still no seeds of the bottomland type germinated.

Water Relations

Owing to obvious differences in the soil water relations of the two study sites, a determination of the water relations of upland and bottomland switchgrass types was of primary importance in this investigation. Due to the lack of viable seed of the bottomland type, clones were used in this and in the following experiment. Three clones of the bottomland type and six of the upland type were collected in November of 1961. Each clone was washed free of soil with cistern water and divided into two parts, each of which was potted in a ten inch pot in a 1:1:1 mixture of sand, soil, and manure. They were then placed in a constant temperature room at 41 C to insure the breaking of dormancy. After 30 days they were placed in the greenhouse where they were watered every fourth day. Approximately two weeks later, when sprouts were well developed, half of each original clone was put in a paraffined five-gallon metal container in which the water level was kept 1-2 cm above the soil surface.

Watering of the other half of each original clone continued on every fourth day. The number of culms in each pot was limited to ten and sprouts were removed daily as necessary. After a growing period of 16 weeks, all culms were harvested and morphological characters were measured according to the procedure given previously. The total dry weight of culms per pot was also determined.

Nitrogen Requirements

The results of soil analyses showed that the concentration of nitrogen in the bottomland soil was quite low in comparison with that of the upland. Therefore, a determination of the nitrogen requirements of the two types seemed desirable. Seven clones of each type were collected in January of 1961, potted, and placed in a constant temperature room at 41 C. After 30 days each clone was washed free of soil with cistern water followed by distilled water. Six rhizomes were separated from each clone, each rhizome of which was determined by water displacement to have a volume of 6 cc. Rhizomes of each clone of each type were grown in sand culture in four inch glazed pots in complete solution (Hoagland's No. 1) and in solutions containing 1/10, 1/100, and 1/1000 of the amount of nitrogen in the complete solution.

The pH of each solution was adjusted to 5.8. Three pots of complete and one pot each with the other concentrations were started from each clone and the number of culms in each pot was limited to three. The day length was extended to 18 hours by means of incandescent lamps to prevent flowering. All plants were watered at the same time with equal amounts of the appropriate solution. After 16 weeks the plants were harvested and dried in a convection oven at 95 C for 48 hours. Dry weights of roots and shoots were determined.

Cytology

Root tips were collected from 25 greenhouse-grown plants of each type for the determination of chromosome numbers. They were pretreated for 2 hours in 0.0029 M 8-hydroxyquinoline and then fixed in acetic alcohol. Chromosome numbers were determined by the squash technique and staining with iron-acetocarmine (Belling 1926).

RESULTS

Comparison of Naturally Occurring Types

Eighteen of 21 morphological characters compared between naturally occurring upland and bottomland switchgrass types differed at the 1% level (Table 1). Plants of the bottomland type were much taller, with longer and wider panicles and a larger number of branches at the second node of the panicle (Figs 1, 2). The first internode was longer, the first and fourth nodes were larger, the first and fourth leaves were longer and wider, and their ligules were longer than those of upland plants. Their rhizomes were also greater in diameter and they had a larger number of leaves. Means of the upland type were greater only for the number of cauline branches, the length of primary rhizomes, and of rhizome internodes. In addition to these characters, the number of primary branches at the first node of the panicle and the caryopsis length differed at the 2% and 5% levels respectively. Only spikelet length was not significantly

different between the two naturally occurring types.

Greenhouse Transplants

Upland and bottomland switchgrass types remained distinct when they were grown under the same environmental conditions (Fig 3). Measurements of 15 of 18 characters compared differed at the 1% level (Table 2). Means of the bottomland type exceeded those of the upland type for all statistically significant comparisons--height, panicle length and width, the diameters of the first and fourth nodes, the lengths and widths of the first and fourth leaves, the lengths of the ligules of the first and fourth leaves, and the dry weight per culm. Spikelet length, caryopsis length, and the length of the first internode were not significantly different. Differences between the two naturally occurring types (Table 1) appear to be in part hereditary, since they retained their individuality when grown under the same conditions.

Development of Bottomland Switchgrass

A discussion of variation and causes of variation in the bottomland type is necessary before proceeding with further comparisons between upland and bottomland types. The

mean height of the smaller bottomland plants after one growing season under greenhouse conditions was 158 cm as compared with an average height of 75 cm during the season prior to transplanting. Despite this considerable increase in size, they were still shorter, had shorter and narrower panicles, smaller spikelets and caryopses, and their culms weighed much less in comparison with bottomland plants of average size grown under the same greenhouse conditions. Of the 18 characters compared between large and small forms, eight differed at the 1% level but several of these were only minor differences (Table 3).

These facts suggest that the variation in the size of bottomland plants may be due not only to local differences in environmental conditions but to differences in age of plants as well.

Plants of the bottomland type definitely become larger as they grow older (Fig 4). It seems probable that a number of years is required for the development of a clone 300 cm tall and 75 cm in diameter. Apparently, plants of this type grow quite slowly for the first year or two and after this period of establishment increase rapidly in size. Growth of the clone in diameter continues for some time after the maximum height is reached.

Soil Analyses

The soil of the upland study area is Quinlan very fine sandy loam and consists of a reddish-brown, calcareous, very fine, sandy loam topsoil over reddish-brown, clay loam subsoil which rests on clay, soft sandstone, and shale (Kelting 1951). The upper six inches of soil in this study contained more sand than both silt and clay (Table 4). At a depth of 18-24 inches there was less sand, approximately the same amount of silt, and considerably more clay.

The bottomland soil consisted of a sandy alluvium in which a profile was not yet developed. In general the amount of silt and clay was less in the bottomland soil than in that of the upland (Table 4). The one exception to this statement is the high clay content at the 0-6 inch level in the bottomland soil. It should be pointed out that the amount of clay was slight (0.8%) at this level near the river but increased gradually away from the stream to a maximum of 44.4%. However, only a small amount of clay occurred at a depth of 18-24 inches (Table 4).

The upland soils were decidedly more acid than those of the bottomland site. The upland site had a mean hydrogen ion concentration equivalent to a pH of 7.3 and 7.8 in the

0-6 and 18-24 inch levels respectively. The 0-6 inch level of the bottomland site had a mean hydrogen ion concentration equivalent to a pH of 8.9 whereas that of the 18-24 inch level was 9.1.

Organic carbon was present in greater amounts in both levels of the upland soil than in the bottomland. The differences were greatest at a depth of 18-24 inches where the means differed at the 1% level (Table 4).

The total phosphorus content of the upland soil was lower in the upper six inches and higher at a depth of 18-24 inches than at corresponding levels of the bottomland soil (Table 4). The greatest differences occurred at a depth of 18-24 inches where the means differed at the 5% level. In view of the above facts, however, it seems probable that differences in the phosphorus content of the two soils are not important.

The upland soil contained greater amounts of exchangeable potassium at both the 0-6 and the 18-24 inch-level than did the bottomland soil but the differences were not statistically significant (Table 4).

The total nitrogen content of the upland soil was considerably higher than that of the bottomland soil. The mean values reported for the upper six inches of soil of the

two sites differed at the 5% level whereas at a depth of 18-24 inches the differences were significant at the 1% level. By comparison with the upland site, the bottomland appears to be quite low in nitrogen (Table 4).

Considerable variation in texture, pH, organic carbon content, and mineral content occurred in the upper six inches of soil of the bottomland site (Table 4). There was an increase in the percentage of clay, a decrease in pH, and an increase in organic carbon as well as phosphorus, potassium, and nitrogen with distance from the river. The texture, pH, organic carbon content, and mineral content of the 18-24 and the 30-36 inch levels were very similar and little variation occurred in either.

Reciprocal Transplants

There were no great differences in the upland plants which were transplanted to upland and bottomland sites (Table 5). Differences occurred at the 1% level for five of 18 characters compared. Total culm height and the length of the first leaf were slightly greater for those transplanted to the bottomland whereas the lengths of the ligules of the first and fourth leaves and the diameter of the fourth node were greater in transplants to the upland.

In general, the bottomland plants which were transplanted to upland and bottomland sites differed much more than the upland type which had been transplanted to similar sites. These bottomland plants differed at the 1% level for 11 of 18 characters compared. Except for caryopsis length and the number of cauline branches, means of characters of the bottomland type were much lower in the upland site than those of similar transplants in the bottomland environment (Table 5). These facts suggest that soil moisture may have been a limiting factor in the upland site.

Plants of upland and bottomland types which were transplanted to the upland site were quite different. With the exception of caryopsis length, differences between the means of all characters compared was significant. Transplants of the upland switchgrass were shorter, they had shorter and narrower panicles and fewer branches at the first and second nodes of the panicle. The first internode was shorter, the first and fourth nodes were smaller, the first and fourth leaves were shorter and narrower, and their ligules were shorter. They also had fewer leaves than plants of the bottomland type but longer spikelets and more cauline branches.

In the lowland site, similar but more extreme

differences in size occurred between transplants of upland and bottomland switchgrasses as a result of the much better development reached by the latter in this habitat (Table 5). The upland type was much the smaller of the two and differed significantly from plants of the bottomland type for 15 of 18 characters compared. It is perhaps noteworthy that both switchgrass types had longer caryopses and more cauline branches in the dry upland site and longer spikelets and more leaves in the bottomland site.

Reciprocal transplants were made prior to soil analyses and for this reason, the areas of transplant were perhaps not the most suitable. With the exception of two plants of the upland type which were transplanted to the bottomland, all transplants lived. However, since some transplants did not produce flowering culms or produced fewer than three culms, the data are not strictly comparable.

Despite these deficiencies, this experiment shows that the upland switchgrass does not grow significantly better in the bottomland environment even though the amount of available water is greater, and that plants of the bottomland type become reduced in size when grown in the drier upland situation. It also demonstrates that the bottomland type is much larger and quite distinct from plants of the

upland type even when grown where the amount of available water is slight.

Water Relations

Upland switchgrass grows much better on a normal watering schedule (every four days) than under flooded conditions (Table 6). Of 19 characters compared, 15 differed at the 1% level. Except for the number of leaves and the number of cauline branches, means of plants growing under moderate conditions of soil moisture greatly exceeded means of those which were flooded (Fig 5). Flooded plants were shorter and only 36.7% of the original culms produced panicles. Many of these panicles were quite small with a reduced number of panicle branches and florets. Furthermore, the length of the first internode was shorter, the diameters of the first and fourth nodes were smaller, the first and fourth leaves were shorter and narrower, and their ligules were not as long in comparison with those of plants grown under conditions of moderate moisture. Leaves, as well as cauline branches, were more numerous in flooded plants but their culms weighed much less. In addition, the amount of anthocyanin was increased, root growth was reduced, and flowering was retarded.

Comparatively few changes occurred in plants of the bottomland type as a result of flooding (Table 6). Mean differences of only five of 19 characters compared between flooded plants and those grown on a four day schedule differed at the 1% level. Two of these differences were particularly noteworthy. Flooded plants grew considerably taller and produced longer panicles than non-flooded plants. Other differences were relatively minor. Although flooded plants were taller, their culms were smaller in diameter and consequently, they weighed less than non-flooded plants. However, differences in culm diameter and in weight were not statistically significant. In general it may be said that the bottomland type is certainly not adversely affected by prolonged flooding and that in some respects flooding appears to be favorable (Fig 6). This is quite in contrast with the upland type.

Upland and bottomland switchgrass types grown on a four day watering schedule differed from each other at the 1% level for 13 of 19 characters compared (Table 6). Of these 13 characters mean values were higher in the bottomland type for all except spikelet length. Bottomland plants were taller and had larger panicles with more branches at the first and second nodes. The diameters of the first and

fourth nodes were greater, the first and fourth leaves were longer, and wider and their ligules were longer. The culms of bottomland plants weighed much more than those of upland switchgrass. In addition to these differences, the number of cauline branches and the number of leaves differed at the 2% and 5% levels respectively. Bottomland plants had fewer branches but more leaves than plants of the upland type (Fig 7).

Under flooded conditions, similar but more extreme differences occurred between upland and bottomland switchgrass types (Fig 8). With the exception of the number of branches at the first node of the panicle, all characters compared differed at the 1% level (Table 6). Means of bottomland plants greatly exceeded those of the upland type for most characters. Exceptions include the lengths of spikelets and caryopses, the number of leaves and the number of cauline branches which were greater in upland plants.

Root growth of upland plants became retarded with the onset of flooding and many roots died. Growth in general then ceased until rhizomes were formed at or above water level from which new shoots and roots were produced. Apparently, roots of bottomland plants were not adversely affected as growth was uninterrupted.

Nitrogen Requirements

In the experiment concerned with nitrogen requirements, the weights of shoots and roots of control plants of the bottomland type differed at the 1% level from those of the upland type. The mean weights of shoots and roots of controls of the bottomland types were 7.91 g and 2.72 g respectively in comparison with values of 4.19 g and 1.48 g for the upland type. Due to these differences, comparisons between the two switchgrasses were made in terms of their respective controls.

In the low-nitrogen solutions, the weights of shoots and roots of bottomland plants were considerably greater in comparison with their controls than were those of upland plants (Table 7). At higher concentrations, however, the rate of growth of plants of the bottomland type was less than that of the upland plants. The weights of both shoots and roots on the N/10 solution were less in bottomland plants than in plants of the upland type when compared with their respective controls. In the N/100 solution, the root mass of bottomland plants was also less but the weight of shoots was somewhat greater than that of upland plants in comparison with their controls. The shoot-root ratios of bottomland plants were consistently higher than those plants

of the upland type. The results discussed above indicate that plants of the bottomland type have a somewhat lower requirement for nitrogen than those of the upland. This correlates well with the fact that the nitrogen content in the bottomland area is usually extremely low, especially close to the river. Although equal volumes of rhizomes were utilized in this experiment it is possible that the same amounts of nitrogen were not present in all clonal segments. It is also possible that results are not strictly comparable since occasional plants of each type died early in the experiment. Contrary to expectation, a number of plants of each type flowered and set seed quite well on an 18 hour day.

Cytology

In view of the morphological differences which occurred between upland and bottomland switchgrass types, it is perhaps not surprising that they also had different chromosome numbers. A tetraploid chromosome number of 36 was found consistently in clones of bottomland switchgrass. In the upland, however, the situation was somewhat more complex due to the occurrence of some plants with 54 and others with 72 somatic chromosomes. Of the plants studied, hexaploids were slightly more numerous than octaploids.

Furthermore, mosaics were encountered during this study on three occasions. In two instances, chromosome numbers of 54, 72, and 90 occurred in cells of the same root tip whereas in the other case the counts were 54, 90, and 108.

DISCUSSION

As previously pointed out, switchgrass, Panicum virgatum L., has been reported as one of the dominant species in both upland prairies and in wet lowlands of the Great Plains region.

According to Rice, Penfound, and Rohrbaugh (1960) the true prairie of central Oklahoma is dominated by little bluestem (Andropogon scoparius), big bluestem (Andropogon gerardi), switchgrass (Panicum virgatum) and Indian grass (Sorghastrum nutans). In an analysis of a tall-grass prairie in Marshall County, Oklahoma, Rice (1952) found switchgrass to be more important as a dominant than little bluestem. Nease (1948) stated that the original tall-grass prairie in sandy areas of South Central Oklahoma was dominated by little bluestem in the drier portions whereas switchgrass, sand bluestem (A. hallii) and Indian grass were dominant in the moister areas.

Panicum virgatum is also one of the dominants of the

grasslands of the floodplains of Illinois rivers (Turner 1933). Hefley (1937) reported that the second level of the South Canadian River floodplain near Norman, Oklahoma was dominated after two years by big bluestem, switchgrass, and Indian grass. In addition to being a dominant of the second level, switchgrass was found in the present investigation to have been locally important to the point of dominance in the third and fourth levels as well. However, big bluestem and Indian grass were observed in association with switchgrass only in some drier isolated areas. According to Weaver and Fitzpatrick (1932), switchgrass occupies areas too poorly aerated for big bluestem and occurs in combination with Spartina and Carex vulpinoidea in the poorly drained bottomlands of the Missouri River.

Despite the taxonomic implication that both upland and lowland sites are occupied by the same entity, the results of this investigation indicate that upland and bottomland switchgrass types in McClain County, Oklahoma are morphologically, ecologically, and cytologically distinct.

The gross morphology of naturally occurring upland and bottomland switchgrass types was found to be quite different. The aerial vegetative organs of bottomland plants were far larger on the average but considerably more variable

than those of the upland type. Throughout this study significant regressions between the height of a plant and the length, width or diameter of the other aerial vegetative organs were apparent but no such relationship was evident between height and the length of spikelets or caryopses. These results are in complete agreement with those of Neilson (1944).

In general aspect, upland plants consisted of scattered culms one to several inches apart. Bottomland plants, by contrast, were quite distinct from each other due to the extremely compact nature of the clones. Weaver and Fitzpatrick (1932) also found these clonal differences between upland and bottomland forms. Such differences can be explained on the basis of rhizome length. Rhizomes of bottomland plants were found in this study to have had a mean length of 4.25 cm whereas those of upland plants averaged 11.92 cm. Bottomland clones were far larger on the average than those of the upland type. Cornelius and Johnson (1941), Harlan (1954), and Weaver and Fitzpatrick (1932) all found the switchgrass of wet lowlands to be taller, and more robust than that of upland areas. It should be pointed out, however, that no reference could be found in the literature concerning the variation in size of plants of the bottomland

type or to the developmental nature of plants of this type.

Since these same morphological differences were evident between upland and bottomland plants grown under similar greenhouse conditions, it seems probable that they are hereditary rather than environmental.

The habitats occupied by upland and bottomland switchgrass types were quite different ecologically. The most outstanding difference between upland and lowland sites was perhaps that of soil water content. Although upland soils occasionally have a high moisture content, they are also subject to drought from time to time. Soils of the lowland site are completely saturated during most of the year due to the presence of a very shallow water table which periodically rises to or above the soil surface. Bottomland switchgrass grows quite well under these conditions and has been observed growing quite well in the field with the basal portion of the clone submerged.

Upland soil generally contained more clay and less sand, especially at lower levels, than the soil of the bottomland site. However, the soil of the upland site was surprisingly sandy, particularly in view of the fact that it supported grassland instead of forest.

Upland soils were considerably more acid than were

those of the bottomland. The differences in reaction between upland and bottomland soils were apparently due in part to the comparatively lower organic carbon content and lower clay content of bottomland soils as well as to the deposition of alkali on these soils by the South Canadian River. An encrustation of CaCO_3 and/or Na_2CO_3 may be observed on the surface of bottomland soils from time to time throughout the year. Kelting (1954) found somewhat lower pH values, 6.6-7.0 for the upper six inches and 6.4-8.2 for the 18-24 inch level, for soils of Central Oklahoma grasslands. Daniel, Elwell, and Cox (1943) reported even lower values, 5.8-6.4 for the 0-6 inch level, but somewhat higher values, 7.8-8.1 for the 18-24 inch level of north central Oklahoma soils.

The organic carbon content of the upland soil was much higher at both levels than was that of the bottomland soil. The upper six inches of soil of the upland site contained an average of 0.81% organic carbon¹ whereas the 18-24 in. level contained 0.41%. By comparison the bottomland soil contained 0.46% organic carbon in the 0-6 in. level and 0.12% in the 18-24 in. level. The lower values reported for the

¹All data concerning organic carbon are Walkley and Black values.

bottomland are apparently due to the young and undifferentiated soil of the bottomland and to a paucity in vegetation. Other workers have reported somewhat larger amounts of organic carbon in upland soils. Kelting (1954) found a mean organic content of 0.98% in the upper six inches and 0.47% in the 18-24 in. level of soils of central Oklahoma grasslands. Rice and Penfound (1954) reported that the soils of a central Oklahoma prairie contained 1.14% organic carbon in the upper six inches and 0.53% at a depth of 12-18 inches. The reasons for the differences between the results obtained in the present investigation and those reported by others are not immediately evident.

Although the pH values reported in this investigation for soils of the upland prairie were somewhat higher than those reported by others, these results are consistent with the lower organic carbon content recorded for these soils in this investigation.

In the bottomland the upper six inches of soil contained considerably more, and the 18-24 inch level less phosphorus than did corresponding levels of upland soil. The lower amounts of phosphorus in the 18-24 inch level of bottomland soil are probably due to a lack of appreciable amounts of organic carbon and clay at this depth. Since

phosphorus combines with calcium at or above pH 7.0 (Russell 1950), much of the phosphorus in the soil of both sites, particularly that of the bottomland, is probably unavailable. Furthermore, in the bottomland the absorption of phosphorus by plants is probably quite low since absorption becomes reduced at pH 9.0 (Arnon and Johnson 1942). However, Emmert and Ball (1933) found that an increase in moisture supply directly favored the availability of phosphate phosphorus.

Differences in the potassium content in the soils of the two sites were not very great. However, the nitrogen content of bottomland soils was consistently lower at both levels than was that of the upland. Since anionic nitrogen is not held by micelles it probably has been, and continues to be, leached out of bottomland soil as a result of the high water content. As a further consequence of the high water content, a low oxygen tension may well be expected in these soils and under anerobic conditions, losses due to volatilization of nitrogen may occur in areas with sufficient organic matter (U. S. Dept. Agr. 1938).

In view of the differences in the soils of upland and bottomland sites it seemed probable that the switch-grasses growing on these two sites would have different ecological requirements. The experiment concerned with

reciprocal transplants substantiated this conclusion quite well. Upland plants were apparently not favored by conditions of higher soil moisture since transplants of this type did not grow significantly better in the bottomland than those in the upland. Bottomland transplants on the other hand were considerably smaller in the upland than were those in the bottomland. Considering the results of soil analyses this difference was probably due to less favorable moisture conditions in the upland site. In addition to the apparent differences in the water requirements of upland and bottomland switchgrass types, it is important to note that plants of the bottomland type were considerably larger in most aspects and quite distinct from plants of the upland type whether grown in the bottomland or in the upland.

It is generally recognized that viable seeds of naturally occurring switchgrass are not produced in abundance. Cornelius (1950) found that the yield of seed, the seed set and the percentage of florets with well-developed caryopses averaged much lower for naturally occurring than for cultivated switchgrass. The amount of seed produced apparently depends upon abundant soil moisture and cool conditions during the period from August to October, the time when switchgrass flowers and sets seed. According to

Cornelius (1950), lowland strains of switchgrass are usually the only strains which produce sufficient seed for harvest under natural conditions. He further commented that the moisture supply of the upland prairie is generally insufficient to produce a good crop of seed. While this may be true in certain years, it was observed during 1959 and 1960 in the area of this study that most spikelets of bottomland plants failed to set seed whereas those of upland plants produced a comparatively abundant supply. Harlan, Ahring, and Kneebone (1956) reported that many spikelets blast and fail to set seed in hot dry years, even when the soil is kept moist. Furthermore, since seed production is slight when the concentration of available nitrogen is low (Harlan and Kneebone 1953), seed production of bottomland plants might be expected to be quite low. It seems likely that differences in ecological conditions between upland and lowland sites may be sufficiently different that the seed production of upland and lowland plants might differ considerably in any given year. Regardless of the number of seed produced by upland and bottomland types, the number of viable seed produced is quite another matter. The dissection of a large number of seed during 1959 and 1960 showed that slightly less than 1% of the bottomland seeds and only 2.4% of those

of the upland switchgrass contained embryos. No seeds of the bottomland type and only a few from upland switchgrass germinated regardless of pretreatment. Blake (1935) found that the percentage germination of switchgrass over each of four years ranged from 2.5 to 14.0% in Nebraska. Robocker, Curtis, and Alhgren (1953) found that switchgrass germinated better when planted the second year after harvest. Although this was true in this study for seeds collected from the upland, none of the bottomland seeds germinated.

Due to the lack of viable seed, a determination of the water relations of upland and bottomland switchgrass types under greenhouse conditions was made with clones. Owing to the developmental nature of bottomland switchgrass the use of clones in this experiment made the results considerably more meaningful.

The results of the experiment concerning water relations were in complete agreement with the data on reciprocal transplants. Upland plants grew notably better in moist soil than under flooded conditions. Bottomland plants, however, grew somewhat better under flooded conditions. Whether grown under conditions of moderate soil moisture or under flooded conditions, bottomland plants were much the larger of the two.

In addition to tolerating a considerable amount of

flooding, bottomland plants also had a somewhat lower requirement for nitrogen than did upland plants. It is further interesting that the weights of roots and shoots of bottomland control plants were greater and statistically different from those of the upland type. Although the experiment on nitrogen requirements was conducted on an 18 hour daylength, a number of plants of both types flowered and set seed quite well. The maximum effective daylength is apparently greater, then, than the $12\frac{1}{2}$ to $15\frac{1}{2}$ hour range given by McMillan (1959).

The switchgrass of the bottomland site was entirely tetraploid whereas both hexaploids and octaploids occurred in the upland. In the area of study, therefore, upland and bottomland types can be distinguished on the basis of chromosome number but, due to the developmental nature of bottomland clones, no consistent correlation between chromosome number and the size of individual plants occurred. If, however, mature plants or entire populations are considered, such a correlation is quite pronounced between upland and bottomland types. Church (1942) found that tall switchgrass plants from the Arkansas River floodplain near Muskogee, Oklahoma were tetraploid whereas shorter upland plants from the same area were octaploid. In a study of variation in

switchgrass Neilsen (1944) analyzed a number of morphological characteristics and found that these differed considerably among plants with the same chromosome number. McMillan and Weiler (1959) also found no correlation between the size of plants and chromosome number. In view of the differences in ecological requirements, in age, etc. occurring between different strains of switchgrass, it is little wonder that a correlation between chromosome number and the size of plants has not been found. McMillan and Weiler (1959) further reported that hexaploids are less common and are always associated with tetraploids and/or octaploids. Although both hexaploids and octaploids were found in the upland study site, hexaploids were slightly more numerous than octaploids if the sample studied was a true indication of their relative abundance.

For taxonomic purposes a distinction between upland and bottomland types can best be made by considering two characters, the size of the rhizome and the nature of the upper surface of the leaf blade just above the ligule. The presence of short, stubby rhizomes and the glabrous upper leaf surface at the base of the blade of bottomland plants contrast sharply with the long, thin rhizomes and the pubescence of the upper leaf surface at the base of the blade of

plants of the upland type. Although characters which were subject to opinion were not generally employed in this study, the nature of the leaf base has consistently proved of value in separating the two switchgrass types regardless of growing conditions.

SUMMARY

The present study consists of a comparison of bottomland and upland types of switchgrass, Panicum virgatum L., during the period from 1959 through 1961, in McClain County, Oklahoma.

Some 21 morphological characters of both vegetative and floral organs were utilized in the comparison of the two types of switchgrass.

In addition to a comparison of naturally occurring types, the following methods of study were employed: greenhouse transplants, developmental studies, soil analyses, reciprocal transplants, seed germination trials, water relations, nitrogen requirements, and cytological investigations.

A comparison of naturally occurring types demonstrated that plants of the bottomland had taller and thicker culms, larger panicles, wider and longer leaves, and shorter but thicker rhizomes than those of the upland. Means of the bottomland type greatly exceeded those of the upland type

for most characters compared.

Comparable differences were evident when bottomland and upland plants were grown in the same environment in a greenhouse.

Although the upland type attained its maximum size by the end of the first growing season, plants of the bottomland type did not reach their maximum stature for several years. Apparently, differences in size of clones as well as the size of individual culms of the bottomland type were due primarily to age.

In general, bottomland plants transplanted to upland and lowland sites differed much more than upland plants transplanted to similar sites. Upland plants did not grow significantly better in the lowland situation despite the greater amount of available water. However, transplants of the bottomland type in the bottomland were considerably larger than those in the upland. In either situation, plants of the bottomland type were larger than those of the upland type and they differed at the 1% level for most of the characters compared.

The soil in which the upland form grew was a very fine sandy loam with a well-developed profile whereas the sandy soil of the bottomland had no observable profile.

Perhaps the greatest difference, other than difference in soil water, was the much lower amount of nitrogen in the bottomland.

Due to the lack of viable seed, clones were used in water relations and nitrogen nutrition experiments conducted under greenhouse conditions. Bottomland plants grew as well as, and in some respects better, in flooded soil than in moist soil whereas upland plants grew poorly in flooded soil. Means of bottomland plants greatly exceeded those of upland plants for most characters compared whether grown in moist or flooded soil.

Bottomland plants appeared to have a somewhat lower requirement for nitrogen than those of the upland. In low-nitrogen solutions, the weights of shoots and roots of bottomland plants were considerably greater in comparison with their controls than were those of the upland type. The shoot-root ratios of bottomland plants were consistently higher than were those of upland plants.

Plants of the bottomland type were tetraploids. In the upland, hexaploids were most common but octaploids were also present.

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APPENDIX

TABLE 1. A comparison of naturally occurring upland and bottomland switchgrass types.*

Character	Upland Type		Bottomland Type	
	Mean $\pm$	Stand-ard Error	Mean $\pm$	Stand-ard Error
Height (cm)**	127.36	2.51	194.93	5.58
Panicle (length, cm)**	35.62	0.72	46.32	1.08
Panicle (width, cm)**	17.92	0.51	25.28	0.88
Branches at first node of panicle (number of)	1.68	0.09	2.09	0.14
Branches at second node of panicle (number of)**	2.31	0.09	3.45	0.14
Spikelet (length, mm)	5.16	0.04	5.15	0.03
Caryopsis (length, mm)	3.10	0.02	3.04	0.01
First internode (length, cm)**	26.44	0.78	30.74	0.75
First node (diameter, mm)**	3.84	0.11	6.24	0.15
First leaf (length, cm)**	32.76	0.85	36.77	0.90
First leaf (width, mm)**	6.94	0.20	10.02	0.22
Ligule of first leaf (length, mm)**	3.59	0.10	4.17	0.07
Fourth node (diameter, mm)**	4.17	0.07	7.22	0.13
Fourth leaf (length, cm)**	42.53	0.70	48.55	1.33
Fourth leaf (width, mm)**	8.13	0.19	11.98	0.30
Ligule of fourth leaf (length, mm)**	3.54	0.07	3.89	0.07
Leaves (number of)**	6.18	0.07	7.25	0.12
Cauline branches (number of)**	0.55	0.09	0.04	0.02
Primary rhizome (length, cm)**	11.92	0.55	4.25	0.15
Primary rhizome (average diameter of 3,4,5 nodes, mm)**	2.47	0.05	5.98	0.10
Primary rhizome (average length of 3,4,5, internodes, mm)**	3.45	0.16	1.96	0.06

* Based on 100 measurements for each character of each type.

** Differences significant at the 1% level.

TABLE 2. A comparison of upland and bottomland switchgrass types grown under greenhouse conditions.*

Character	Upland Type		Bottomland Type	
	Mean $\pm$	Standard Error	Mean $\pm$	Standard Error
Height (cm)**	95.12	4.10	178.09	2.36
Panicle (length, cm)**	30.96	2.62	53.53	2.86
Panicle (width, cm)**	13.78	1.78	32.22	2.26
Branches at first node of panicle (number of)**	1.19	0.10	4.25	0.61
Branches at second node of panicle (number of)**	2.19	0.21	4.75	0.50
Spikelet (length, mm)	5.09	0.16	5.33	0.10
Caryopsis (length, mm)	2.78	0.19	2.90	0.03
First internode (length, cm)	27.72	1.19	29.25	2.33
First node (diameter, mm)**	2.89	0.18	4.65	0.10
First leaf (length, cm)**	26.81	2.60	47.00	1.65
First leaf (width, cm)**	7.66	0.44	12.50	0.70
Ligule of first leaf (length, mm)**	1.72	0.18	4.41	0.18
Fourth node (diameter, mm)**	3.19	0.12	5.19	0.16
Fourth leaf (length, cm)**	28.97	2.68	56.34	2.24
Fourth leaf (width, mm)**	8.30	0.35	13.56	0.54
Ligule of fourth leaf (length, mm)**	1.77	0.10	3.94	0.16
Leaves (number of)**	4.94	0.11	6.25	0.14
Culm (dry weight, gms)**	2.00	0.24	7.65	0.25

*Based on 16 measurements for each character of each type.

**Differences significant at the 1% level.

TABLE 3. A comparison of small and large plants of bottomland switchgrass grown under greenhouse conditions.*

Character	Bottomland Switchgrass			
	Small Clones		Large Clones	
	Mean $\pm$	Standard Error	Mean $\pm$	Standard Error
Height (cm)**	158.34	2.70	178.09	2.36
Panicle (length, cm)**	32.91	1.88	52.53	2.86
Panicle (width, cm)**	17.28	1.29	32.22	2.26
Branches at first node of panicle (number of)	3.19	0.53	4.25	0.61
Branches at second node of panicle (number of)	3.75	0.34	4.75	0.50
Spikelet (length, mm)**	4.89	0.05	5.33	0.10
Caryopsis (length, mm)**	2.74	0.05	2.90	0.03
First internode (length, cm)	30.00	1.65	29.25	2.23
First node (diameter, mm)**	3.66	0.13	4.65	0.10
First leaf (length, cm)	42.52	2.53	47.00	1.65
First leaf (width, cm)	11.50	0.58	12.50	0.70
Ligule of first leaf (length, mm)	4.06	0.24	4.41	0.18
Fourth node (diameter, mm)	4.88	0.14	5.19	0.16
Fourth leaf (length, cm)	53.10	1.43	56.34	2.24
Fourth leaf (width, mm)**	11.33	0.19	13.56	0.54
Ligule of fourth leaf (length, mm)	4.00	0.13	3.94	0.16
Leaves (number of)	6.00	0.13	6.25	0.14
Culm (dry weight, gms)**	5.10	0.23	7.65	0.25

*Based on 16 measurements for each character of small and of large clones.

**Differences significant at the 1% level.

TABLE 4. Results of soil analyses of upland and bottomland study sites.*

		Upland Site					
		0-6 inch level			18-24 inch level		
		Mean	Range		Mean	Range	
	% Sand	79.96	72.4	-88.0	72.48	54.5	-84.6
Texture	% Silt	7.20	5.6	- 9.2	6.80	0.8	-13.2
	% Clay	12.84	4.8	-20.6	20.72	10.1	-32.4
pH		7.3	6.9	- 8.0	7.8	7.2	- 8.7
% Organic Carbon		0.8065	0.5460 - 1.1520		0.4119	0.1821 - 0.5460	
% Total Phosphorus		0.0181	0.0125 - 0.0239		0.0234	0.0170 - 0.0337	
% Exchangeable Potassium		0.0084	0.0070 - 0.0095		0.0075	0.0041 - 0.0180	
% Total Nitrogen		0.1098	0.0690 - 0.1394		0.0579	0.0424 - 0.0671	

* Means based on four samples from each level of each site.

TABLE 4. Continued.

	Bottomland Site								
	0-6 inch level			18-24 inch level			30-36 inch level		
	Mean	Range		Mean	Range		Mean	Range	
% Sand	70.72	38.0	-96.4	98.16	97.6	-98.8	98.12	97.6	-98.4
Texture % Silt	9.84	2.8	-17.6	1.20	0.8	- 1.8	1.28	0.8	- 1.8
% Clay	19.44	0.8	-44.4	0.64	0.2	- 1.2	0.60	0.4	- 0.8
pH	8.9	8.6	- 9.6	9.1	9.0	- 9.1	9.1	8.9	- 9.1
% Organic Carbon	0.4552	0.1215-	0.9708	0.1215	0.1215-	0.1215	0.1215	0.1215-	0.1215
% Total Phosphorus	0.0303	0.0128-	0.0561	0.0140	0.0096-	0.0185	0.0142	0.0070-	0.0209
% Exchangeable Potassium	0.0074	0.0042-	0.0129	0.0022	0.0017-	0.0023	0.0022	0.0017-	0.0024
% Total Nitrogen	0.0543	0.0211-	0.1005	0.0084	0.0070-	0.0091	0.0082	0.0070-	0.0093

TABLE 5. A comparison of reciprocal transplants of upland and bottomland switchgrass types.*

Character	Upland Type				Bottomland Type				Statistical			
	To Upland (1)		To Bottomland (2)		To Upland (3)		To Bottomland (4)		Comparisons			
	Mean $\pm$ Stand- Error	ard	Mean $\pm$ Stand- Error	ard	Mean $\pm$ Stand- Error	ard	Mean $\pm$ Stand- Error	ard	1 vs 2	3 vs 4	1 vs 3	2 vs 4
Height (cm)	87.02	3.44	103.21	2.95	142.42	3.98	207.80	2.19	**	**	**	**
Panicle (length, cm)	22.90	1.04	22.78	0.87	32.57	1.38	41.46	0.73		**	**	**
Panicle (width, cm)	7.26	0.46	6.51	0.42	10.42	0.52	13.58	0.41		**	**	**
Branches at first node of panicle (number of)	1.05	0.05	1.13	0.07	2.44	0.31	3.42	0.24			**	**
Branches at second node of panicle (number of)	1.42	0.15	1.52	0.14	4.48	0.30	4.71	0.17			**	**
Spikelet (length, mm)	4.97	0.02	5.01	0.01	4.65	0.04	4.99	0.02		**	**	
Caryopsis (length, mm)	3.00	0.01	2.97	0.02	2.99	0.01	2.97	0.01				
First internode (length, cm)	21.28	1.33	21.00	1.32	26.26	1.24	31.12	0.61		**	**	**
First node (diameter, mm)	1.62	0.11	1.41	0.07	3.26	0.13	4.12	0.08		**	**	**
First leaf (length, cm)	17.21	1.23	21.69	0.58	22.91	0.98	30.32	0.70	**	**	**	**
First leaf (width, cm)	4.21	0.23	4.15	0.15	8.11	0.22	9.27	0.30		**	**	**
Ligule of first leaf (length, mm)	1.61	0.20	0.99	0.02	3.14	0.09	3.26	0.07	**		**	**
Fourth node (diameter, mm)	2.41	0.09	2.03	0.06	4.18	0.09	4.83	0.10	**	**	**	**
Fourth leaf (length, cm)	28.31	1.36	30.45	1.25	35.55	1.23	46.08	0.49		**	**	**
Fourth leaf (width, mm)	6.63	0.18	6.20	0.16	11.00	0.19	12.78	0.18		**	**	**
Ligule of fourth leaf (length, mm)	1.91	0.12	1.01	0.02	3.73	0.10	4.00	0.07	**		**	**
Leaves (number of)	5.28	0.10	5.39	0.10	6.60	0.14	6.67	0.08			**	**
Cauline branches (number of)	0.81	0.18	0.35	0.14	0.08	0.06	0.04	0.03			**	

*The number of measurements for each character varied from 18-21 in No. 1, 20-23 in No. 2, 17-25 in No. 3, and 42-45 in No. 4.

**Differences significant at the 1% level.

TABLE 6. A comparison of the growth of upland and bottomland types of switchgrass under moist and flooded conditions in the greenhouse.*

Character	Upland Type				Bottomland Type				Statistical			
	Moist (1)		Flooded (2)		Moist (3)		Flooded (4)		Comparisons			
	Mean $\pm$	Stand- ard Error	Mean $\pm$	Stand- ard Error	Mean $\pm$	Stand- ard Error	Mean $\pm$	Stand- ard Error	1 vs 2	3 vs 4	1 vs 3	2 vs 4
Height (cm)	119.73	3.84	68.42	4.13	143.38	3.06	196.28	6.71	**	**	**	**
Panicle (length, cm)	41.19	1.58	21.24	1.90	40.93	1.41	51.50	2.90	**	**		**
Panicle (width, cm)	14.59	-.79	7.93	1.11	16.22	0.64	17.60	0.84	**			**
Branches at first node of panicle (number of)	1.40	0.07	1.36	0.26	2.73	0.27	1.57	0.16		**	**	
Branches at second node of panicle (number of)	2.10	0.12	1.45	0.21	3.20	0.33	3.07	0.24	**		**	**
Spikelet (length, mm)	5.15	0.08	5.15	0.06	4.39	0.78	4.66	0.09			**	**
Caryopsis (length, mm)	3.03	0.03	2.99	0.01	2.92	0.07	2.77	0.06				**
First internode (length, cm)	29.98	1.39	16.09	1.88	28.13	0.99	41.57	1.54	**			**
First node (diameter, mm)	3.41	0.15	1.11	0.05	4.53	0.14	4.61	0.17	**		**	**
First leaf (length, cm)	36.66	1.50	24.68	0.66	42.15	0.87	45.90	2.38	**		**	**
First leaf (width, cm)	8.07	0.29	4.52	0.13	10.68	0.21	10.89	0.29	**		**	**
Ligule of first leaf (length, mm)	2.91	0.14	2.37	0.07	4.05	0.15	4.87	0.13	**	**	**	**
Fourth node (diameter, mm)	3.45	0.12	1.74	0.05	5.16	0.10	4.91	0.13	**		**	**
Fourth leaf (length, cm)	38.63	1.53	26.02	0.91	46.63	1.36	44.25	1.86	**		**	**
Fourth leaf (width, mm)	8.30	0.19	5.36	0.13	10.49	0.24	10.50	0.27	**		**	**
Ligule of fourth leaf (length, mm)	2.44	0.08	2.41	0.06	3.65	0.11	3.63	0.12			**	**
Leaves (number of)	5.45	0.07	7.68	0.20	5.77	0.12	6.10	0.06	**			**
Cauline branches (number of)	0.33	0.09	0.97	0.16	0.07	0.05	0.17	0.08	**	**		**
Total culm wt/pot (gms)	31.72	4.09	13.36	1.38	50.75	1.17	70.97	1.46	**		**	**

*The number of measurements for each character varied from 52-60 in No. 1 and from 22-60 in No. 2 (60 for characters other than those dealing with panicles). In Nos. 3 and 4 the number of measurements for each character was consistently 60. The one exception to the above was the total culm wt/pot which was based on 6 pots each for Nos. 1 and 2, and 3 pots each for Nos. 3 and 4.

**Differences significant at the 1% level.

TABLE 7. A comparison of the nitrogen requirements of upland and bottomland switchgrass types.

Nitrogen Concentration	Plant Part	Upland		Bottomland	
		% of Control	Shoot-Root	% of Control	Shoot-Root
		Weight	Ratio	Weight	Ratio
Control*	Shoots	100	2.83	100	2.91
	Roots	100		100	
N/10 (21 ppm)	Shoots	92.9	1.86	84.7	2.24
	Roots	141.2		108.5	
N/100 (2.1 ppm)	Shoots	56.3	1.57	61.8	1.94
	Roots	101.4		92.6	
N/1000 (0.21 ppm)	Shoots	27.4	1.67	58.1	1.78
	Roots	46.6		96.0	

*Control solution (Hoagland's No. 1) contained among other elements the following amounts of N, P, and K: 210 ppm of N, 30.98 ppm of P, and 244.9 ppm of K.

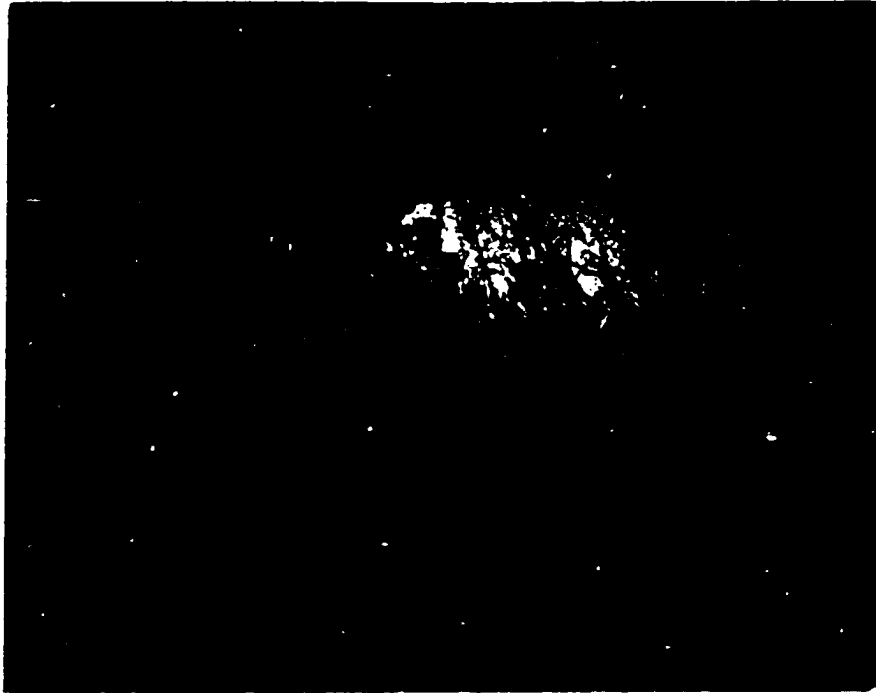


Fig 1. Naturally occurring upland switchgrass (Note meter stick).



Fig 2. Naturally occurring bottomland switchgrass (Note meter stick).



Fig 3. Upland (left) and bottomland switchgrass (right) grown under greenhouse conditions.

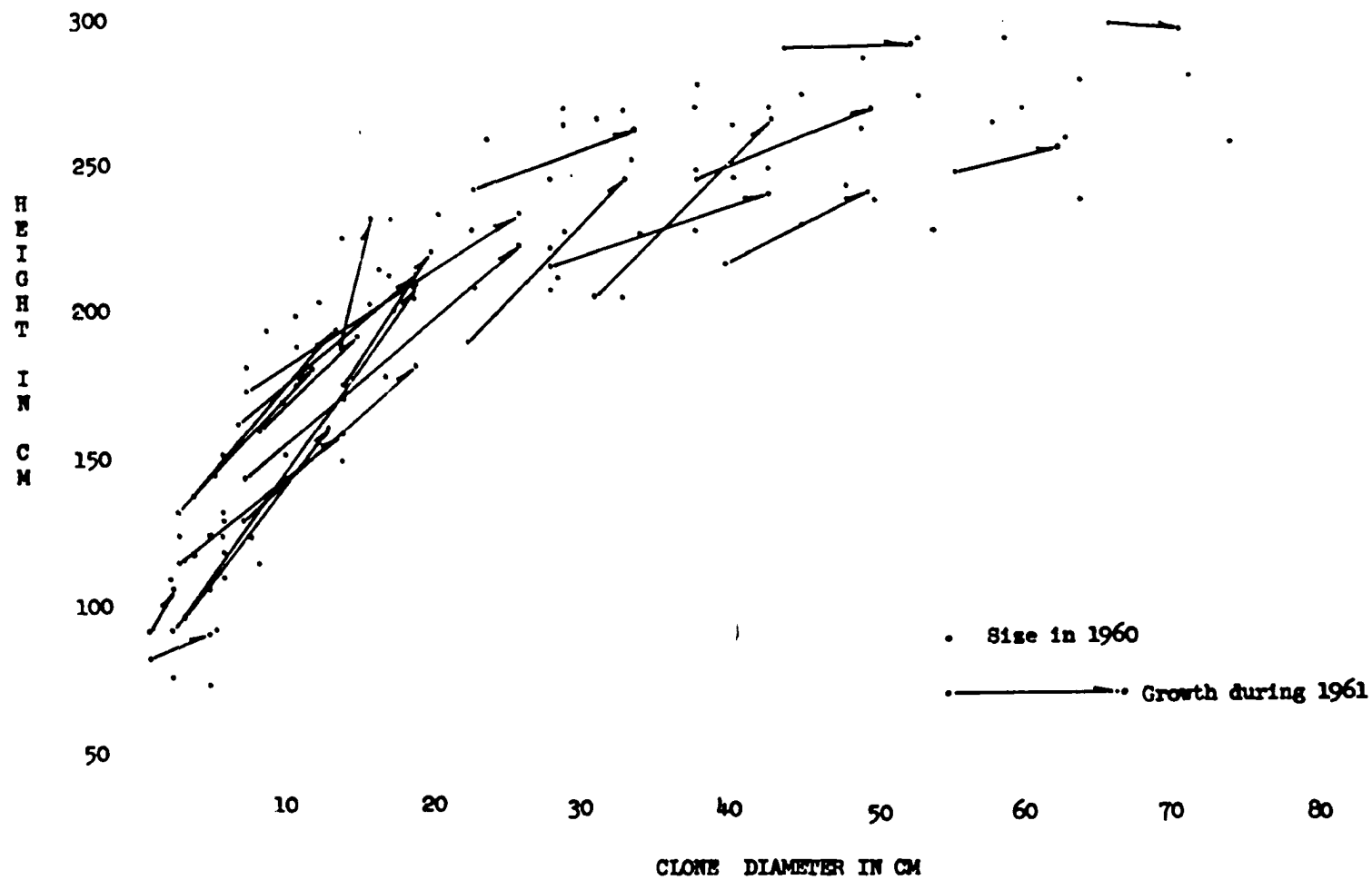


Fig 4. A comparison of the growth of bottomland plants of various sizes.

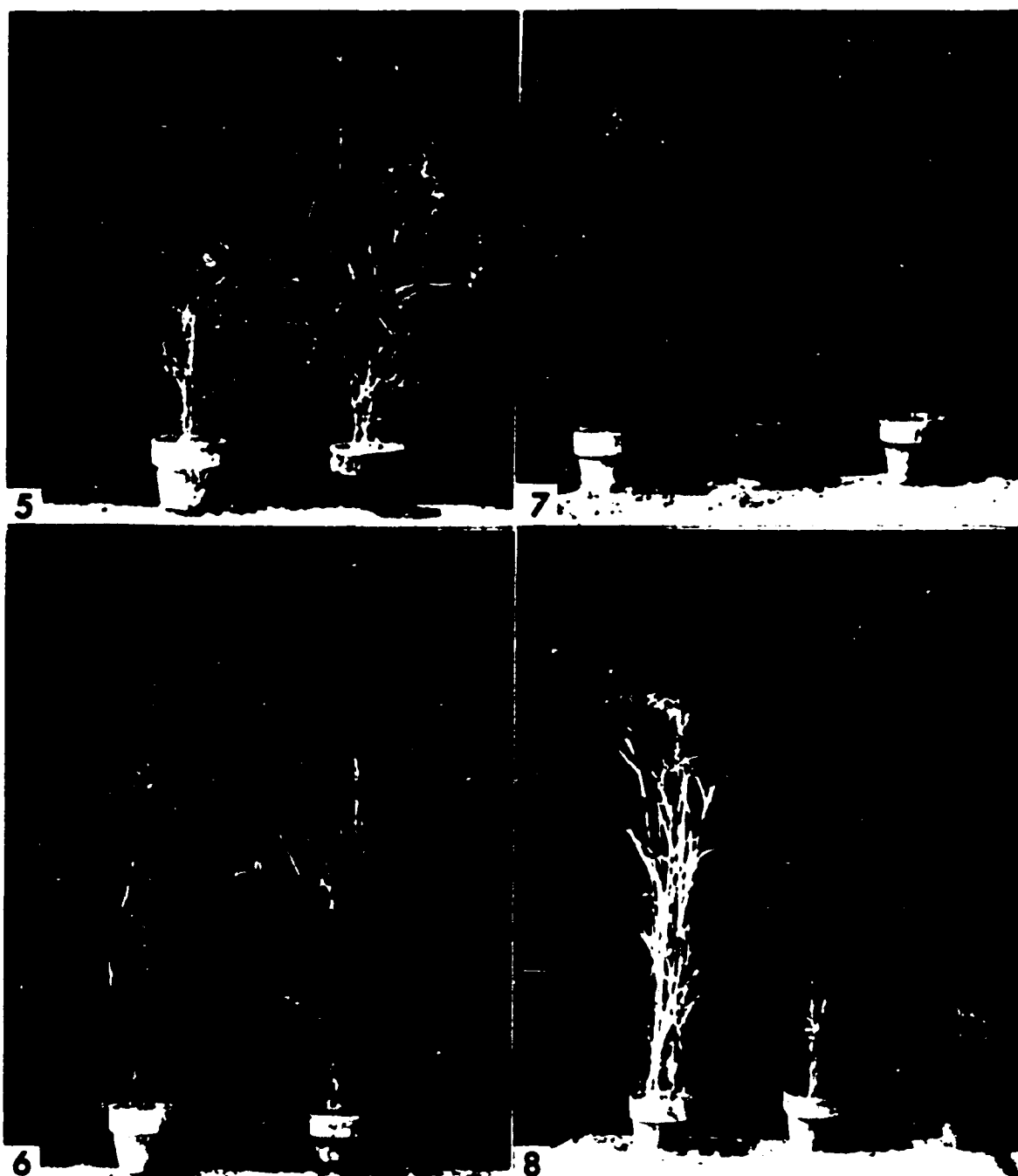


Fig 5. Upland plants grown under moist conditions (right) and flooded conditions (left). Fig 6. Bottomland plants grown under moist conditions (left) and flooded conditions (right). Fig 7. Upland (center and right) and bottomland plants (left) grown under moist conditions. Fig 8. Upland (center and right) and bottomland plants (left) grown under flooded conditions.