TAXONOMIC AND ECOLOGICAL RELATIONSHIPS OF

SCIRPUS ACUTUS MUHL. AND *S. VALIDUS* VAHL

(CYPERACEAE) IN SOUTHERN MANITOBA

A Thesis

Submitted to

The Faculty of Graduate Studies and Research

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Doctor of Philosophy

by

Alexander James Macaulay

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ABSTRACT

This study was conducted in the period 1970 to 1972 and was designed to examine the taxonomic and ecological relationships between *Scirpus acutus* Muhl. and *S. validus* Vahl in southern Manitoba. Taxonomic assessment of the stands was accomplished using the hybrid index based on six characters selected in part from a factor analysis of 13 morphological features. The response of the taxa so defined to a number of environmental parameters was measured using a 'stand performance' index, the product of culm density and fertility.

S. acutus and *S. validus* show morphological discontinuity when six characters are used in combination. *S. acutus* is characterized by inflorescences less than 80 mm long; less than 13 primary rays; rare development of secondary rays and absence of tertiary and quaternary rays; spikelets borne in clusters, with at least one cluster of five or more present; and culms dark green to olive green with aerenchymal lacunae less than 1.5 mm, and usually less than 0.86 mm in diameter. *S. validus* has inflorescences longer than 47 mm, usually longer than 80.5 mm; the number of primary rays usually exceeds 13, but never is less than seven; ray development is extensive with secondary and usually tertiary rays numerous; spikelets are borne singly or in groups of less than five; culms are light green to glaucous with lacunar diameters always greater than 0.87 mm and usually more than 1.5 mm.

The habitat requirements of *S. acutus* and *S. validus* differ with

respect to water depth tolerance, the pattern of water level fluctu-
ations, and the range of tolerance for conductivity and the concentra-
tions of magnesium and sulfate ions. *S. acutus* is typically found at
mean fall water depths of 0 to 80 cm (optimum between 15 and 40 cm) in
habitats with relatively stable water levels. It is capable of toler-
ating waters with conductivity readings as high as 2,600 micromhos/cm^2,
magnesium concentrations of 2,180 mg/l and sulfate concentrations of
1,900 mg/l. *S. validus*, however, is usually found at mean fall water
depths less than 30 cm (optimum 0 to 20 cm) in habitats with unstable
water levels. It has not been found in waters with conductivity in
excess of 494 micromhos/cm^2, magnesium ion concentrations greater
than 230 mg/l and sulfate ion concentrations more than 700 mg/l. Mag-
nesium and/or sulfate ion concentrations are probably limiting the dis-
tribution of *S. validus* in Manitoba to sites with a non-calcareous
substrate.

The occurrence of morphological intermediates of suspected
hybrid origin is infrequent, suggesting that significant barriers
to gene flow exist between the two taxa.

This reproductive isolation combined with the morphological
and ecological distinctions indicate that, within central North America
at least, *S. acutus* and *S. validus* should be considered as distinct
species.

The implications of these findings are discussed, with
particular reference to marsh management for waterfowl and muskrats.

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CHAPTER I

INTRODUCTION

A. Statement of the problem

The genus *Scirpus* L. (Cyperaceae) is represented in Manitoba by 12 species (Scoggan, 1957). Within this group *S. acutus* Muhl. and *S. validus* Vahl are distinguished by having a single, erect involucral bract, a paniculate inflorescence, and a terete, leafless culm.

S. acutus and *S. validus* are sympatric throughout central North America and are commonly found in the shallow waters of many marshes and lakes within this area. They frequently are dominant members of the reedswamp community and, as such, they have a significant role in the dynamic processes of the ecosystem. By virtue of their extensive root and rhizome systems, they contribute to delta formation and the prevention of erosion; while the stout culms are effective in reducing water turbulence (Steenis, 1939). The culms and achenes of both *S. acutus* and *S. validus* are used for cover and food by a wide variety of wildlife, principally waterfowl and muskrats (*Ondatra zibethica* L.)[1] (Martin *et. al.*, 1951).

In view of their prominent role in North American marsh ecosystems, it is paradoxical that *S. acutus* and *S. validus* have been the subject of considerable taxonomic confusion since 1806. This confusion has existed for both taxonomists and ecologists and has been generated for two reasons.

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[1] Nomenclature of mammals follows Burt and Grossenheider (1963).

Firstly, the two taxa are morphologically similar and show considerable variation in morphological characters. This factor, along with inconsistent use and interpretation of diagnostic characters in the literature has produced a poorly-defined morphological concept of the two taxa.

The second source of confusion arises because *S. acutus* and *S. validus* are found in similar habitats and the lack of a comprehensive comparative study of their environmental requirements has resulted in confusion of the habitat types occupied by each.

The present study was designed with two basic objectives:

1. To determine the degree of morphological discontinuity between these two taxa by an objective reappraisal of a number of morphological characters.

2. To compare the response of the two taxa to a number of environmental parameters.

If met, these objectives should provide a clearer understanding of the taxonomic and environmental relationships of *S. acutus*[1] and *S. validus*.

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[1] Throughout this study, the existence of the two taxa is accepted, but reference to them by their binomials does not imply an acceptance of their specific status; the binomials are used solely in deference to tradition to avoid further confusion.

B. <u>Literature review</u>

1. <u>Taxonomic</u>

The genus *Scirpus* is composed of two natural groups, the
leafy and the non-leafy species. Beetle (1940) delimited them as
the subgenera Euscirpus (Grisebach) and Aphylloides, based on the
nature of the involucral bract (foliaceous or a single erect bract)
and the cauline leaves (blades well-developed as opposed to reduced
or wanting). The section Pterolepis Schrader, series Lacustres
(Beetle, 1944; section Eulacustres of Beetle, 1941) was defined to
include the non-leafy species with paniculate inflorescences,
setulose perianth bristles, and bi- or trifid styles. This treat-
ment of the subgeneric categories has been generally accepted. At
the specific level and lower, however, there has been no general
agreement on the disposition of the taxa involved.

The first-named taxon within the series is *S. lacustris* L.;
prior to 1806, all specimens, European or North American, were as-
signed to *S. lacustris*. *S. tabernaemontani* Gmelin, of Eurasian
distribution, was described in 1805, and a year later Vahl des-
cribed *S. validus* from the West Indies. The third species to be
distinguished from *S. lacustris* was *S. acutus* Muhl., described by
Bigelow in 1814 from specimens collected in the eastern United
States.

Poor acceptance of all the newly-named taxa prompted Chase
(1904) to publish a clarification of the North American allies of
S. lacustris. She assigned many North American specimens to
S. validus Vahl, thereby extending the range of this species well

beyond its former tropical distribution. Chase also described the
North American *S. heterochaetus*, clearly distinguishing between
it, *S. validus*, and *S. lacustris*. A third taxon described by
Chase was *S. occidentalis* (Watson), which was later confirmed to
be a synonym of the earlier *S. acutus* Muhl. (Fernald, 1920).
Despite the confusion created by *S. occidentalis*, the North American
taxa began to achieve recognition as a result of Chase's paper
(see Brainerd, 1904). In 1941, Beetle summarized the generally
accepted status of the taxa as follows:

1. *S. lacustris* L.   of European distribution

2. *S. lacustris* L. var. *tabernaemontani* (Gmelin) Doll
                  of Eurasia

3. *S. heterochaetus* Chase   of eastern Canada,
                                 eastern and central
                                 United States

4. *S. validus* Vahl   of North America, South
                                 America, Australia, New
                                 Zealand, China, Japan,
                                 and the Phillipines

5. *S. acutus* Muhl.   of central North America

Fernald (1943) disagreed, however, and stated that the
North American representatives of *S. validus* were sufficiently
distinct from their tropical counterparts that they should be
distinguished. He therefore proposed the name *S. validus* Vahl var.
creber f. *megastachyus*.

Some authors have expressed doubt as to the validity of
the specific distinction between *S. acutus* and *S. validus* (Martin
and Uhler,1939;Koyama, 1962 and 1963). Koyama (1962) em-
phasized that the whole "*Scirpus lacustris* complex", composed of

the five taxa mentioned above, needed revision. He stated that
there was insufficient morphological difference to separate any
from *S. lacustris* above the subspecific level. In his view, *S.
lacustris* would be composed of three subspecies and would include
the following taxa;

1. subsp. *lacustris* var. *lacustris*, including
   S. lacustris L. and *S. heterochaetus* Chase

2. subsp. *glaucus*, incorporating *S. tabernaemontani*
   Gmelin and *S. acutus* Muhl.

3. subsp. *validus* (Vahl), the former *S. validus* Vahl

Koyama's treatment has been disputed by Smith (1969);
Smith states that there <u>is</u> sufficient morphological difference to
distinguish the North American representatives at the species level.
He qualifies his view by stating that extensive hybridization oc-
curs between all three.

Dabbs (1971) also suspected hybridization between *S. acutus*
and *S. validus* in the Saskatchewan River Delta, based upon morpho-
logically intermediate specimens which were sterile. He felt,
however, that there was sufficient morphological and ecological
evidence to consider them as distinct species.

The taxonomic treatment of the North American representa-
tives of the *"Scirpus lacustris* complex" has now come full circle.
Prior to 1806, all non-leafy round-stemmed bulrushes were refer-
rable to *S. lacustris*. Beginning with Vahl in 1806, the des-
cription and gradual acceptance of three distinct North American
species occurred. In 1962, however, Koyama (*op. cit.*) stated that
all three should be re-united with *S. lacustris*. The more recent

literature of Smith (*op. cit.*) and Dabbs (*op. cit.*), however, reaffirm the specific status of the North American taxa.

The taxonomic confusion has been caused in part by the use of different diagnostic characters by different authors and also by lack of agreement in data when the same characters are used.

Chase (1904) used the larger achenes, larger scales, spikelet shape and viscid pubescence of the scale to distinguish *S. acutus* (*S. occidentalis* (Watson) Chase) from *S. validus*.

Beetle (1941) agreed that spikelet shape and larger scales were diagnostic of *S. acutus*, but states that the achenes of *S. validus* are larger (2.5 x 2.0 mm) than *S. acutus* (2.0 x 1.75 mm) and the scales are "...frequently viscid dotted...", in *S. validus*, while he does not describe this character for *S. acutus*. Beetle (*op. cit.*, p. 692) used the fibrous roots and ovoid spikelets of *S. validus* to distinguish it from *S. acutus* (roots spongy and spikelets subcylindric).

Fernald (1950, p. 264) described the spikelets of *S. acutus* as "slenderly ovoid to linear cylindric" and those of *S. validus* as "ovoid to cylindric"; this fine distinction was obscured, however, by his description (*op. cit.*, p. 270) of the spikelets of *S. validus* (Vahl) var. *creber* Fern. f. *megastachyus* Fern. as "ovoid to linearly cylindric". Fernald does not use the root morphology as a diagnostic character, nor does he mention root morphology in his descriptions.

Gleason (1952, p. 271) distinguishes *S. acutus* from *S. validus* by the length of the scale in relation to the achene

("scales much exceeding the achenes" in *S. acutus*; "scales about as long as the achenes" in *S. validus*).

Koyama (1962) based his distinction (at the subspecific level) of *S. acutus* and *S. validus* on the scales (papillose, punctate and fimbriate-margined in *S. acutus*; glabrescent, usually non-punctate and less fimbriate in *S. validus*) and the scale-achene length (the scales exceeding the achenes in *S. acutus*).

Smith (1969) considered the number of air spaces (aerenchymal lacunae) in a cross section of the culm, the proportion of spikelets borne singly, and the floral scale color as diagnostic.

Dabbs (1971) used stem color, secondary ray length, presence of tertiary rays, spikelet color and scale length to distinguish populations of *S. acutus* and *S. validus*. The contrast between Dabb's (1971) characters and those of Beetle (1941), who attempted the first clarification of the group are noteworthy at this point. Beetle did not recognize a color difference of the culms (he described both as 'green'), while Dabbs found that the 'dark green' culms of *S. acutus* contrasted with the 'light green' culms of *S. validus*. The treatment of the ray development by Beetle and Dabbs is also conflicting. Beetle stated that secondary ray length was greater in *S. acutus* ("...to 3 cm..." in *S. acutus* as opposed to "...to 2 cm..." in *S. validus*) and that in both species the development of tertiary rays was 'rare'. Dabbs (*op. cit.*) stated that secondary ray lengths were greater in *S. validus*, being 10 mm or more in length, while those of *S. acutus* were "...very short or absent..." (*op. cit.*, p. 151). Dabbs found the development

of tertiary rays characteristic of *S. validus*, whereas they were
absent in *S. acutus*.

2. Ecological

The environmental requirements of *S. acutus* and *S. validus*
have not been clearly defined in the literature. This is due in
part to the similarities of the habitats occupied by the plants,
but also due to a lack of comparative data for a number of envir-
onmental parameters. The confusion has been compounded by simpli-
fied statements in the literature, particularly in floras or other
works briefly describing plant habitats, which indicate that *S.
acutus* and *S. validus* occupy the same habitat; these statements
are very often based on one environmental parameter.

Of all the environmental factors acting upon emergent hy-
drophytes, water depth is the most obvious and the most easily
measured. As a result, attempts to typify the habitat of emergents
in a short statement are usually based on this parameter. Muenscher
(1944), Fernald (1952), Gleason (1952) and Moss (1959) give brief
statements on habitat, but do not indicate any differences between
the two species. Sigler (1948), however, does indicate a water
depth "preference", stating that *S. acutus* grows "at depths of 5 to
7½ feet" while *S. validus* is "abundant in very shallow water or
marshy areas...". Smith (1969) indicated that *S. acutus* was found
in deeper water to 3 m, whereas *S. validus* grows in "...wet mud
and very shallow water along the shores", and was never found at
depths greater than 1 m. Similarly Dabbs (1971) found that

S. validus rarely grew at depths greater than 60 cm, whereas
S. acutus was found at depths of 1.5 m.

Similarly, little information is available from the litera-
ture on the chemical quality of water in which *S. acutus* and
S. validus grow. Metcalf (1931) found *S. acutus* had a wide range
of tolerance for saline and alkaline waters. He described *S. acutus*
as being common to rare in saline, saline-alkaline, and fresh water,
while *S. validus* was found only in fresh water. Martin and Uhler
(1939) found that *S. validus* was restricted to fresh water, while
S. acutus "...thrives in mildly alkaline or slightly brackish
waters...". Fassett (1940) described *S. acutus* as "common in hard
water...". Muenscher (1944, p. 167) said of *S. acutus*: "In cal-
careous areas this species often covers extensive areas, the so-
called 'tule marshes'". Martin *et. al.* (1951) indicate that *S.
acutus* is somewhat alkali-tolerant, though less so than the alkali
bulrush (*S. paludosus*). Curtis (1959, p. 390) described the optimum
for *S. validus* as medium hard waters (50 - 150 ppm $CaCO_3$) and that of
S. acutus as very hard water (150+ ppm). Stewart and Kantrud (1969)
described *S. acutus* as most abundant in slightly to moderately
brackish (300 - 8,000 micromhos/cm^2), whereas *S. validus* is found
in fresh or slightly brackish waters (40 - 2,200 micromhos/cm^2).
Smith (1969) found that *S. acutus* tolerated conductivities in ex-
cess of 18,000 micromhos/cm^2 while *S. validus* was generally found
at values below 2,000 micromhos/cm^2.

The utilization of *S. acutus* and *S. validus* as a source of
food and cover for waterfowl has been well-documented. Many

species of diving and dabbling ducks eat the achenes (Metcalf, 1931; Martin and Uhler, 1939; Martin *et al.*,1951; Chamberlain, 1948; and Keith and Stanislowski, 1960). Martin *et al.*(*op. cit.*) also list 22 species of wading birds, seven species of songbirds, and two species of upland gamebirds which feed on the achenes. Steenis (1939), Wolf (1955), and Lokomon (1966) indicate the strong preference of ducks, particularly diving ducks, for these bulrushes as a source of nesting cover. Williams and Sooter (1941) found that Canada geese (*Branta canadensis* L.)[1] will also nest in bulrushes (*S. acutus*).

Muskrats (*Ondatra zibethica*) eat the succulent bases of both *S. acutus* and *S. validus* and use the rhizomes and culms for constructing their lodges (Yeager, 1945; Errington, 1948; Bellrose, 1950; Arata, 1959).

Both species of bulrush have been used extensively by aboriginal tribes in North America (Beetle, 1950). The culms were collected for thatching and weaving baskets and mats. Steenis (*op. cit.*) considers that the genus on a world-wide scale, represents one of the most important uncultivated textile materials.

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[1] Nomenclature of birds follows Godfrey (1966).

C. Description of the area

1. General description of southern Manitoba

Physiographically, southern Manitoba (south of 54°N) can be visualized as a central triangular basin with upland plateaus on the east and west borders. Altitudes vary from a maximum in the west of 827 m above sea level to approximately 216 m in the lowest portion of the basin, Lake Winnipeg (Weir, 1960). The eastern uplands, formed by the Canadian Shield, reach an altitude of approximately 364 m above sea level.

The most prominent feature of the western upland is the Manitoba Escarpment, underlain by Cretaceous shales and sandstone (Figure 1). The surface deposits are predominantly glacial drift composed of shale and limestone with some admixture of granitic materials (Figure 2).

The central basin, or Manitoba Lowland (Weir, 1960), has a mixture of lacustrine and calcareous drift material, which forms a mantle of various thickness over bedrock of several geological ages (Figure 2). The bedrock of the western portion of the Manitoba Lowland is mainly limestone of the Jurassic, Devonian, and Silurian periods. These are replaced further east successively by older Ordovician limestone, Ordovician sandstone and shale and finally the Precambrian granites, gneisses and sedimentary rock of the Canadian (or Precambrian) Shield (Figure 1). The Precambrian Shield has a discontinuous mantle of surface material interspersed with bedrock outcroppings. The surface deposits are primarily glacial drift of granitic origin.

Figure 1: Geology of southern Manitoba (Weir, 1960).
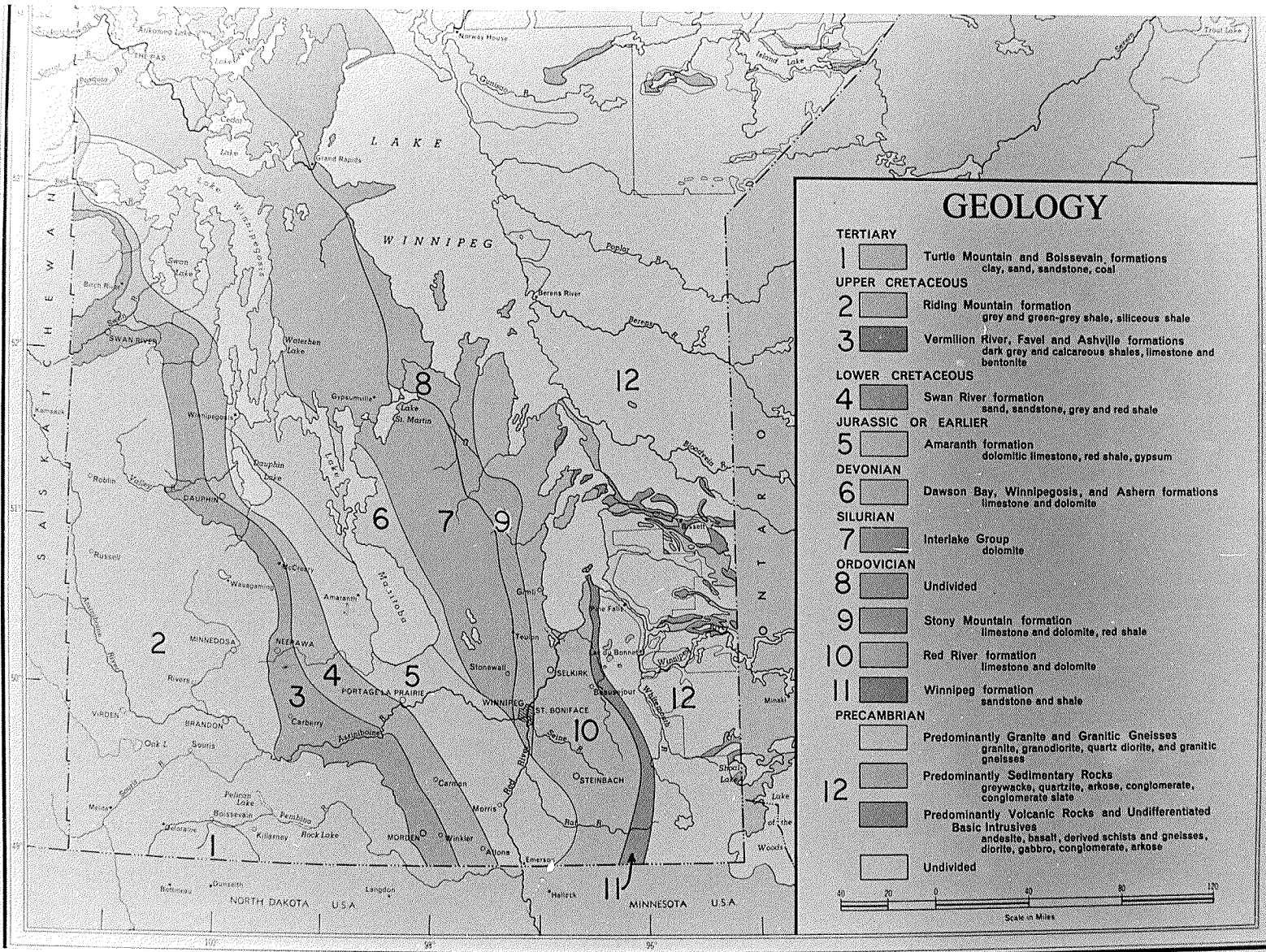
GEOLOGY

TERTIARY

1 Turtle Mountain and Boissevain formations
clay, sand, sandstone, coal

UPPER CRETACEOUS

2 Riding Mountain formation
grey and green-grey shale, siliceous shale

3 Vermilion River, Favel and Ashville formations
dark grey and calcareous shales, limestone and bentonite

LOWER CRETACEOUS

4 Swan River formation
sand, sandstone, grey and red shale

JURASSIC OR EARLIER

5 Amaranth formation
dolomitic limestone, red shale, gypsum

DEVONIAN

6 Dawson Bay, Winnipegosis, and Ashern formations
limestone and dolomite

SILURIAN

7 Interlake Group
dolomite

ORDOVICIAN

8 Undivided

9 Stony Mountain formation
limestone and dolomite, red shale

10 Red River formation
limestone and dolomite

11 Winnipeg formation
sandstone and shale

PRECAMBRIAN

Predominantly Granite and Granitic Gneisses
granite, granodiorite, quartz diorite, and granitic gneisses

12 Predominantly Sedimentary Rocks
greywacke, quartzite, arkose, conglomerate, conglomerate slate

Predominantly Volcanic Rocks and Undifferentiated Basic Intrusives
andesite, basalt, derived schists and gneisses, diorite, gabbro, conglomerate, arkose

Undivided

Scale in Miles
40   20   0   40   80   120

14
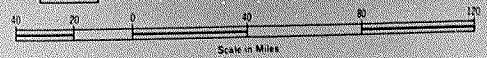
Figure 2:   Surface deposits of southern Manitoba (Weir, 1960).
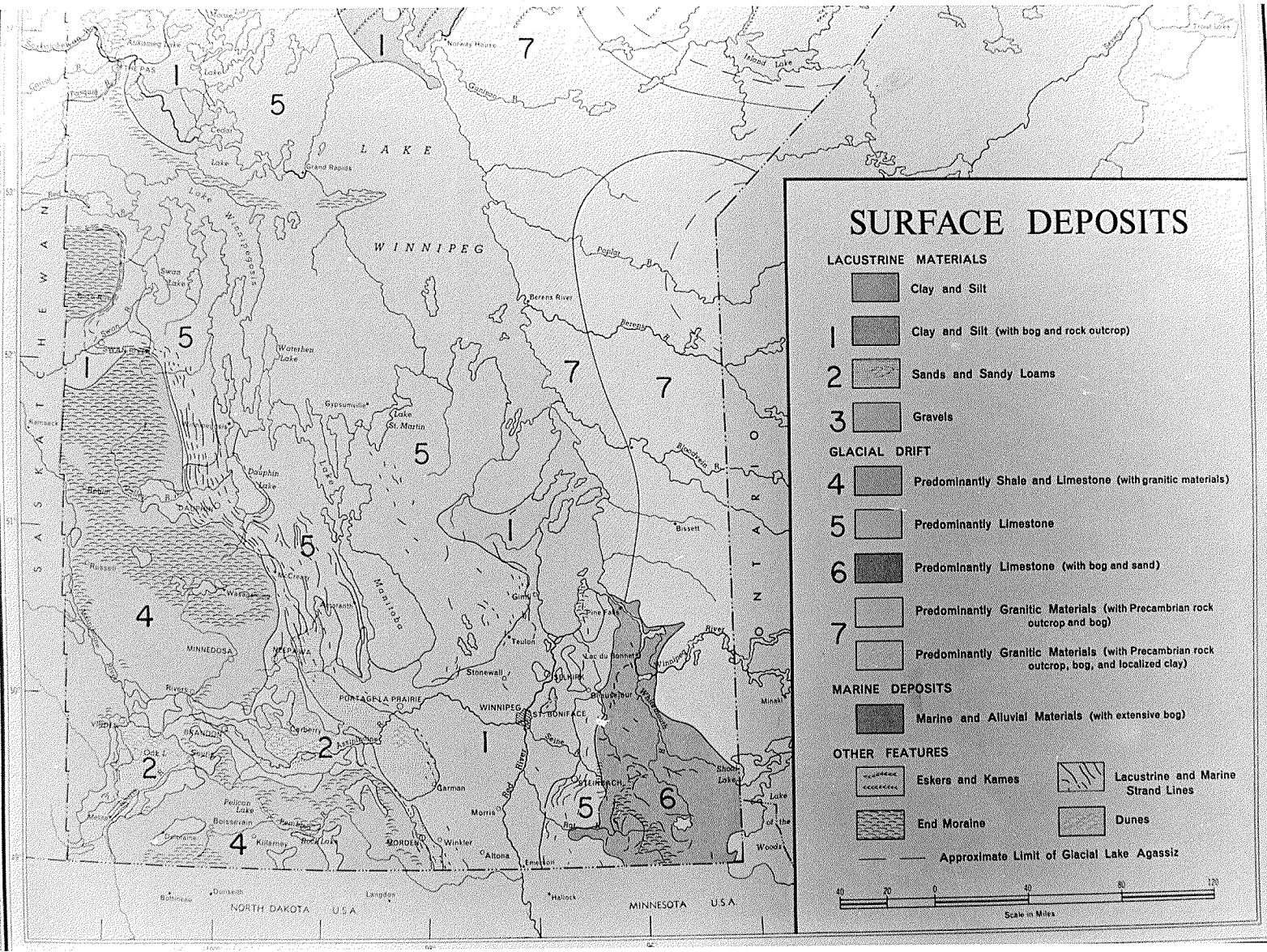
SURFACE DEPOSITS

LACUSTRINE MATERIALS

Clay and Silt

| Clay and Silt (with bog and rock outcrop)

2 Sands and Sandy Loams

3 Gravels

GLACIAL DRIFT

4 Predominantly Shale and Limestone (with granitic materials)

5 Predominantly Limestone

6 Predominantly Limestone (with bog and sand)

7 Predominantly Granitic Materials (with Precambrian rock outcrop and bog)

Predominantly Granitic Materials (with Precambrian rock outcrop, bog, and localized clay)

MARINE DEPOSITS

Marine and Alluvial Materials (with extensive bog)

OTHER FEATURES

Eskers and Kames

Lacustrine and Marine Strand Lines

End Moraine

Dunes

Approximate Limit of Glacial Lake Agassiz

40   20   0   40   80   120
Scale in Miles
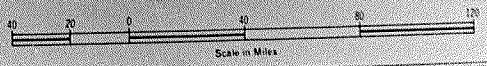
The climate of southern Manitoba is described as Continental, with extreme mean temperatures of -21°C in January and $+21^{\circ}$C in July (Weir, *op. cit.*, p. 14). The average number of frost-free days varies from 100 in the north to 120 in the south. Average annual precipitation varies from 43 cm in the northwest to 56 cm in the southeast, approximately 70% occurring as rain.

A north-south gradient in climatic factors is in part responsible for the northwest-southeast orientation of the five major natural vegetation types in southern Manitoba: the open grasslands in the south and southwest, the aspen parklands, the deciduous (broadleaf) forests, the mixed woods, and the northern coniferous forest in the north and northeast.

Open grasslands were a prominent feature of southern Manitoba prior to the advent of agriculture. Mixed grass prairie extended into southwestern Manitoba from Saskatchewan and North Dakota, while tall grass prairie was found in the Red River valley to a latitude of approximately 52°N. A transition zone of wooded grassland, the aspen parkland, formed the ecotone between the grasslands and the deciduous forest further north. The scattered groves of aspen (*Populus tremuloides* Michx.)[1] and balsam poplar (*Populus balsamifera* L.) increase in size and coalesce in the north, with birch (*Betula papyrifera* March) and white spruce (*Picea glauca*

---

[1] Nomenclature of plants follows Scoggan (1957).

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(Moench) Voss) beginning to appear. Still further north this deciduous woodland becomes a transition, the mixed woods, with white spruce, the balsam fir (*Abies balsamea* (L.) Mill.) mixed with the aspen and birch. The deciduous trees are gradually replaced until white spruce and balsam fir are dominant on the higher well-drained sites, and black spruce (*Picea mariana* (Mill.) BSP.) and larch (*Larix laricina* (Du Roi) K. Koch) occupy the lower, poorly drained areas. These species are the dominants of the northern coniferous forest.

Five study areas were located in southern Manitoba in order to examine the range of marsh habitats produced by the complex of parent materials and climate described above. Each of the study areas has a distinctive topography and different parent materials, which contribute to differences in the water chemistry, type of rooting medium, and patterns of water level fluctuations throughout the summer. The areas are referred to as The Pas, Langruth, Minnedosa, Delta, and Netley (Figure 3); some of the distinctive features as well as the sites located in each study area are described below.

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Figure 3: Location of five study areas in southern Manitoba.

MANITOBA
south of 55°N

Scale: 20 miles

THE PAS

LAKE WINNIPEG

LAKE WINNIPEGOSIS

N

LANGRUTH

MINNEDOSA

L. MANITOBA

DELTA

NETLEY

WINNIPEG
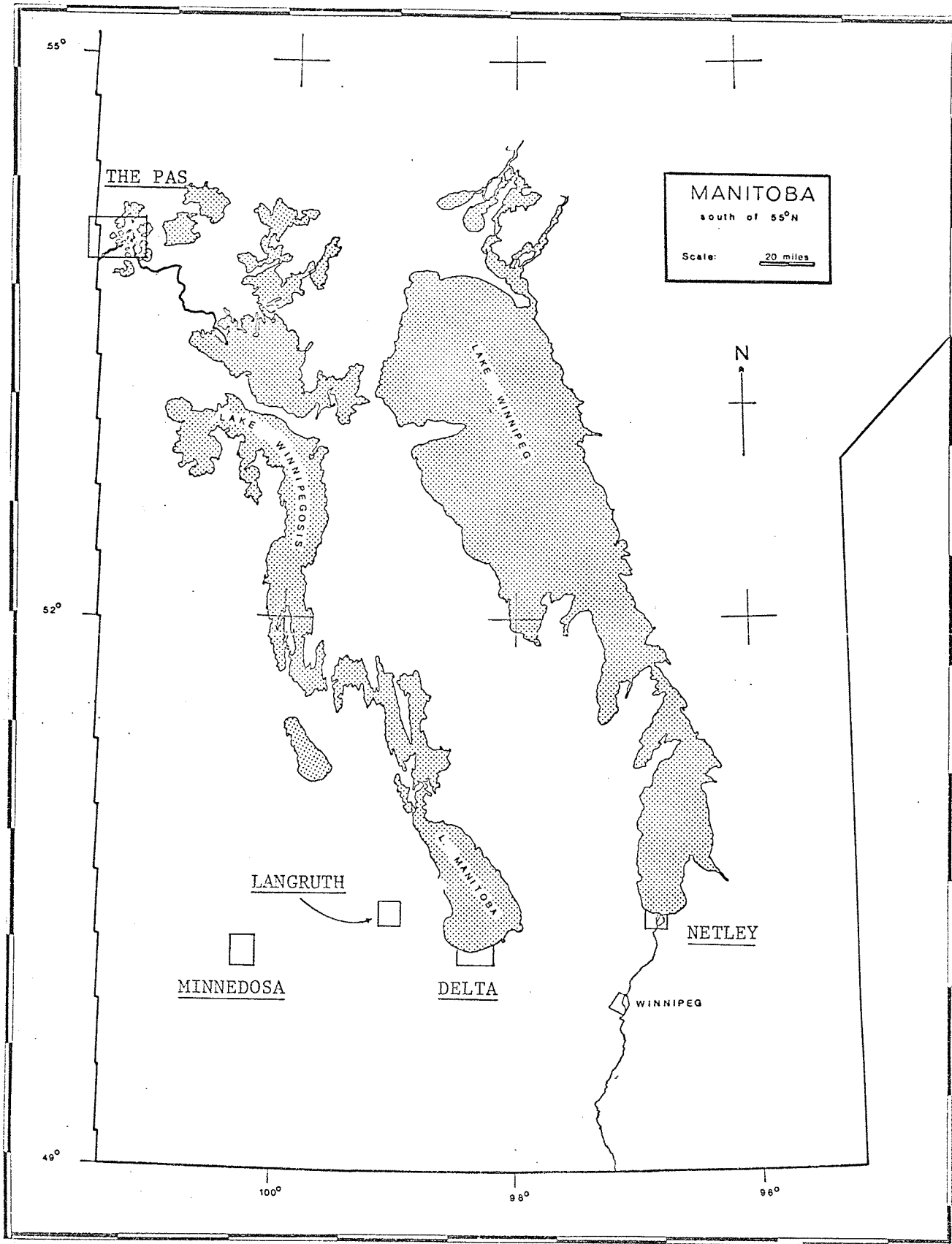
2. Description of the study areas and site locations

(a) The Pas

The marshes of this area are associated with the floodplain of the Saskatchewan River. The topography is flat, the major relief feature being the natural levees and man-made dikes associated with the river system. West of The Pas townsite (Figure 4), rich surficial deposits of alluvium provide a good agricultural soil. Numerous dikes have been constructed, particularly along the Carrot River, to alleviate the flooding of the farmlands. Sites 24 and 31 are located on this alluvium, in wild rice (*Zizania aquatica* L. var. *interior* Fassett) paddies constructed by The Pas Indian Band (Figures 5 and 6).

Further west, the drainage becomes progressively poorer, with the accumulation of peat in many areas. Sites 34, 35, 41, and 42 are located in the Murphy Lake-Murphy Extension complex (Figure 7). The margins of these lakes have substantial stands of aspen, balsam poplar, and some white spruce on the higher sites (Figure 8); lower, poorly drained areas are dominated by willows (*Salix* spp.). The emergent zone is dominated by *Phragmites communis* Trin., bulrushes (*Scirpus* spp.), sedges (*Carex* spp.), spikerush (*Eleocharis palustris* (L.) R. & S.), and water horsetail (*Equisetum fluviatile* L.). The rooting medium in most instances is a floating mat which is continuous into open water by the extensive rhizome network of yellow pond lily (*Nuphar variegatum* Engelm.). Murphy Lake and Murphy Extension are interconnected and the water levels are controlled artificially by Ducks Unlimited.

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Figure 4: Location of sites in The Pas study area.
Composite of National Topographic System
The Pas map sheets, 63 F/14W and 63 F/14E,
Edition 1. See Appendix I for grid refer-
ence location to nearest 100 m reference
point for each site. Map scale 1:50,000.

36 ●

INDIAN RESERVE 21 E

INDIAN RESERVE 21 E

IR 21 J

Microwave ○

Pas River Lot 7

Tanks

INDIAN RESERVE 21 B

Historic Site

PAS

Dam

INDIAN RESERVE 21 D

Radio

The Pas (seaplane base)

Dump

RIVER LOTS

● **43**

24 ●

31

IR 21 C

Dam

Dyke

B

1 TO 6

Airfield

Grace Lake (seaplane base)

Dyke

Lot 9

Park

Water

The Pas

INDIAN RESERVE 21-I

Golf Course

The Pas

Turntable

528

Airfield

N

INDIAN RESERVE 21 A

Ditch

Cemetery Lake

Cemetery Lake
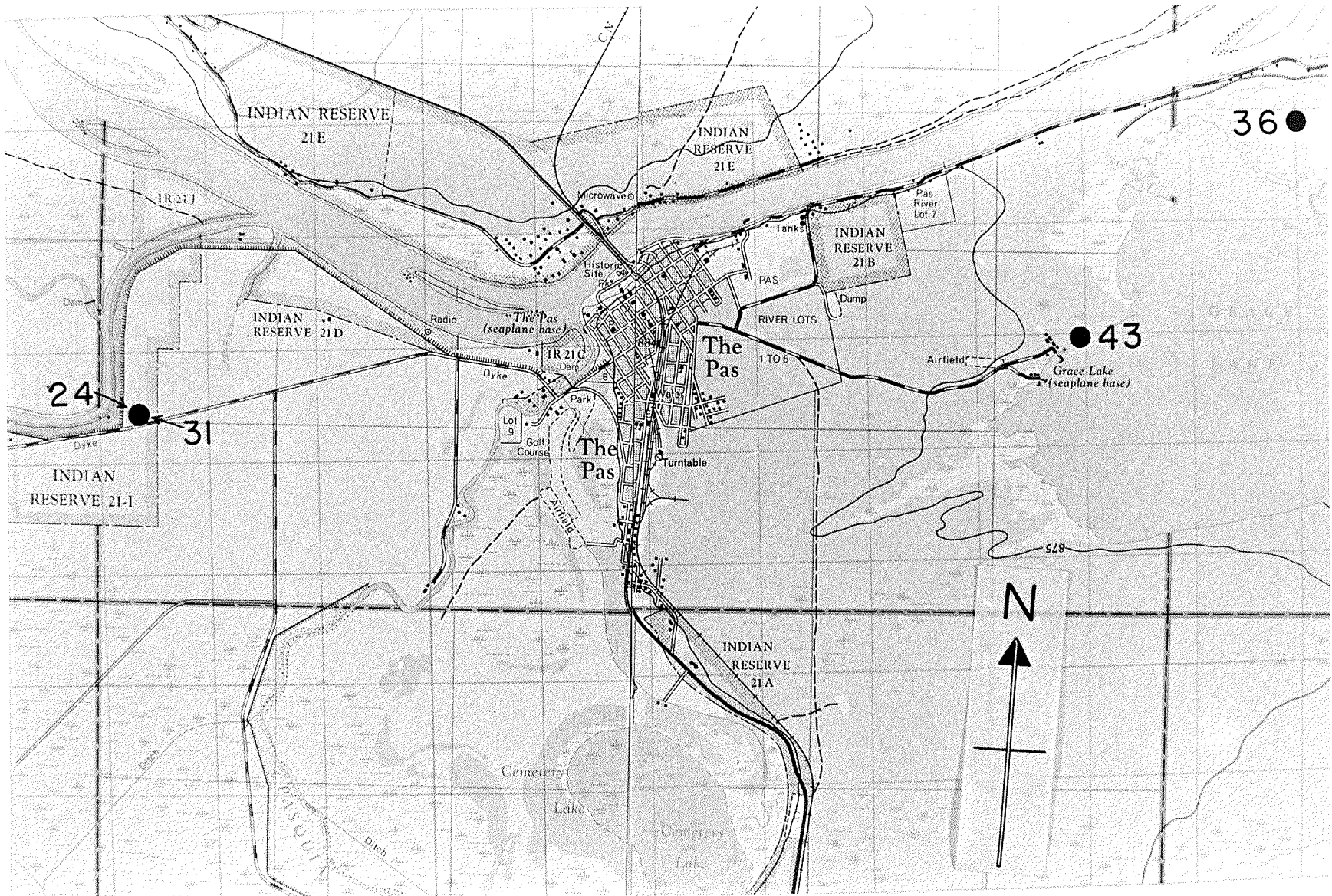
Figure 5. Site 24, located in a wild
           rice (*Zizania aquatica*) paddy.
           S. validus on the edge of water
           in background (August 9, 1972).

Figure 6. Site 31, located immediately east
           of site 24 (above). *S. validus*
           growing at maximum depth of 35 cm
           (August 9, 1972).

Figure 7: Location of sites in The Pas study area,
Murphy Lake-Murphy Extension. Taken
from National Topographic System,
Culdesac Lake map sheet 63 F/12W,
Edition 1. See Appendix I for grid
reference location to nearest 100 m
reference point for each site.
Map scale 1:50,000.

22
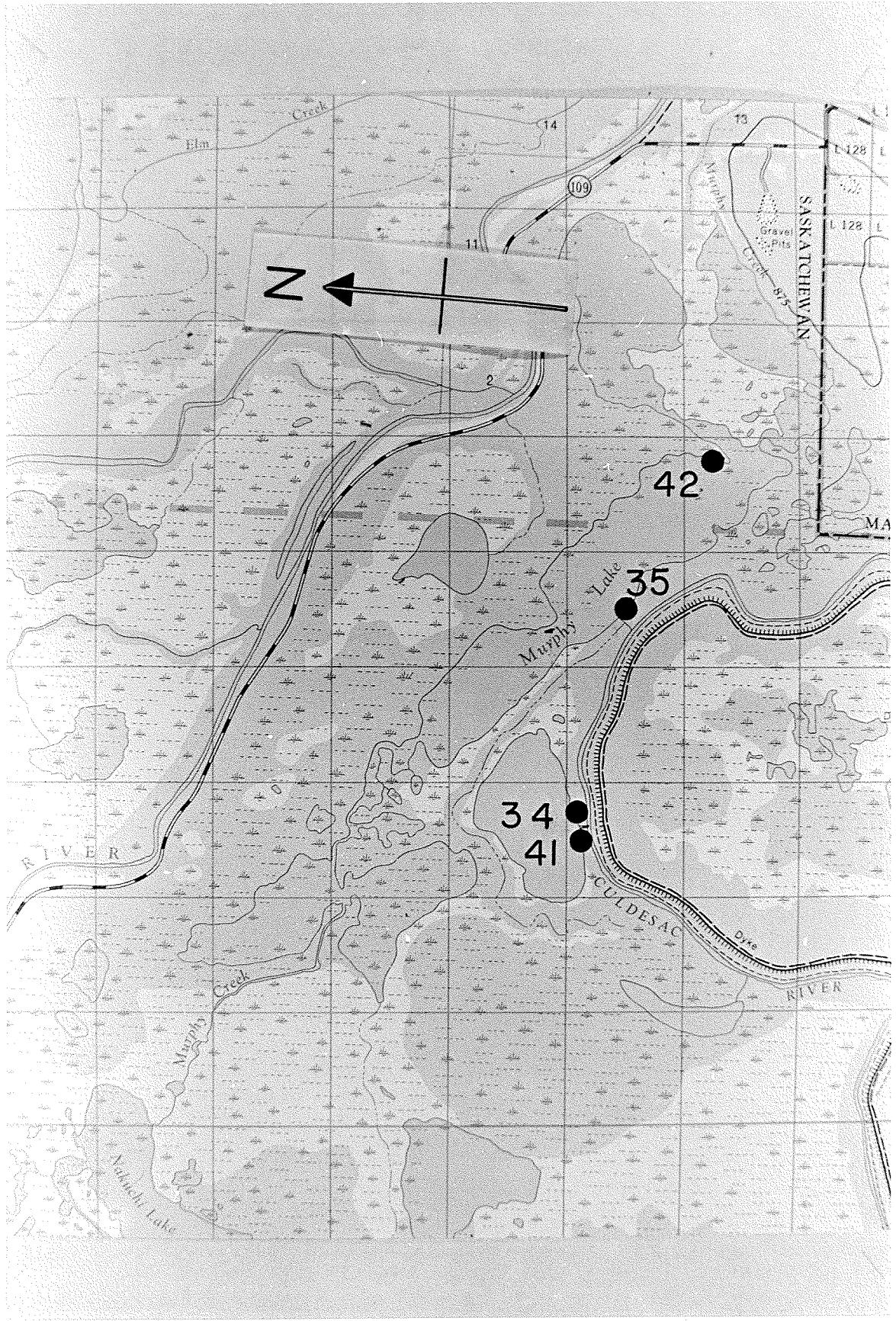
Figure 8: Site 35, Murphy Lake. *S. acutus*
           growing on floating mat in water
           depths from 150 to 200 cm
           (August 11, 1972).

Figure 9: Site 43, Grace Lake. *S. acutus*
           growing in water depths from
           25 to 85 cm (August 14, 1972).

Sites 36 and 43 are located east of The Pas townsite on Grace Lake (Figures 4 and 9). The lake bottom is composed of calcareous coarse sand and gravel with many large boulders interspersed. At the eastern end, the bottom is overlain by organic material and silt 25 to 50 cm thick. A fixed-level control structure on the north-east side and moderately good drainage into the lake appear to provide relatively stable water levels throughout the summer.

Figure 10: Location of sites in Langruth study area, 9.7 km
            west of Langruth. Taken from National Topo-
            graphic System, Langruth map sheet 62 J/7W,
            Edition 1. See Appendix I for grid reference
            location to nearest 100 m reference point for
            each site. Map scale 1:50,000.

(b) Langruth

The topography of the Langruth study area is smooth to un-
dulating. Numerous beach ridges oriented perpendicular to the land
fall, which is from west to east, create abundant permanent, semi-
permanent, and temporary bodies of surface water. Sites 1, 2, 9,
13, 14, 15, 38 are located in the vicinity of Big Grass Marsh
(Figure 10), which covers an area of approximately 18,647 ha
The parent material is medium to coarse-textured very calcareous
till, which is rarely covered by more than a few centimeters of
organic debris and silt. Extensive ditching for agricultural
drainage results in pronounced declines in water levels over the
summer.

Aspen (*Populus tremuloides*), poplar (*P. balsamifera*), and
burr oak (*Quercus macrocarpa* Michx.) are the prevalent tree species
on the uplands. Bluffs of these trees are interspersed with grass-
lands dominated by *Poa pratensis* L., *Agropyron* spp., *Andropogon
scoparius* Michx., and *Bromus* spp.

The reed-swamp community associated with Big Grass Marsh
and in other low-lying areas is dominated by *Phragmites communis*,
bulrush (*Scirpus acutus*), numerous sedges (*Carex* spp.), and
sprangletop grass (*Scolochloa festucacea* (Willd.) Link). The most
abundant submerged hydrophytes are *Potamogeton richardsonii* (Benn.)
Rydb. and *Utricularia vulgaris* L., the bladderwort. *Potamogeton
vaginatus* L. is locally abundant in deeper water.
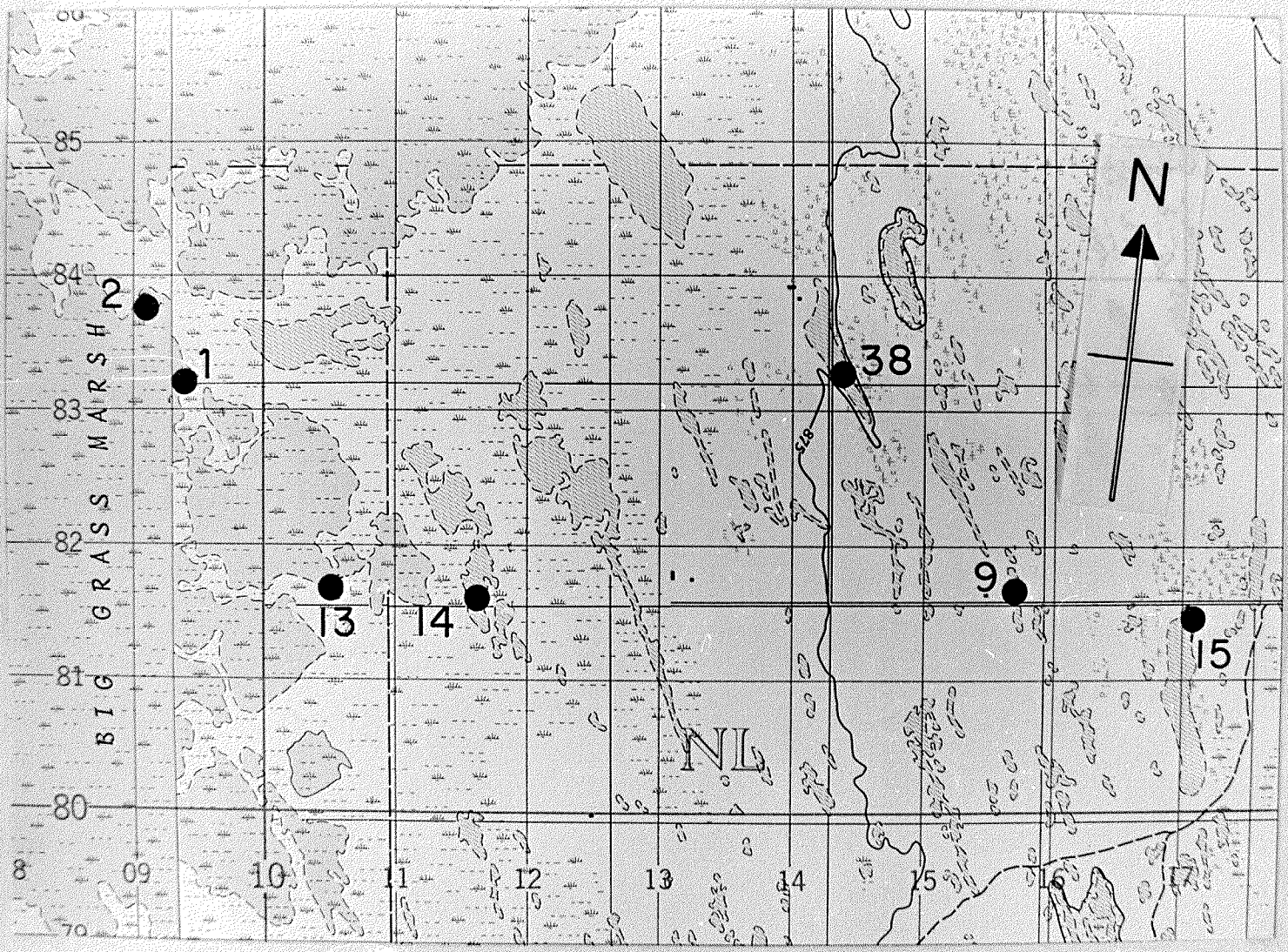
(c) Minnedosa

Sites 6, 11, 16, 21, 25, 26, 27 and 29 are located along highway 10 south of Minnedosa (Figure 11) in an area of dead ice moraine. The topography is smooth to rolling, with the upland aspen groves interspersed with cultivated land. The numerous 'potholes' are a prominent physiographic feature. The parent material is a medium to coarse-textured moderately calcareous boulder till of mixed shale, limestone, and granitic rock (Ehrlich *et al.*,1957).

The 'potholes' vary greatly in size from less than 2 ha to approximately 65 ha. The open water areas in the center are usually devoid of vegetation. An emergent zone usually exists, consisting of pure or mixed stands of cattail (*Typha latifolia* L. and *Typha angustifolia* L.), sprangletop grass (*Scolochloa festucacea*) and bulrush (*S. acutus*) (Figure 12).

The water level fluctuations are quite variable in different 'potholes' due in part to suspected differences in groundwater flow patterns. Generally, there is a progressive decline in water levels throught the growing season, suggesting that these are groundwater recharge depressions; other 'potholes', however, will show a relatively stable water level through the entire summer, indicating a discharge area (Lissey, 1962).

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Figure 11: Location of sites in Minnedosa study
area, 8 km south of Minnedosa.
Taken from National Topographic System,
Moore Park map sheet 62 J/4W, Edition 1.
See Appendix I for nearest 100 m grid
reference point for each site.
Map scale 1:50,000.

29

58

57

33   34   35   36   37   38   39   40   4

56

55

CANADIAN   Rufford Elevator   1776   NATIONAL   1747   1727

11

16

54

53

26   25   6

Tremaine   10

52

27   51

N

50

49

48

34   35   36   37   38   39   40   4

47

1697   1675   1648   46   1637   CANADIAN   1620

Fourth   Base

45

1600

21

28
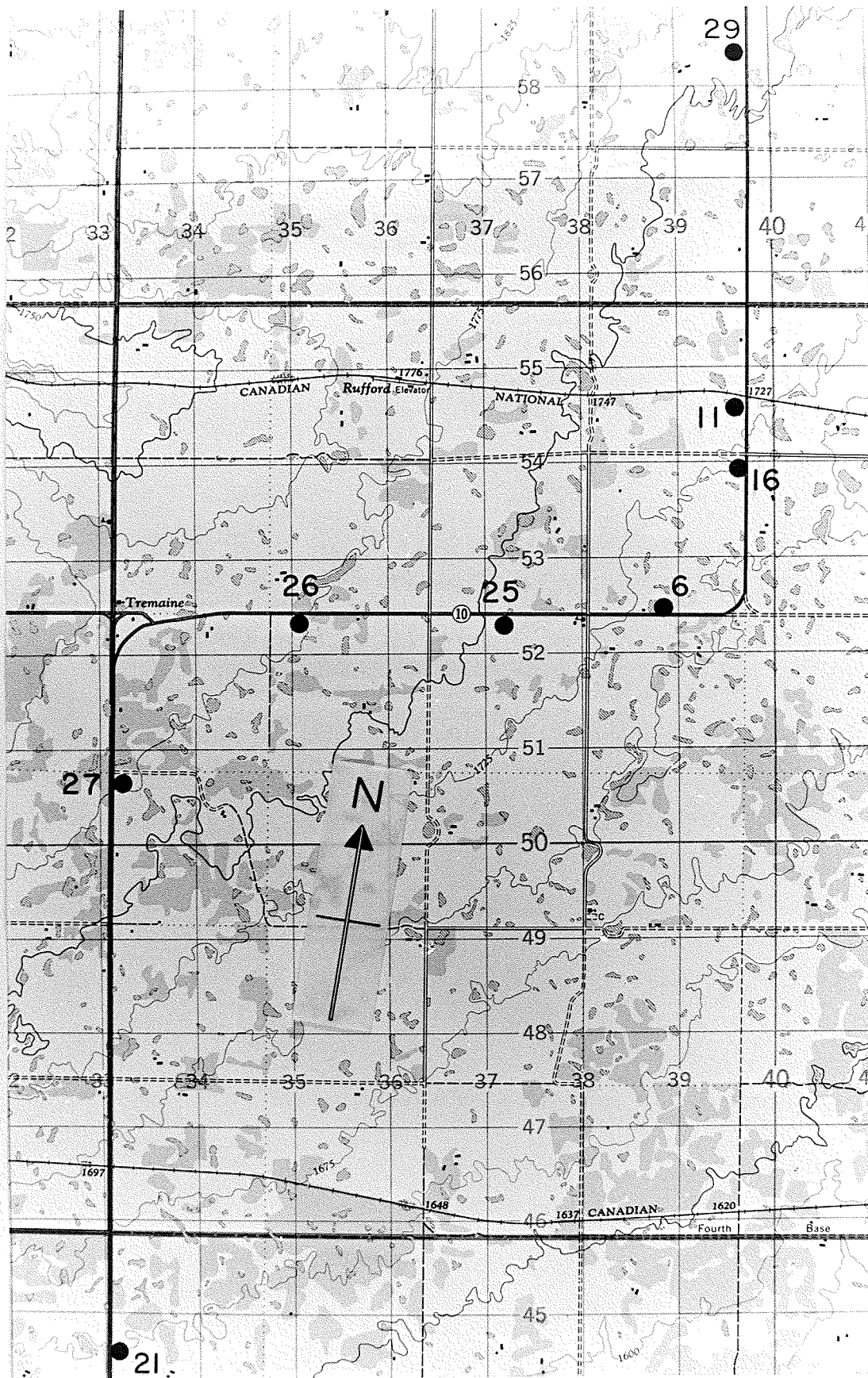
Figure 12: View of Site 21, looking east from
            Provincial Highway number 10.
            S. acutus forms the emergent zone
            bordering open water (August 5, 1972).

(d) Delta

The study area referred to as Delta includes the Delta Marsh, tributary streams leading into it from the south, and the adjacent areas of the Portage Plains. Sites 20, 22, 23, 28, 30, 32, 33, 37, 39, 44-60 and 100-103 were located within this area (Figures 13, 14, and 15). The topography is smooth to gently undulating, with numerous meandering channels.

The Delta Marsh is located at the southern end of Lake Manitoba; it is separated from the lake by a barrier ridge with three major channels connecting lake and marsh. Water levels of the marsh tend to fluctuate with those of the lake, but controlled lake levels in recent years have reduced the amplitude of water level fluctuations; the major fluctuations at present are due to wind tides. The substrate of the marsh is composed of silt and fine sand with a thick layer of undecomposed organic matter and muck overlying it. Water depths are usually less than one metre, although in some areas, depths of 3 m occur. The shallower bays and channels have vigorous stands of submerged aquatics growing in them. *Potamogeton pectinatus* L. is the most abundant; *Myriophyllum exalbescens* Fern., *Utricularia vulgaris* and *Potamogeton richardsonii* are also found throughout the area. The reed-swamp community is dominated by *Phragmites communis* (Walker, 1965), which is the common emergent around most of the bays and along the channels. Cattails (*Typha latifolia* and *Typha angustifolia*) and bulrushes (*Scirpus* spp.) replace the *Phragmites* in some of the sheltered bays and channels (Figure 16). Wet meadow

species such as *Scolochloa festucacea*, *Spartina pectinata* Link and *Sonchus* spp. are prominent on the higher better drained sites. Walker (1959, 1965) gives detailed descriptions of the vegetation.

Several old channels traverse the Portage Plains and appear to have been connected with the marsh in the past. Most of these channels now hold temporary water in the spring only. Many are sufficiently dry by late summer to permit vehicle access for haying operations.

The substrate in these channels is composed of silt and fine sand. The frequent exposure of the mud has resulted in incorporation of the organic detritus into the mineral material; as a result, the substratum has many of the characteristics of a terrestrial soil which is periodically inundated. The vegetation of these creek channels is dominated by slough grass (*Beckmannia syzigachne* (Stend.) Fern.), water plantain (*Alisma triviale* Pursh), water parsnip (*Sium suave* Walt.), spikerush (*Eleocharis palustris* (L.) R. & S.) and *E. acicularis* (L.) R. & S.) and bulrush (*Scirpus validus*) (Figure 17). Drier sites have in addition a large number of composites (*Aster* spp., *Sonchus* spp. and *Bidens cernua* L.).

Figure 13: Location of sites in Delta study area,
            western portion. Taken from National
            Topographic System, MacDonald map sheet
            62 J/1W, Edition 2. See Appendix I for
            nearest 100 m grid reference point for
            each site. Map scale 1:50,000.

LAKE MANITOBA

Delta Beach
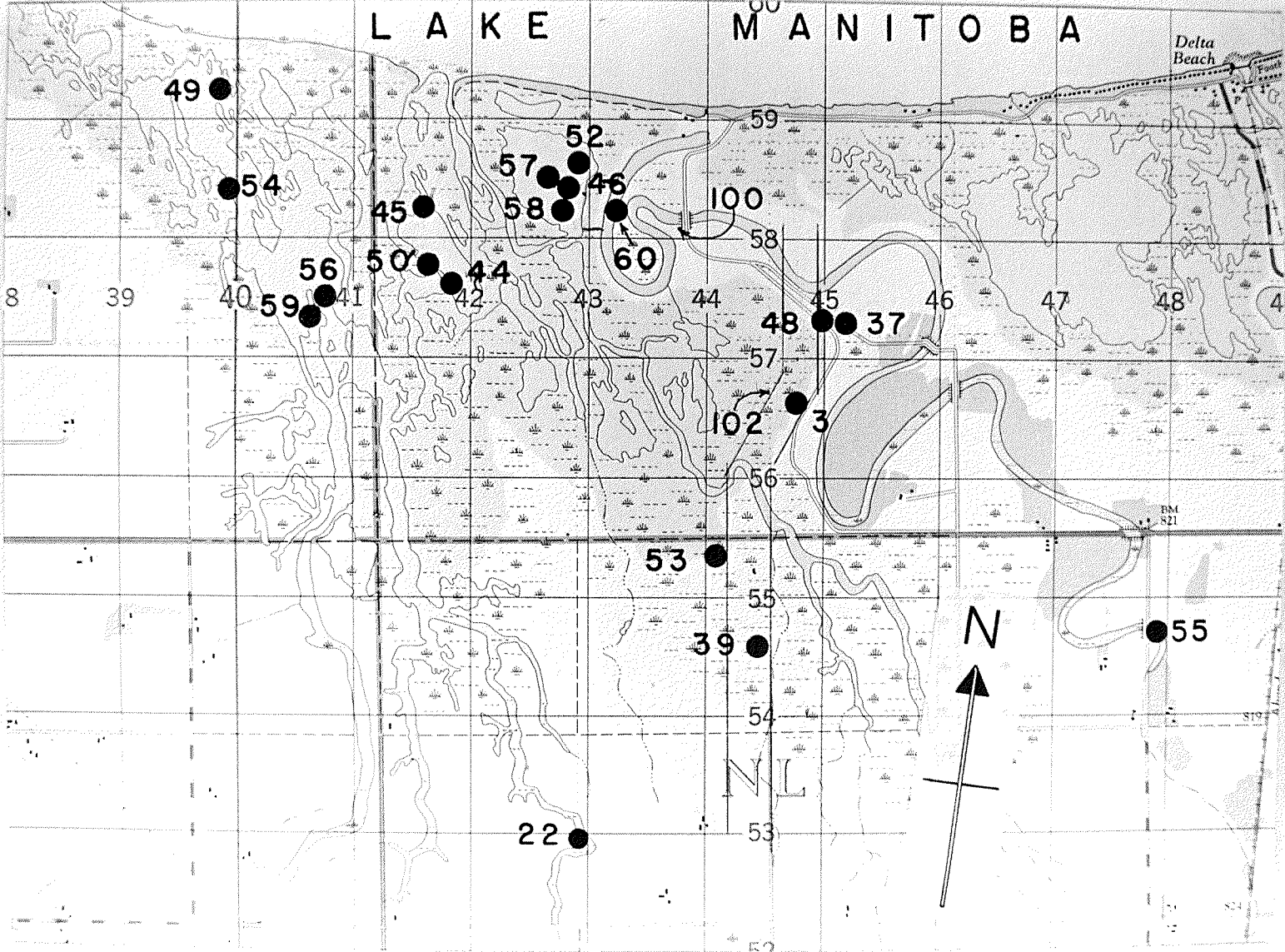
Figure 14: Location of sites in Delta study area,
            central portion. Taken from National
            Topographic System, MacDonald map sheet
            62 J/1E, Edition 1. See Appendix I for
            nearest 100 m grid reference point for
            each site. Map scale 1:50,000.

Cadham
Bay

Simpson
Bay

Bay

0   51   52   53   54   55   56   57   5

PORTAGE

CREEK

●28

●20

N

●32

PORTAGE

33
●

●30

103

825

825

CREEK

●22

101
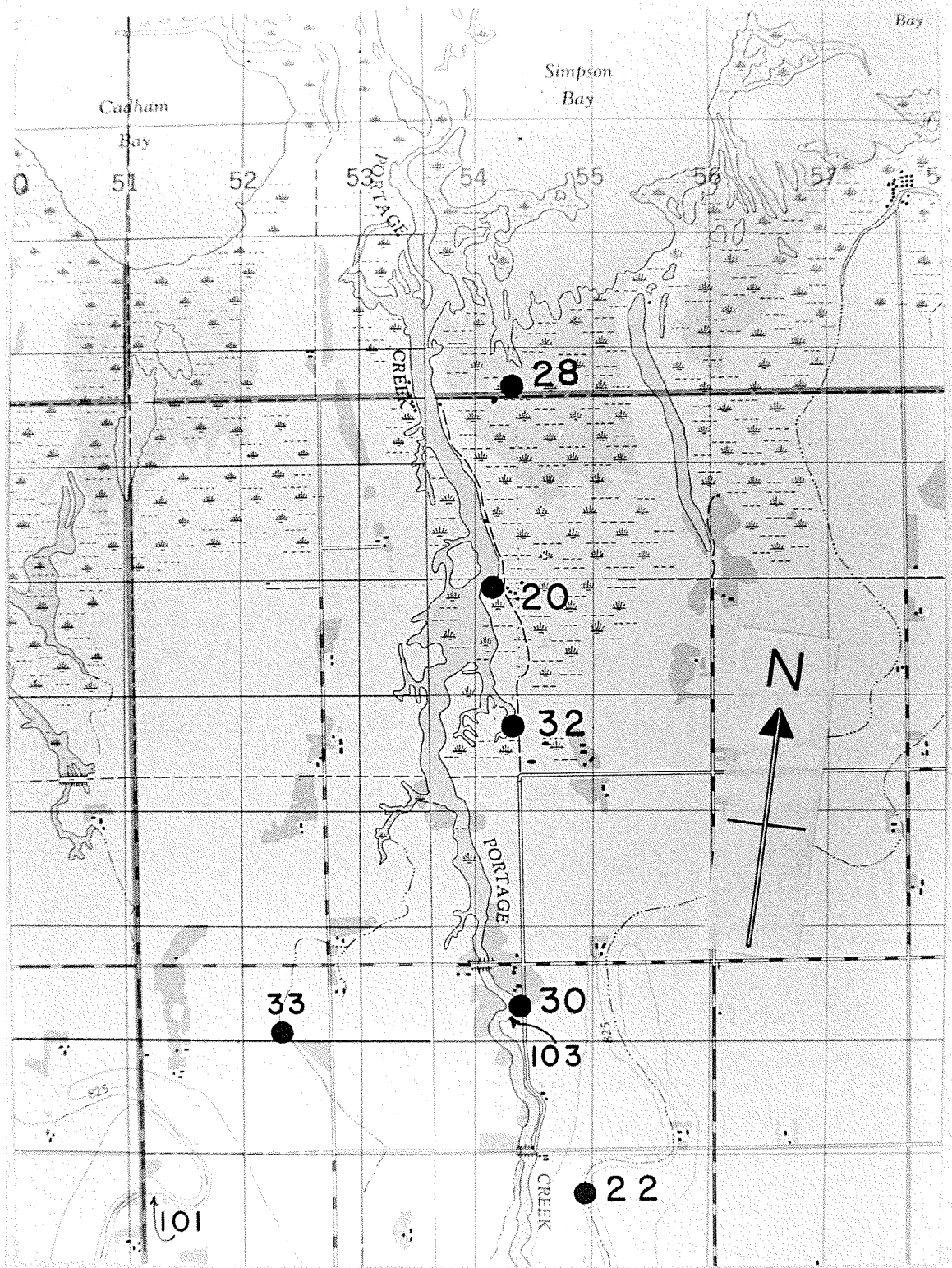
Figure 15: Location of Site 51 in eastern portion
            of Delta study area. Taken from
            National Topographic System, MacDonald
            map sheet 62 J/1E, Edition 2. See
            Appendix I for nearest 100 m grid
            reference point. Map scale 1:50,000.

St Ambroise ½ m

| 64 | 65 | 05′ | R 5 | 67 | 68 | 69 | 70 | R 4 | 71 | 98°00′ |

50°15′

Tp15

66

Clandeboye Bay

Historical Site ⊕

825

65

64

terhen Bay

N

↑

63

C: 825

62

● 5I

St Marks Lake

CI

P· St Marks

828

61

PASTURE

Tp14

60

COMMUNITY

832

59

GOVERNMENT

58

825

834

| 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 10 |

833

57

GOVERNMENT

COMMUN
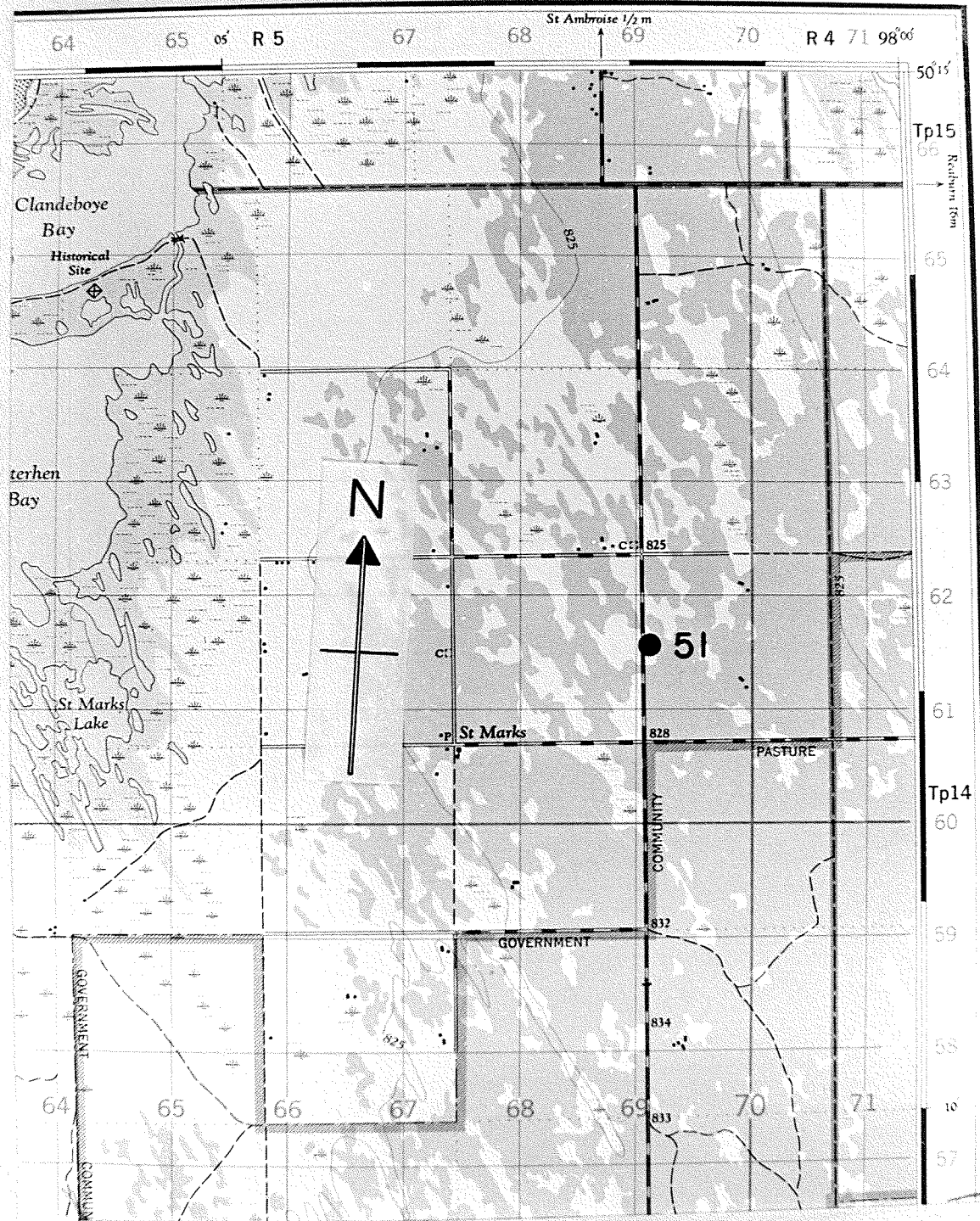
Figure 16:   Site 46, *S. acutus* growing in
              water from 30 to 50 cm deep.
              Male yellowheaded blackbird
              (*Xanthocephalus xanthocephalus*)
              in centre of photograph
              (July 5, 1971).

Figure 17:   Site 30, *S. validus* along stagnant
              creek. The area in the foreground
              has been heavily grazed by cattle
              (July 26, 1971).

(e) Netley

Sites 4, 7, 8, 12, 17, 19, and 40 are located in the
Netley Marsh (Figure 18). The marsh has formed at the mouth of
the Red River, where numerous channels and bays have developed
and are separated only by the levees created by the channels.
The marsh is connected with Lake Winnipeg, consequently the water
levels of the marsh fluctuate with lake levels. Since 1966, the
level of Lake Winnipeg has been continuously above the to year
mean by as much as 1 m. This high water has been compounded by
the frequent wind tides which raise the water levels an additional
0.3 m or more (Parlour *et. al.*, 1972). These recent years of
high water have eliminated most of the aquatic vegetation; very
few open water areas have any submerged aquatics, and the emergent
vegetation is now restricted to the higher ground of the levees
and around the marsh periphery. The dominant vegetation is the reed,
Phragmites communis, with burreed (*Sparganium* spp.), bulrushes
(*Scirpus* spp.)(Figure 19), sedges (*Carex* spp.), and sprangletop
grass (*Scolochloa festucacea*) being locally abundant. The parent
material is the fine-textured non-calcareous deltaic material de-
posited by the Red River.

Figure 18: Location of sites in the Netley study area,
            immediately south of Lake Winnipeg. Taken
            from National Topographic System, Red River
            Delta map sheet 62 I/7, Edition 2.
            See Appendix I for nearest 100 m grid re-
            ference for each site. Map scale 1:50,000.
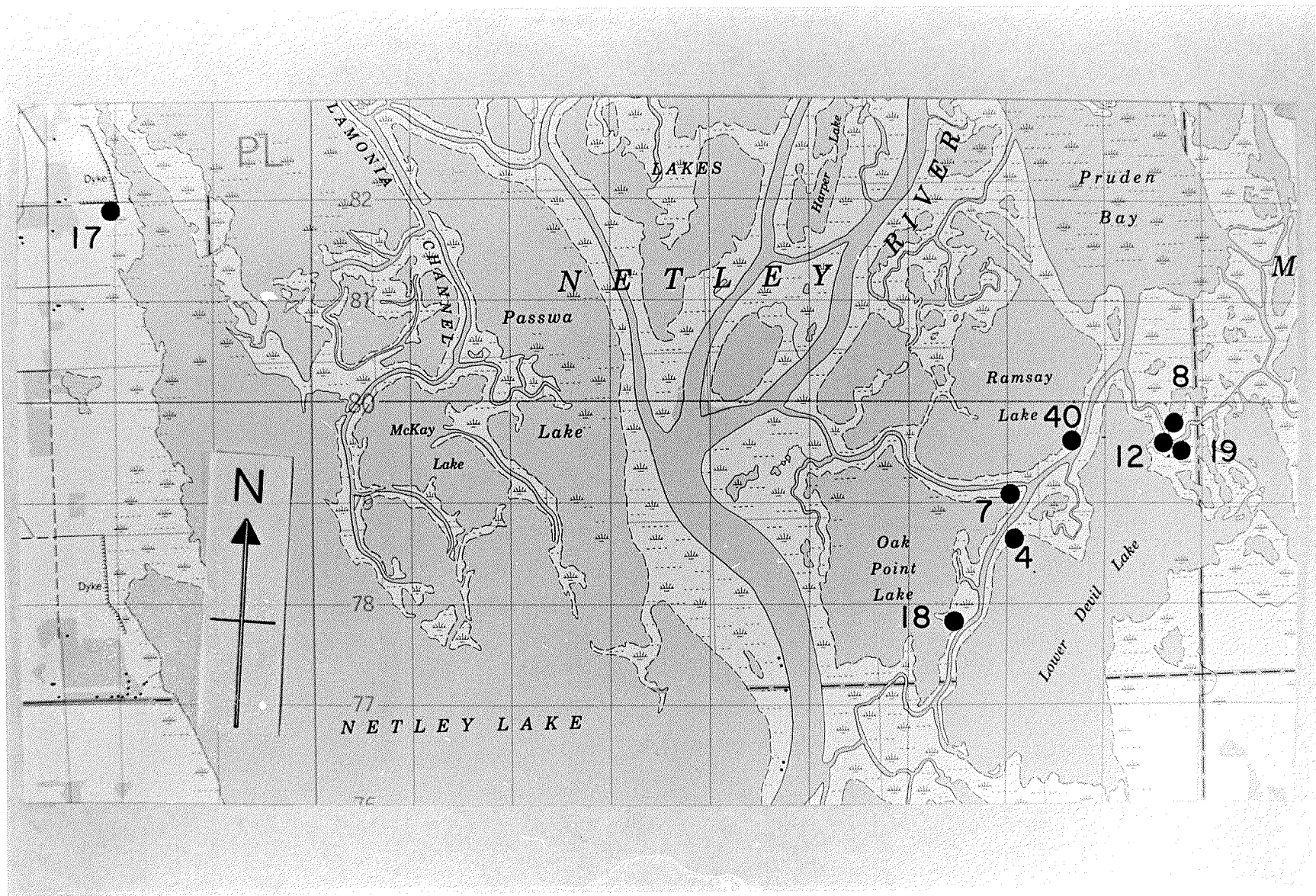
Figure 19: Site 8, *S. validus* growing in water from 30 to 50 cm deep. Note the large number of sterile culms (August 24, 1972).

CHAPTER II

METHODS

A. Site selection

During the summer of 1970, a preliminary survey of sites
was conducted throughout southern Manitoba in order to become fam-
iliar with the general biology and the range of habitats occupied
by *S. acutus* and *S. validus*. Many of the sites visited in 1970
were revisited in 1971 or 1972 for more detailed analysis.

Site selection in 1971 and 1972 was based upon several
arbitrary criteria. To be considered for analysis, a site had to
have a bulrush stand with a minimum size of 5 m by 5 m, visually
dominated by one or both of the taxa under study, and be relatively
free from human disturbance.

In 1971, all sites selected for study were located on or
adjacent to the Delta Marsh. Preliminary site selection was made
from aerial photographs of the area prior to the field season. In
mid-May these sites were visited and the decision for acceptance
or rejection made. Sites were selected so that the greatest di-
versity of environments and morphological types for the region
would be included in the sample. The Delta Marsh was selected be-
cause both *S. acutus* and *S. validus* occur in this area, and also
because the University of Manitoba Field Station (Delta Marsh) pro-
vided convenient living and laboratory facilities.

During 1972, similar procedures for site selection were
followed, except that sites were selected in five major study areas
in southern Manitoba. These study areas were selected because they
represent different combinations of parent material, soils, and
climate, and would therefore reflect divergent habitat types.

B. General biology

1. Growth and reproduction

The patterns of growth and flowering of *S. acutus* and *S. validus* at Delta were monitored in the summer of 1971. Delta was chosen because both forms occur there, thus eliminating any effect of different environmental and climatic conditions. The sites are referred to as sites 100 (*S. acutus*) and 101 (*S. validus*) and are located on Figures 13 and 14. Two 1m by 1m quadrats were established at each site in early spring, and as the new culms appeared in these quadrats, they were individually marked with a ring of plastic embossing tape (Figure 20). Culm heights were measured and floral development noted at three-day intervals.

In 1972, comparisons of net annual production of aerial shoots of *S. acutus* and *S. validus* were obtained from 12 sites in conjunction with the vegetation analysis described below. Five 1m by 1m quadrats were spaced equidistant along the main vegetation transect. The culms were individually cut below the mud surface as close to the rhizome as possible. The basal sheaths and the culms were washed to remove any extraneous material. The shoots were then bagged, dried at $95^{o}C$ for 48 h and weighed. All samples were obtained in the period from August 1 to 11.

The above-ground and below-ground components of the total plant biomass were measured at sites 102 and 103 (see Figures 13 and 14), where ten 0.5 m by 0.5m plots of aerial shoots were

clipped, bagged, and oven-dried at $105^{\circ}C$ for 48 hours before weighing. From the centre of each plot a core 13 cm in diameter and 50 cm deep (Figure 21) was removed intact and transported back to the laboratory for analysis. A five-compartment "washing table" with 2 mm mesh screen on the bottom of each compartment was used to hold the cores while a jet of water 2.5 cm in diameter washed the soil through the screen, leaving the roots and rhizomes intact. Living roots and rhizomes were removed and dried at $105^{\circ}C$ for 48 hours and weighed. Living roots were detected by the presence of an apical meristem and an intact cortex. Living rhizomes were verified by the presence of live buds, white cortex tissue which tested positive for starch with iodine and the absence of black surface discoloration, which was attributed to hydrogen sulfide in the mud.

The sexual phase of reproduction of *S. acutus* and *S. validus*, particularly the aspect of achene germination, is difficult to study under field conditions. There are relatively few instances of germination encountered during a study of this type, and even when found, it is impossible to determine the pre-germination environmental conditions to which the achenes were exposed. The most satisfactory method of studying germination in such circumstances is to artificially subject achenes to the types of environmental conditions to which they would likely be exposed naturally.

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Figure 20: A loop of plastic embossing tape was
used for individual culm markers.
The ends of the loop were stapled
together.

Figure 21: Root cores 50 cm long and 13 cm in
diameter were extracted for deter-
mination of below-ground biomass.

2. Germination tests

Fifteen experiments were designed to determine the field requirements for germination of *S. acutus* and *S. validus* achenes. Achenes collected in late September of 1970 from sites 100 and 101 were subjected to combinations of several storage and germination conditions, and in six tests specific treatments were applied to the achenes (Table I). In test 2, the embryos were excised by removing one half of the seed coat and extracting the intact embryos and as much of the endosperm as possible. They were placed in a vial of standard nutrient culture solution (Arnon and Hoagland, 1940). The achenes of test 3 were immersed in concentrated sulfuric acid for approximately ten minutes, then removed and rinsed in distilled water. In test 4, achenes were fed to two captive female mallard ducks which had not been fed for eight hours previously. The achenes were floated on the surface of the drinking water, from which they were readily ingested by the ducks. Feces were collected six hours later and the achenes separated from the fecal material in a 250-mesh sieve. Both birds were fed the achenes of *S. validus*, and six days later given those of *S. acutus*. The scarification of the achenes in test 9 was done with a scalpel by 'notching' the seed coat progressively deeper until it was pierced.

TABLE I . STORAGE, TREATMENT, AND GERMINATION CONDITIONS FOR 15
GERMINATION TESTS OF S. ACUTUS AND S. VALIDUS ACHENES

Test No.	Storage Conditions				Treatment	Germination Conditions		
	Time (days)	Temperature (^{o}C)	Light (hours)	Medium		Temperature (^{o}C)	Light (hours)	Medium
1		no storage			none	20	12	moist filter paper
2		no storage			embryo excision	20	12	standard 'R' solution
3		no storage			sulfuric acid	20	12	distilled water
4		no storage			fed to ducks	20	12	distilled water
5	30	5	0	peat moss	none	20	12	peat moss
6	30	5	0	silica sand	none	20	12	silica sand
7	30	5	0	humus	none	20	12	humus
8	150	5	0	stored dry	none	20	12	moist filter paper
9	150	5	0	stored dry	scarification	20	12	distilled water
10	150	5	0	distilled water	none	20	12	distilled water
11	150	5	0	wet mud	none	20	12	wet mud
12	120	5	0	distilled water	frozen 30 days	20	12	distilled water
13	120	5	0	wet mud	frozen 30 days	20	12	wet mud
14	150	20	12	distilled water	none	20	12	distilled water
15	150	20	0	distilled water	none	20	12	distilled water

3. Stand performance

During the initial visit to each site in spring, a base-
line transect was established along the water depth gradient, be-
ginning in the shallow portion of the stand and terminating at the
deep water edge. Five perpendicular side transects were marked
with wooden stakes at equal intervals along the main transect line.

On a second visit during the August to mid-September period,
when each site was revisited for vegetation analysis, five 0.5 m
by 0.5 m plots were selected at 1 m intervals along each of the
five side transects. Density and fertility were recorded for each
plot. Fertility was defined as the proportion of total culms which
bore inflorescences with apparently normal achenes. The product
of culm density and per cent fertility was used as an index of
stand performance. This is an attempt to combine the parameters
of vitality (reproductive success) and vigor (relative size and
health, without reference to reproductive success) as defined by
Daubenmire (1968).

4. Community relationships

Both plants and animals are a part of the environment of
any organism; therefore, even an autecological study should be
done with the perspective of the whole community in mind. In order
to put the data obtained on growth and environmental response of
these bulrushes into a community context, the associated plant and
animal species were recorded at each site. A list of associated
plant species was compiled from presence-absence data collected for

each of the vegetation quadrats. Floating aquatics such as the

duckweeds (*Lemna* spp.) were not recorded. Interaction of animals

with bulrushes (e.g. nesting and feeding) were recorded whenever

encountered; no specific searching methods (e.g. to locate duck

nests in bulrush stands) were employed

C. Taxonomic assessment

   1. The rationale for methods of character selection and
      taxonomic assessment

         Throughout this study the existence of the taxa *S. acutus*

and *S. validus* was recognized. The extreme forms present entirely

distinct facies which superficially become a continuous range of

variation when less 'typical' specimens are considered. Figure 22

portrays the gradation of inflorescence form encountered in the

examination of herbarium specimens[1] and the author's field collections.

         The taxonomic problem in this study was to determine the

degree of morphological distinction between these two taxa. The

confusion over diagnostic characters in the literature led the

author to conclude that no single character was of diagnostic value.

The hypothesis resulting from these observations has been clearly

stated by Heslop-Harrison (1952, p. 77):

> "The basic postulate is simply that two populations
> may show intergradation in every character considered
> separately, but that complete discrimination of the two
> (including the potentiality of referring any small sample
> or even individuals to one or the other) should be pos-
> sible if a combination of enough reasonably independent
> measurements can be taken into account."

         Heslop-Harrison was referring to the various techniques of

discriminant analysis, including discriminant function analysis

and the hybrid index of Anderson (1936), which have been employed

to solve the type of problem encountered here (see Riley, 1938).

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[1] See Appendix IV for a list of herbarium specimens examined.

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Figure 22:   The range of inflorescence types between
             S. acutus (extreme left) and *S. validus*
             (extreme right) indicates the gradation
             from one morphological type to the other.

a   b   c   d   e   f
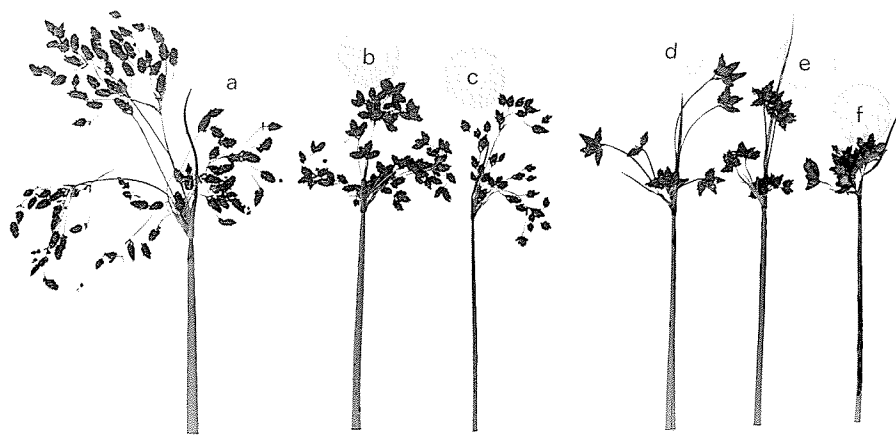
The criticism of all these techniques is that they assume an ability to distinguish the groups involved (Heslop-Harrison, *op. cit.*, p. 77; Cattell, 1965, p. 414), and secondly, the characters are chosen *a priori* from these subjectively-defined groups. These criticisms also apply to all previous studies of *S. acutus* and *S. validus*.

The possibility of hybridization between *S. validus* and *S. acutus* (Smith, 1969 and Dabbs, 1971) and the success of the hybrid index technique (see Riley, *op. cit.* and Davis and Heywood, 1963, p. 479) in such cases suggested this technique as a logical means of portraying the variation between *S. acutus* and *S. validus*. Even if hybridization is not responsible for the variation, the method is still valid, although Davis and Heywood (*op. cit.*, p. 325) suggest the name "biometric index" in such instances. The former name is retained, here, however, in view of the possibility of hybridization.

The hybrid index technique involves scoring specimens (0, 1, or 2) for a number of characters, the score indicating whether the specimen shows the extreme expressions of the character (0 or 2) or an intermediate state (1). The sum of the scores represents the hybrid index of the specimen. The mean index value can be applied to the sample from a stand, but intermediate mean values must be clearly distinguished as being of hybrid origin and therefore morphologically intermediate, or due to a mixture of two morphological types; in either case, the result is an intermediate value (Davis and Heywood, *op. cit.*, p. 479).

The hybrid index technique has been used in the analysis of *S. acutus* and *S. validus* populations (Smith, 1969; Dabbs, 1971), but the characters used in its construction were in both cases chosen subjectively. For objective selection of characters, a technique was required which could isolate those characters responsible for the variation within a number of samples of *S. acutus* and *S. validus*. A basic requirement of the desired technique is that no assumption be made that the groups can be distinguished. Factor analysis meets these requirements (Cattell, *op. cit.*, p. 412). The technique has as its purpose the definition of "factors", composed of one or more variables (morphological characters in this case), which account for the variability in a set of data. Factors and their associated variables are extracted in descending order of their importance in accounting for the observed variability. The involvement of two or more variables in one factor indicates covariation of these variables.

Theoretically such a factor analysis of morphological data should provide a number of characters useful in diagnosing the variation within a sample. The question arises of how many characters should be used in the construction of the hybrid index. As Davis and Heywood (*op. cit.*, p. 110) indicate, the possible choice of characters is limited only by practical considerations. Ideally, every attribute of an organism should be measured, but this is impossible. The problem then is to maximize effort by considering those characters most important in the variability of

the sample. Sneath (1948) suggests that a minimum number of five

characters is usually required by mathematical techniques, although

a much greater number proves more satisfactory. On the choice of

characters, Heslop-Harrison (*op. cit.*) suggests that the charact-

ers be obtained from as wide a range of plant organs as possible.

On the basis of this reasoning, a number of morphological

measurements were obtained and analyzed by factor analysis tech-

niques. From this analysis the most important characters (a mini-

mum of five) would be used in the hybrid index assessment of mor-

phological affinity between *S. acutus* and *S. validus*.

2. Morphological analysis

Specimens for taxonomic assessment were collected from

each stand in conjunction with the vegetation analysis. Twenty-

five mature specimens were collected, one from each of the vegeta-

tion plots. Inflorescences were placed in plant presses with the

longest ray extended to facilitate subsequent measuring. All

material was dried in an herbarium drier for 48 hours at 65°C.

The following morphological features were evaluated for

each specimen and served as the basis for the morphological char-

acters selected for analysis:

    1. inflorescence length: distance from the base of
                                                the involucral bract to the
                                              tip of the most distal
                                              spikelet.

    2. involucral bract length: distance from base of bract
                                                  to intact tip.

3. ray development: number of primary, secondary, tertiary, and quaternary rays in the inflorescence.

4. spikelet clustering: number of spikelets borne singly, in groups of two to 12, and more than 12.

5. spikelet length: maximum length from bases of lowermost scale to tip of most distal projection including projecting awn.

6. spikelet width: maximum width of spikelet regardless of position, perpendicular to the long axis.

7. scale length: distance from basal portion of midrib to most distal portion of scale excluding awn.

8. scale width: maximum width of scale, regardless of position, perpendicular to long axis.

9. awn length: straight-line distance from base where midrib becomes excurrent to intact tip.

10. achene length: distance from base of achene to base of the "beak".

11. achene width: maximum width, regardless of position, perpendicular to long axis.

12. lacunar diameter: This character was measured in the field, since it would be subject to change when pressed. The culm diameter measured midway from the base to the tip is divided by the number of aerenchymal lacunae in cross section. Often the culms are strongly oval in cross section, necessitating two diameter measurements, maximum and minimum.

13. culm color: arbitrarily scored in the
                               field as 1, 2, or 3 as
                               follows:

                               1 - Munsell[1] colors 10 GY5/4,
                                   10.0 GY5/6, 2.5 G5/6

                               2 - 7.5 GY5/6, 10.0 GY4/6

                               3 - 5.0 GY4/4, 5.0 GY4/6,
                                   7.5 GY3/4, 7.5 GY4/4,
                                   7.5 GY4/6, 10.0 GY4/4

All linear dimensions, with the exception of inflorescence

and bract lengths, were measured using apparatus modified from

Anderson (1968) (Figure 23). This consisted of a movable mechani-

cal microscope stage (Olympus Model 206769) mounted on a plexi-

glas base. A metal extension arm was attached to the movable

portion of the stage and modified to incorporate a dial indicator

(Mitutoyo, Model 2050) graduated in 0.01 mm. Material for

measurement was placed on a plexiglas 'slide' with a modified

inset centrepiece which could be turned 360°. Measurements were

recorded on a line-operated taperecorder (Sony, Model TC 222)

with a foot-controlled record switch, and later transferred to

data sheets.

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[1] Munsell Book of Colors, 1967 (12 ed.) Munsell Color Co.,
Baltimore, Md.

Figure 23: The apparatus used for linear morphological measure-
ments. The movable microscope stage is mounted on a
plexiglas base. Movement of the 'slide' backward
or forward moves the dial indicator, which is gradu-
ated in 0.01 mm. (Modified from Anderson, 1968)
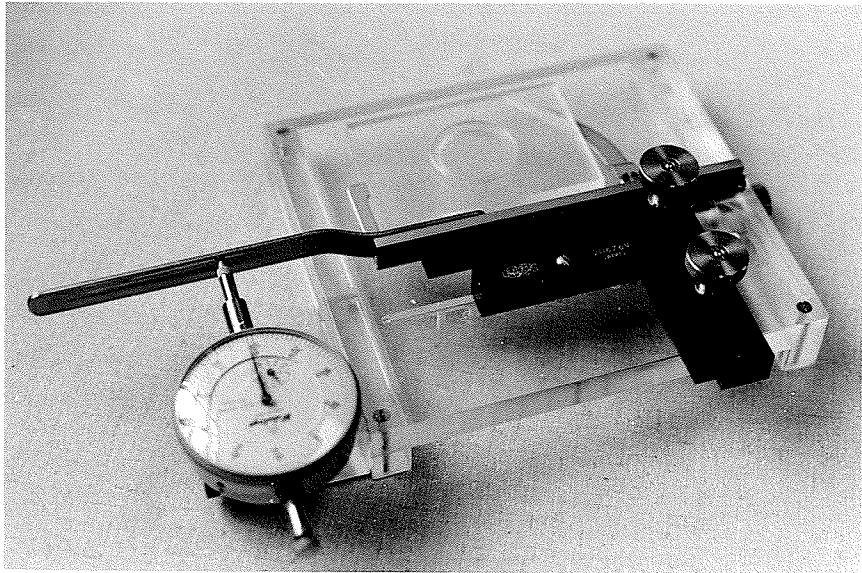
3. <u>Mathematical treatment</u>

Thirteen characters were used in the analysis: inflorescence length; bract length; spikelet length; spikelet width; floral scale length; floral scale width; awn length; achene length; achene width; number of spikelet clusters with two or less spikelets; number of spikelet clusters with five or more spikelets; number of primary rays; total number of secondary, tertiary, and quaternary rays. Lacunar diameter and culm color were not included because they were not always referrable to the specimen from which the other 13 characters were measured. A factor analysis program was used to assess the relative contribution of each of the previously-mentioned characters to the total variability in the sample of 60 stands. The program was written in Fortan IV for the University of Manitoba IBM 360/65 computer.[1] In order to meet the requirement of the factor analysis procedure for constant variance (Cattell, 1965) a log transformation was made on linear measurements, and a square root transformation was performed on 'count data' (number of primary ray, for example), as recommended by Bartlett (1947) and Snedecor (1956) respectively. Those characters with high loadings on the resulting factors were retained for possible use in the construction of the hybrid index.

This technique involves scoring specimens on an arbitrary

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[1] See University of Manitoba Computer Centre's *Programmer's Guide (Part B): Statistical Package*, Program 20.

scale of values for a number of characters; the extreme values of

the scale represent the expressions of the character typical of

the two species. The scores for each specimen on each character

are summed to give the index value. The mean index value for a

number of specimens from the same stand is then used to represent

the hybrid index for that stand. A three-state coding system of

0, 1, and 2 was used to correspond to the 'validus-like' expres-

sion of the character (0), intermediate (1), and the 'acutus-like'

state (2).

Quantitative characters in this technique, where possible,

should show no overlap between the two species (Riley, 1938). In

order to determine which of the characters selected from the factor

analysis were discontinuous in their distribution between the

'acutus' and 'validus' states, histograms were plotted of 1,500

observations on each character. Those which displayed a unimodal

distribution were discarded, while those showing a bimodal dis-

tribution were retained. For those characters retained, the char-

acter state to be associated with each of the index scores was

assigned using the technique of Riley (*op. cit.*). The frequency

distribution of inflorescence lengths is used in Figure 24 as an

example of how the character states of the quantitative characters

were defined.

The point of discontinuity (A in Figure 24) was considered

to be the centre of the area of overlap between the two character

states. The mean ($\bar{x}_1$ and $\bar{x}_2$) and standard deviation (sd_1 and sd_2)

were computed for each of the 'states' so defined. The range of

values to be associated with the intermediate score was then de-fined as extending from sd_1 to sd_2. The extreme scores were then assigned to the ranges lying to the left of sd_1 and to the right of sd_2.

Figure 24: Frequency histogram of 1,500 inflorescence lengths from sites 1 to 60 illustrating the method of determining the three character states ('0', '1', and '2'). The means ($\overline{x}_1$ and $\overline{x}_2$) and standard deviation (sd_1 and sd_2) for the two distributions separated at 'A' as indicated.
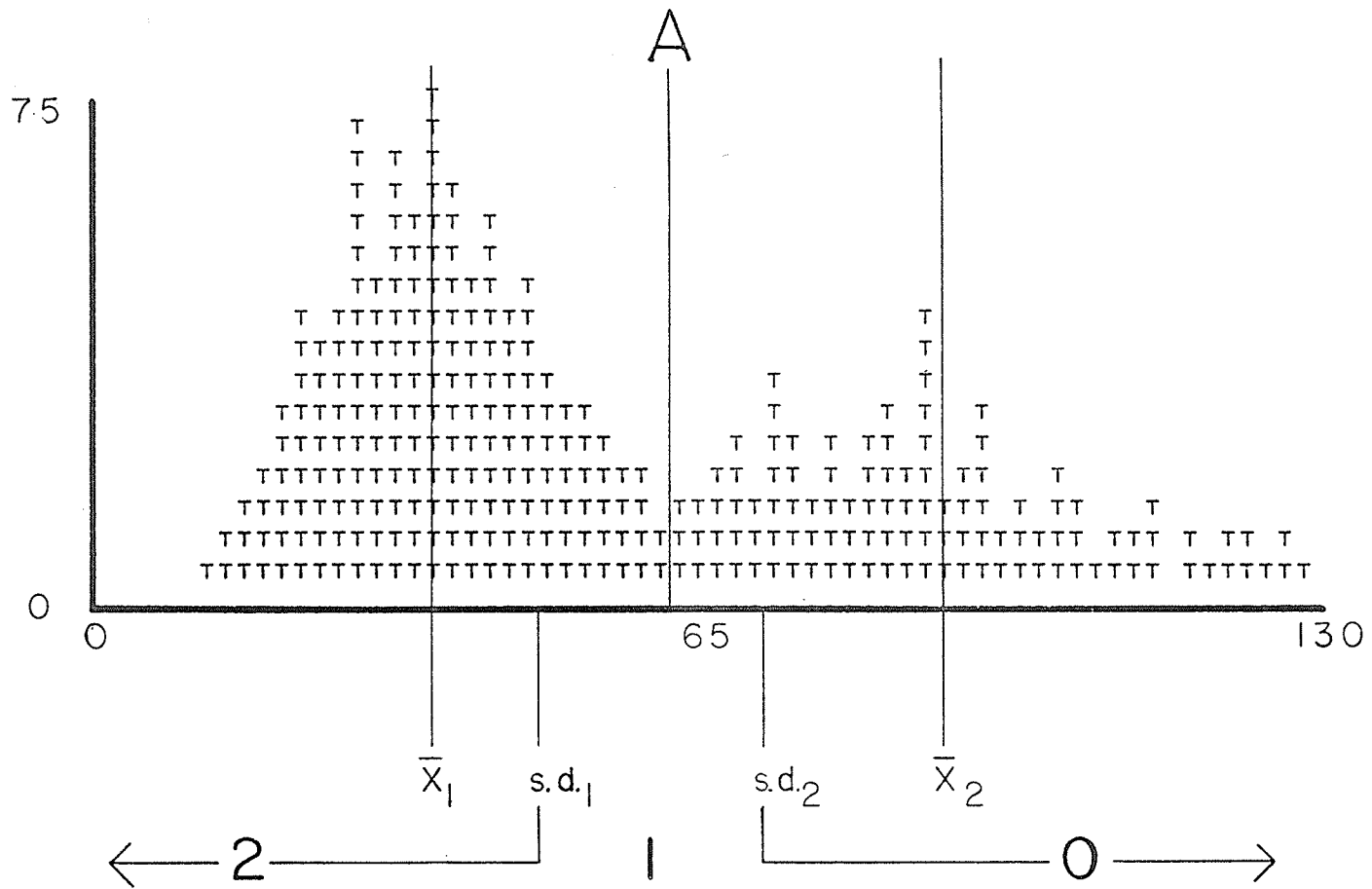
D. Environmental parameters

1. Substrate texture

Samples of the rooting medium were collected when the transects were established. One sample was collected from each of the five points of intersection of baseline and side transect. The sample was obtained by removing a soil core 30 cm deep with a narrow-bladed spade. A tangential slice of the core, sufficiently wide to give approximately 500 g air-dried sediment, was removed with a knife, bagged and oven-dried for 48 hours at 105°C. After drying, each sample was ground with a mortar and pestle, care being taken to avoid breaking pebbles.

Particle size distribution of each sample was determined using the "pipette method" of Killmer and Alexander (1949) with modifications.

Modified Pipette Method

Two subsamples of approximately 10 g each were taken from each sample, placed in labelled 250 ml beakers and sufficient distilled water added to make a thin paste. Organic material was digested with 30% hydrogen peroxide. Five milliliters of 30 per cent hydrogen peroxide were added and the mixture stirred. The samples were placed on a hot plate and heated gently until an effervescing reaction occurred. They were then removed from the hot plate and allowed to stand until the reaction subsided. More hydrogen peroxide was added and the procedure repeated until no reaction occurred. Excess hydrogen peroxide was driven off by

heating.

Ten milliliters of sodium hexametaphosphate solution[1] were added to the samples and the volume of the mixture brought to 200 ml by adding distilled water. The beakers were placed on a magnetic stirrer for ten minutes, removed and allowed to settle for five minutes. The supernatant was poured through a 250-mesh sieve into a 1,000 ml graduated cylinder. The sediment remaining in the beaker was repeatedly washed with a jet of distilled water and the supernatant poured through the sieve until clear. The particles remaining on the sieve were washed back into the beaker, dried at $105^{o}C$ for eight hours, and weighed.

The volume of the suspension in the graduated cylinder was made up to 1,000 ml with distilled water. The soil was then mixed in the cylinder by vigorous stirring with a plunger. Forty seconds after stirring a 25 ml sample was withdrawn with a transfer pipette from a depth of 10 cm. This was placed in a clean, pre-weighed 50 ml beaker and dried at $105^{o}C$ for 12 hours. The beaker was removed from the oven and allowed to cool to room temperature in a dessicator, weighed and the weight of sediment calculated. A second sample was withdrawn at 7 hours, 4 minutes, dried and weighed as above.

The 250-mesh sieve retained all particles of 62μ or greater, while the sample taken at 40 seconds (t_1) included all particles less than 50μ. The final reading at 7 hours, 4 minutes

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[1] 35.7 gm Calgon/liter distilled water.

(t_2) included all particles less than 2μ. Particle size distribution was calculated as follows:

1. weight of sand =

2. weight of silt + clay + Calgon in 25 ml (t_1) =

3. weight of clay + Calgon in 25 ml (t_2) =

4. weight of Calgon in 25 ml = 35.7 x 0.01 x 0.025 = 0.0089 g

5. weight of clay in 25 ml = (3) - (4)

6. weight of silt in 25 ml = (2) - (3)

7. weight of silt in 1,000 ml = (6) x 1,000 ÷ 25

8. weight of clay in 1,000 ml = (5) x 1,000 ÷ 25

9. total weight of soil = (1) + (7) + (8)

10. % sand = (1) ÷ (9) x 100%

11. % silt = (6) ÷ (9) x 100%

12. % clay = (8) ÷ (9) x 100%

2. Water depth and water level fluctuations

Water depth measurements were recorded in the centre of each of the vegetation analysis plots using a meter stick resting vertically on the mud surface. The mean water depth of a stand calculated from these measurements would represent the mean depth at the end of the growing season.

Continuous records of water level changes throughout the summer were obtained for 17 sites, eight in 1971 and nine in 1972. Leupold and Stevens Type F water level recorders equipped with two-week chart drives and battery-operated clocks were located at sites

Figure 25: Water level recorder at site 29. The
float and weight which operate the chart
drum are hidden from view. The stilling
well housing the float can be seen at
the base of the stand.

which would provide the range in water level fluctuation in the
five study areas (sites 2, 3, 14, 19, 21, 22, 25, 29, 32-34, 49,
50, 52, 55, and 60). Stilling wells were installed with each re-
corder in order to dampen the oscillation due to wave and wind
action (Figure 25). The distance between sites and the neces-
sity of servicing the recorders twice monthly made continuous
water level recording for all sites impossible.

3. Water chemistry

Alkalinity, pH, and total dissolved solids are commonly
used parameters for examining surface waters (Moyle, 1956; Stewart
and Kantrud, 1969); these aspects of the water chemistry were
chosen to provide the general information on water quality. The
predominance of calcite ($CaCO_3$), dolomite ($CaMg(CO_3)_2$) and gypsum
($CaSO_4$) in some Manitoba soils suggested that calcium, magnesium
and sulfate ions should also be included in the analysis.

The following water chemistry parameters therefore were
examined:

    1. alkalinity

    2. pH

    3. total dissolved solids

    4. calcium ion concentration

    5. magnesium ion concentration

    6. sulfate ion concentration

Alkalinity, calcium, magnesium, pH, and sulphate determina-
tions were made using the Hach water analysis kit (Model DR-EL).

Standard curves were produced to check the accuracy of the equipment against known standards. The total dissolved solids were determined using a Barnstead Model PM-70CB portable conductivity bridge; it was checked periodically against a Radiometer Model CDM2 line-operater conductivity meter to ensure battery performance.

Water samples were collected in 500 ml polyethylene bottles from the deep-water margin of each stand after completing the vegetation analysis and placed on ice until ready for analysis. All analyses were conducted within six hours of the time of collection, samples being allowed to return to 15°C beforehand.

Glassware used in the analyses was soaked approximately 12 hours in "Contrad 70', a surfactant manufactured by Harleco, then rinsed in three washes of distilled water. A small trailer was used as a field laboratory.

4. Nutrient culture experiment

The analysis of water chemistry parameters as described above would not allow the investigator to isolate the effects on growth of single ions. In order to examine the effect of different concentrations of a single ion with all other parameters controlled, overwintering rhizomes of *S. acutus* and *S. validus* were grown in nutrient culture solutions. The effects of different concentrations of calcium, magnesium, and sulfate ions on the growth of the rhizomes and culms were measured. A modified standard 'R' solution (Arnon and Hoagland, 1940) was used both as the stock solution and a control. Concentrations of calcium and

magnesium were produced by the addition of their chloride salts; sodium sulfate was used to increase the level of sulfate ions.

The concentrations of calcium and magnesium in the stock solution were within the observed tolerance range of both *S. acutus* and *S. validus* under field conditions. Sulfate, however, was higher than observed under natural conditions, therefore magnesium chloride was substituted for magnesium sulfate in the stock solution. This resulted in the same concentration of magnesium, but raised the chloride concentration by 130 ppm. Final concentrations in the stock and fortified solutions are given in Table II.

TABLE II. CONCENTRATION OF CALCIUM, MAGNESIUM, AND SULFATE IONS IN THE CONTROL (STOCK) AND EXPERIMENTAL (FORTIFIED) NUTRIENT SOLUTIONS (ppm)

	Nutrient Solution Ion Concentrations (ppm)			
	Control	Experimental		
		1	2	3
calcium	234	228	400	600
magnesium	60	200	400	800
sulfate	18	100	300	900

Overwintering rhizomes were removed from sites 100 and 101 in 0.25 m^2 soil blocks in mid-January. The blocks were allowed to warm slowly to room temperature before carefully washing all soil away from the roots and rhizomes. Excessively long rhizomes were

cut to lengths of 30 cm.

Twenty-two styrofoam boxes (40 by 40 by 25 cm deep) were
filled to a depth of 10 cm with acid-washed, autoclaved silica
sand. Eleven were planted with five rhizomes each of *S. validus*
and the remaining eleven with *S. acutus* rhizomes. Attempts were
made to have an equal number of overwintering buds in each con-
tainer. An additional 5 cm of sand was then poured over the
rhizomes to cover them. Pairs of the containers, one containing
each type, were filled to 10 cm above the sand surface with the
nutrient solutions of varying ion concentrations. Growing con-
ditions were held constant at a light intensity of 8500 foot-
candles, photoperiod of 16h light, and temperature of $20^{\circ}C$. The
containers were drained and flushed with distilled water weekly to
prevent accumulation of salts. In addition to the control using
the standard stock solution, a control with distilled water and
silica sand and one with distilled water and marsh mud were used.

As culms developed, they were individually labelled and
the heights recorded daily from February 19 to April 26, 1971.
On April 26, rhizomes and culms were removed, the increase in
rhizome length noted, then the entire plant oven-dried and weighed.

CHAPTER III

RESULTS
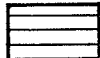
A. General Biology

1. Distribution in Southern Manitoba

 S. acutus and *S. validus* show different distribution pattern
in southern Manitoba despite their widespread sympatric distributions
throughout central North America. Figure 26 represents this distri-
bution based on collections made in this study as well as on herbar-
ium collections from the Botany Department, University of Manitoba
and the National Museum in Ottawa. *S. acutus* is widely distributed
throughout southern Manitoba on limestone, non-calcareous lacustrine,
and granitic surficial deposits. *S. validus*, however, is absent from
the calcareous till of the Manitoba Lowland, and tends to be re-
stricted to the less calcareous lacustrine and granitic deposits.
Four apparent exceptions occur, one on the northwest side of Lake
Winnipeg, two in Riding Mountain Park north of Minnedosa and one in
southwestern Manitoba (approximately 49°N 100°W). All four are her-
barium specimens and not records of the author. In view of the
heterogeneous geological formations in the latter three areas, with
shale and granitic rock being prominent, local edaphic factors may
be suitable for *S. validus*. The collection from the northwest
side of Lake Winnipeg may be associated with fluvial deposits at the
mouth of the Saskatchewan River. With the exception of these four
sites, which the author has not visited, no records of occurrence of
S. validus on highly calcareous soils have been obtained.

 The absence of *S. validus* from the region of kettle lakes
south of Minnedosa illustrates this restricted distribution. The
knob and kettle topography of this area results in abundant kettle

Figure 26. Map of southern Manitoba showing locations
of *S. acutus* (triangles) and *S. validus*
(circles) stands in relation to the sur-
ficial deposits of southern Manitoba. Each
triangle or circle represents one or more
stands for that location.

            non-calcareous, lacustrine
            or deltaic

            calcareous

            granitic (Precambrian Shield)
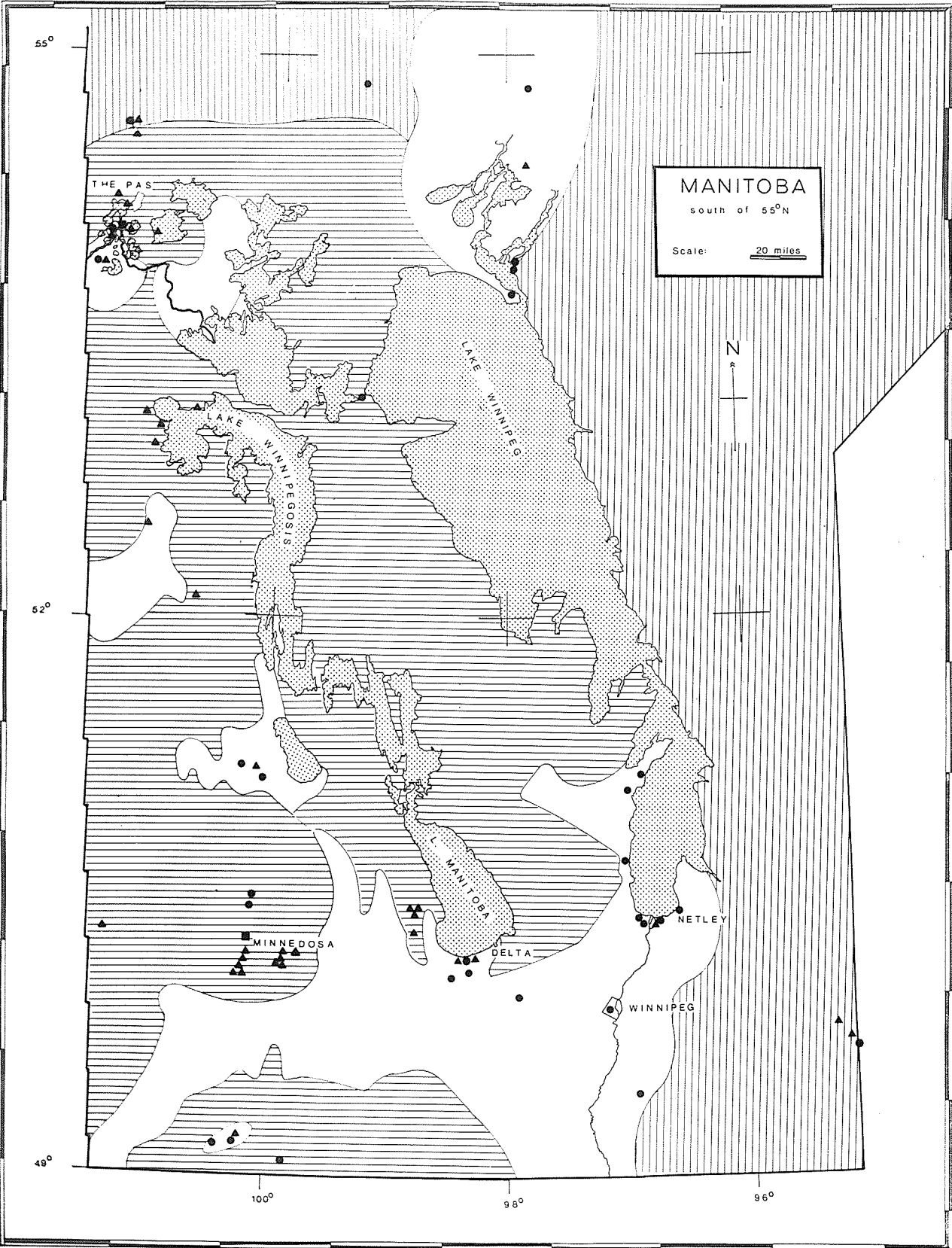
MANITOBA
south of 55°N

Scale: 20 miles

N

THE PAS

LAKE WINNIPEG

LAKE WINNIPEGOSIS

L. MANITOBA

MINNEDOSA

DELTA

NETLEY

WINNIPEG

55°

52°

49°

100°

98°

96°

lakes or 'potholes' of varying degrees of permanence. In 1972, an

attempt was made to locate five sites each of *S. acutus* and *S.*

validus in this area in order to obtain comparative data on habitat

requirements and response to the environment. Of 226 potholes ex-

amined, 120 had prominent emergent zones of *Scirpus*, and all were

typical *S. acutus*. Three small *S. validus* stands have been found

in this area, none exceeding 6 m^2 in extent. One of these, found

in 1970, was revisited in 1972, but only dead culms of the previous

year were found, and in June, 1973, there were no remnants of the

stand. A second stand growing in a shallow depression adjacent to a

'pothole' in 1972 had produced 40 culms which were scattered among

S. paludosus, *Typha* sp. and *Scolochloa festucacea*. These culms

persisted in 1973, but in reduced numbers. The third site consisted

of several small clones of short culms (30 to 50 cm) with reduced

or undeveloped inflorescences. This site was revisited in 1973 and

most of the clones had disappeared; those which persisted were

growing with *Juncus balticus, Ranunculus cymbalaria, Eleocharis*

acicularis, and *Triglochin maritima*, all of which had increased in

numbers. The inability of *S. validus* to become established in this

area, despite abundant seed sources to the east and south, suggests

that there are limiting factors operating to exclude it.

2. Growth and reproduction

A comparative study of annual growth and flowering of

S. acutus (site 100) and *S. validus* (site 101) was undertaken in the

Delta Marsh to determine if there were genetically based differences

in any aspects of annual shoot production. The following description progresses through the life cycle of the plants, beginning with culm initiation from the perennial rhizome, the growth of the annual culms, flowering , fruit maturation, and, to complete the cycle, the pattern of seedling establishment. This is followed by a consideration of some of the factors involved in achene germination as determined in the laboratory. Finally, the biomass resulting from a single year's growth is considered and comparisons are made between *S. acutus* and *S. validus* production.

(a) Growth of the annual culms

Culm initiation begins in May when the overwintering buds begin to elongate and the tips appear above the mud surface. Figure 27 describes the pattern of culm initiation at site 100 (*S. acutus*). During the first three weeks of May, 84% of the year's culms are initiated, although occasional new culms develop until the end of July. The culms produced in late June and July are sterile, the inflorescences failing to develop.

A similar pattern of culm initiation occurs for *S. validus* (Figure 28). During May, 74% of the culms appear; 12% begin growth during June, the remaining 14% developing during July and August. The culms produced in July and August are usually sterile, although occasional very small inflorescences develop. At both sites, sterile culms were produced throughout the growing season, but the percentage increased from less than 20% to complete sterility by midsummer..

Figure 27. Culm initiation at Site 100 (*S. acutus*),
            1971. Cross-hatched portion of each bar
            represents the number of culms which did
            not produce inflorescences, the open
            portion represents culms which produced
            inflorescences.

Figure 28. Culm initiation at site 101 (*S. validus*),
            1971. Cross-hatched portion of each bar
            represents the number of culms which did
            not produce inflorescences, the open
            portion represents culms which produced
            inflorescences.
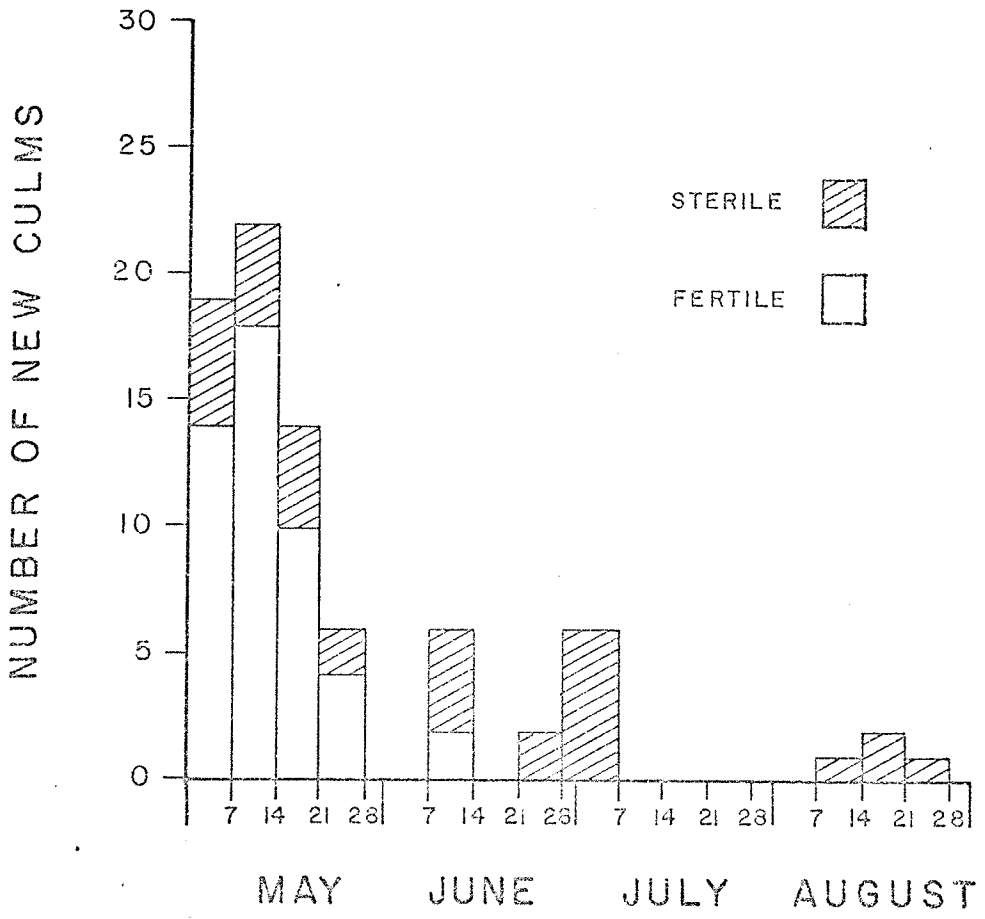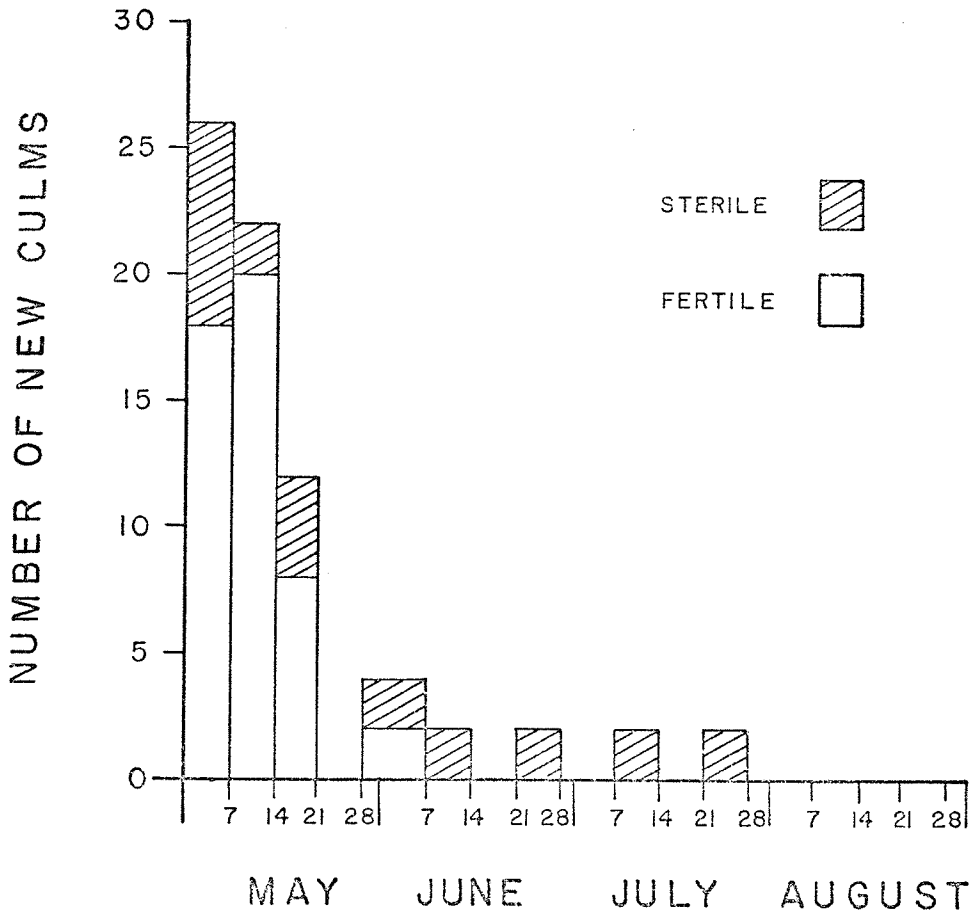
Figure 29 describes the increasing heights of the first 25 culms marked in each of the quadrats at sites 100 and 101. The mean height of culms in both quadrats at site 100 increased more rapidly than those of site 101. The culms in the deep water quadrat at site 100 could not be measured until the tips approached the surface of the water on May 18. The greater height of these culms at this time compared with those of the shallow water quadrat is attributed to higher mud temperatures throughout the winter in deep water. The mud at the shallow water quadrat was $-3^{o}C$ on February 25, 1971, while that of the deep water quadrat was $+2^{o}C$ on the same date. These early culms in both quadrats reached maximum height by the third week of June, although growth of younger culms was still in progress.

The first 25 culms in each quadrat at site 101 showed a marked difference in time of growth (Figure 27). The soil of both quadrats was frozen during the winter, but the soil of the shallow water quadrat thawed earlier in the spring because it was not covered by water; the soil of the deep water quadrat had not completely thawed when the first culms appeared at the shallow water quadrat. When growth began on May 22 at the deep water quadrat, the culms in the shallow quadrat were already 22 cm high. Maximum height was attained by June 9, but was considerably less than for culms at site 100. This is thought to be environmentally produced rather than genetic, because the height of *S. validus* at other sites often exceeded 150 cm. The surface runoff through this creek channel was very rapid in the spring, with most of the surface water gone by mid-

Figure 29.   Mean height of the first 25 culms ini-
             tiated in deep-water and shallow-water
             quadrats at site 100 (*S. acutus*) and
             site 101 (*S. validus*).

Figure 30.   Mean rate of culm elongation for both
             quadrats at site 100 (*S. acutus*) and
             site 101 (*S. validus*).
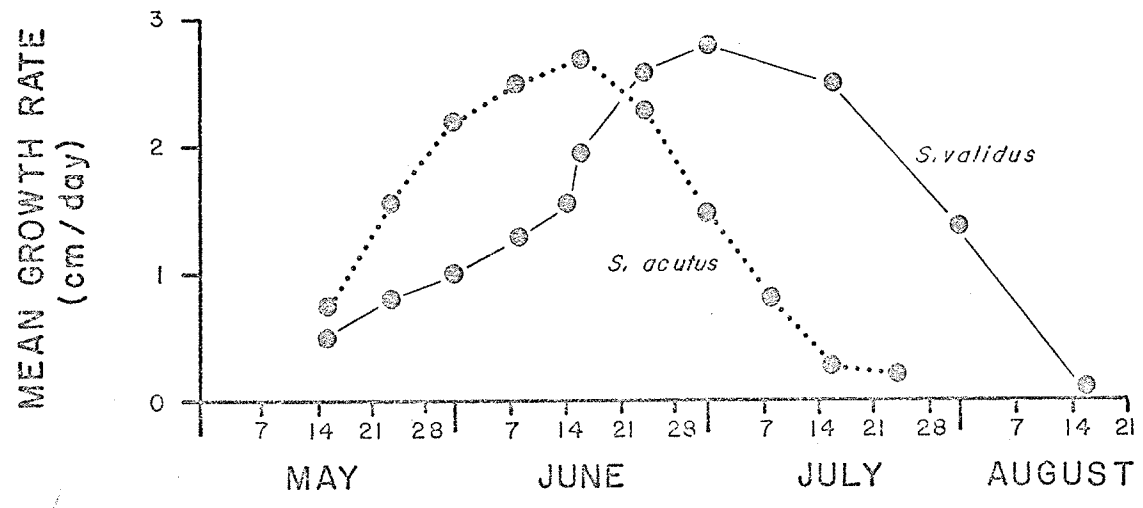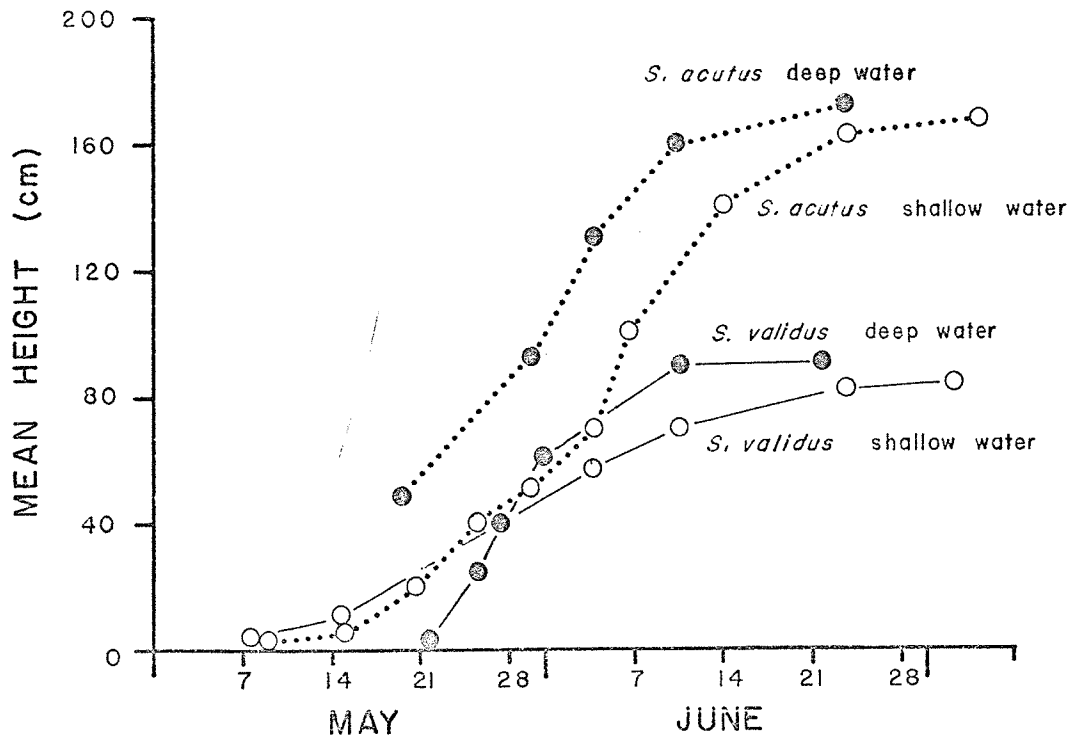
May. A water deficit probably occurred and resulted in earlier

maturation and stunted height of the culms.

The mean rates of culm elongation for the entire growing

season at sites 100 and 101 are presented in Figure 30. This figure

illustrates the effect of the growth rate of individual culms (Fig-

ure 29) coupled with the prolonged period of culm initiation (Fig-

ures 27 and 28). The maximum growth rate (culm elongation) of the

S. acutus stand at site 100 occurred during the second week of June.

At this time, the earliest culms had almost reached maximum height

(Figure 29), but the younger culms were in the period of most rapid

growth. From a maximum rate of elongation of 2.6 cm per day in mid-

June the rate declined rapidly to mid-July, when only occasional

new culms were being produced (Figure 27).

A lower initial growth rate is exhibited by the *S. validus*

culms at site 101, as shown in Figure 30. A maximum of 2.8 cm per

day occurred in late June, with a gradual decline until the end of

July. The growth rate of new culms in August (Figure 28) was not

followed; if these had been measured, there would have been slight

rise in the mean growth of the stand during this period.

The length of the growing season can be determined from Fig-

ure 30. For *S. acutus*, it is approximately 65 days, whereas for

S. validus it is approximately 90 days. The greater length of the

growing season for *S. validus* is mainly due to a greater number of

culms produced in June and July (Figures 27 and 28), although the

rate of growth also may be greater for *S. acutus* (Figure 29). Com-

parisons to determine if the differences are genetically controlled

would require monitoring the growth of both taxa under identical conditions.

As the new culms are elongating, a progressive swelling of the tip occurs at the base of the bract. When the culm is approximately three weeks old, the sheath enclosing the developing inflorescence splits, and this is followed by a rapid elongation of the rays. Ray elongation is accompanied by exsertion of the receptive styles in all but a few apical florets of each spikelet. The styles wither within 48 hours, and four to six days later the anthers begin shedding pollen. Pollination is probably anemophilous as this is true for most of the Cyperaceae (Willis, 1955).

The pattern of flowering in the apical florets is similar, but the timing is variable. The styles occasionally are exserted simultaneously with those of the basal florets, but most frequently they appear just prior to anthesis in the basal florets; occasionally enlarged fertilized ovaries are present basally before the apical florets flower. The number of apical florets with delayed flowering varies from one or two to as much as 1/3 of the total in the spikelet. This pattern was observed in both *S. acutus* and *S. validus* with no apparent differences.

In summary, culms produced in early May will flower in mid-June and fertilized ovaries are apparent by the third week of June. Ripe achenes will be present 85 days after culm initiation; thus, culms initiated in the first week of May will have ripe achenes beginning to appear in the basal florets by the first week of August.

S. validus achenes are all shed at once, within a period of

about two weeks, whereas *S. acutus* achenes tend to be shed less syn-
chronously over a period of about two months; occasionally, achenes
of *S. acutus* are retained in the inflorescence through the winter.

Although the achenes are denser than water, they will float
for as long as 22 days. Achenes of *S. acutus* and *S. validus* were
collected from sites 100 and 101 and placed in separate beakers of
tap water to compare their abilities to float. With gentle stirring
once per day, all the *S. acutus* achenes sank within 8 days (Figure
31), whereas some *S. validus* achenes remained on the surface for 22
days (Figure 32). Both types of achenes have a waxy, pitted seed
coat and perianth bristles which aid in flotation, but under con-
stantly turbulent conditions it is unlikely that they would remain
afloat for more than a few hours.

(b) Natural seedling establishment

The achenes of *S. validus* germinate more readily under nat-
ural conditions than do those of *S. acutus*. During the study period,
seven stands of *S. validus* were found which are known to have dev-
eloped from seedlings. In contrast, no examples of seedling estab-
lishment of *S. acutus* were found. Drawdown[1] conditions which expose
mud containing *S. validus* achenes result in their rapid germination.
Although the author was unable to follow the events of a single
drawdown through the study period, three were examined at various

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[1] The term 'drawdown' is used here to refer to a rapid
decline in water levels, produced naturally or by man,
which exposes the mud surface.

Figure 31. Floating ability of *S. acutus* achenes,
showing the number of achenes remain-
ing on the surface on consecutive days
(initial number = 60).

Figure 32. Floating ability of *S. validus* achenes,
showing the number of achenes remain-
ing on the surface on consecutive days
(initial number = 60).
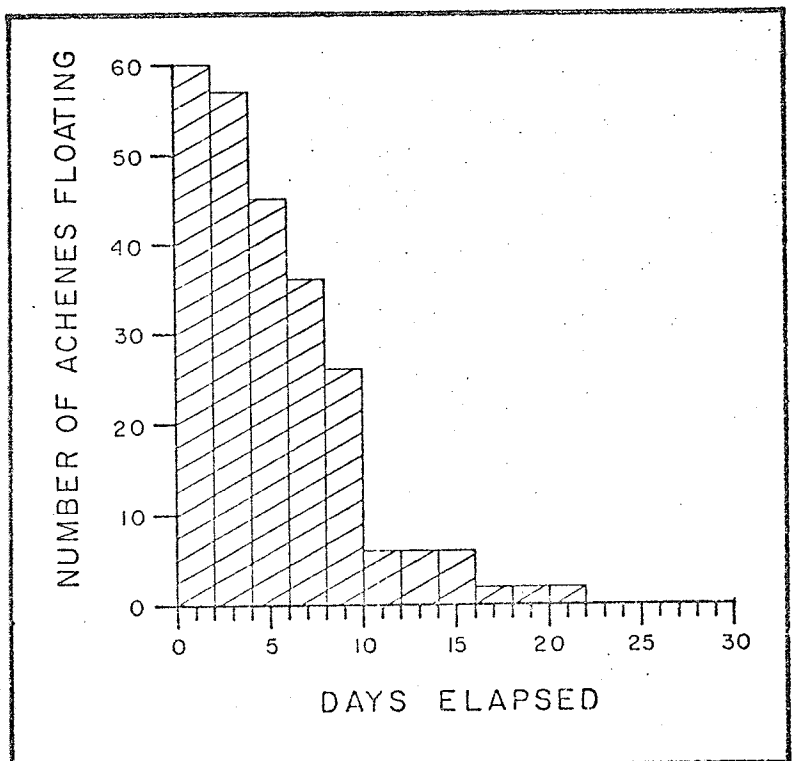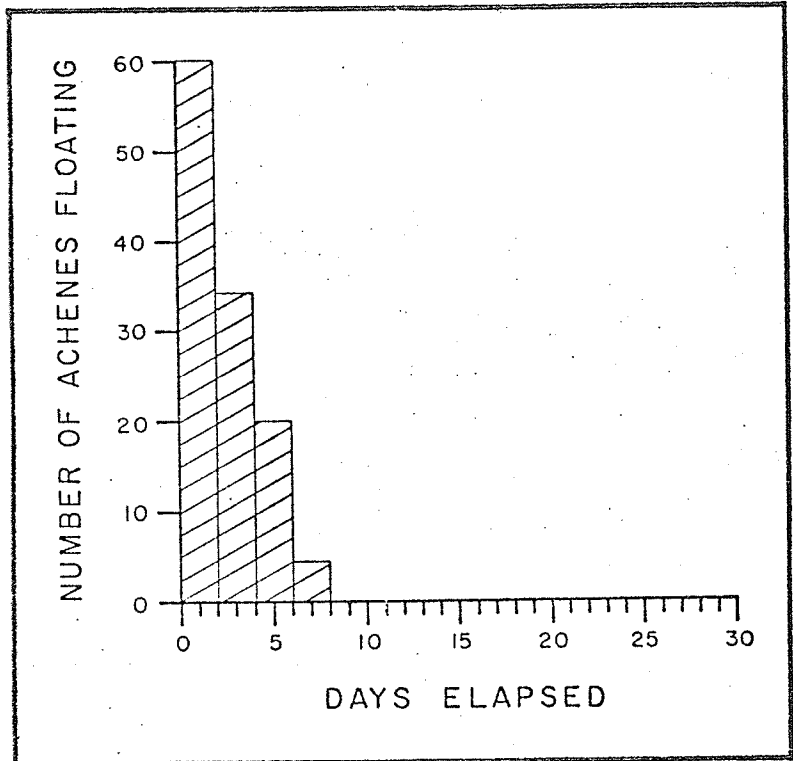
stages of establishment and, together with the history provided by

persons involved, it is possible to obtain a general pattern of the

establishment of *S. validus* from seedlings[1]. Drawdowns in the fall

which are maintained through the following summer result in the

germination of *S. validus* achenes during late June and early July.

Initially the seedlings form a dense mat which becomes less dense

as the seedlings grow (Figure 33). By the end of August, the seed-

lings have reached a height of 30 to 50 cm (Figure 34) and have es-

tablished a short rhizome; the culms do not flower in the first

growing season. Observations during the second growing season in-

dicate that a rapid proliferation of the rhizome system occurs (Fig-

ure 35); by the end of the summer it covers an area of 0.2 to 0.5 m^2

and has produced 30 to 40 flowering culms (Figure 36). At this time

the seedling origin of the stand is still evident by the clumped

pattern of the culms which have developed from individual seedlings

(Figure 37). Continued vigorous growth during the third season will

result in these clumps coalescing to produce a more random pattern

of culms.

(c) Achene germination in the laboratory

The absence of information on the germination conditions re-

quired for *S. acutus* achenes to germinate naturally prompted a number

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[1] I am indebted to Messrs. W. G. Leitch, K. A. Pugh, and
G. H. Townsend for information on Ducks Unlimited's draw-
downs at the Murphy Extension #2 and Cumberland Marsh
(Willow Lakes) projects; and to Mr. P. Ward who provided
information for a drawdown which he undertook in the
'Back Marsh' area of the Delta Marsh.

Figure 33. Germination of *S. validus* achenes on
                the mud surface at Lake 36 (The Pas).
                S. validus seedlings immediately be-
                hind Mr. Jichuk, *Eleocharis acicularis*
                in foreground, and a mature stand of
                S. acutus in background.
                (August 12, 1972)

Figure 34. Single *S. validus* seedling approximately
                25 cm high, showing the development of
                3 culms and an overwintering bud from a
                short rhizome. Ruler graduated in
                inches. (Lake 36, The Pas, August 12,
                1972)

Figure 35.   Mature rhizome of *S. validus*, showing
             the extensive root system developed.
             Shoot near rhizome apex (at right) will
             not develop until following Spring.
             Reddish-brown roots of previous growing
             seasons contrast sharply with newly-
             produced roots near apex. (Delta,
             September 14, 1970)

Figure 36.   Clone of *S. validus* produced by one
             seedling by the end of second growing
             season. (Willow Lakes, near Cumberland
             House, August 17, 1973)

Figure 37. *S. validus* stand established from seed-
           lings; end of second growing season.
           The clumped pattern of culms represents
           individual clones which have established
           from a single seedling. (Willow Lakes,
           near Cumberland House, August 17, 1972.
           Water depth at time of photo was 5 to
           15 cm.)

of germination tests in the laboratory. These were designed to determine what factors were important in triggering the germination of
S. acutus achenes, and also to compare the germination behavior of
S. acutus with *S. validus*.

Table III summarizes the results of the fifteen tests conducted. In test number 1, freshly-collected achenes were subjected
to the germination conditions without a period of storage or treatment; both *S. acutus* and *S. validus* failed to germinate.

In tests 2, 3, and 4 fresh achenes were subjected to three
treatments, embryo excision, sulfuric acid, and fed to ducks respectively, in order to determine whether or not germination was being inhibited by seed coat restrictions. Negative results were also
obtained for these tests.

Tests 5, 6, and 7 examined the effect on germination of a
1-month cold treatment in the dark using different media (peat moss,
silica sand, and humus). Both *S. acutus* and *S. validus* showed no
evidence of germinating at the end of the tests.

The storage period was increased to 150 days in tests 8 to
12, with several different storage and germination media used. In
test 8 under dry storage conditions, no germination occurred. Dry
storage and germination test in distilled water (test 9) following
scarification of the seed coat produced no germination in *S. acutus*,
but 15% of the *S. validus* achenes germinated. Storage in distilled
water with no scarification (test 10) produced a lower germination
rate (6%) in *S. validus*; *S. acutus* achenes did not respond.

Wet mud as a medium for the storage and germination test

TABLE III.   RESULTS OF GERMINATION TESTS (SAMPLE SIZE IN PARENTHESES)

Test	% Germination	
Number*	*S. acutus*	*S. validus*
1	0 (100)	0 (100)
2	0 (10)	0 (10)
3	0 (100)	0 (100)
4	0 (undetermined)	0 (undetermined)
5	0 (50)	0 (50)
6	0 (50)	0 (50)
7	0 (50)	0 (50)
8	0 (50)	0 (50)
9	0 (20)	15 (20)
10	0 (100)	6 (100)
11	2 (100)	74 (100)
12	0 (100)	10 (100)
13	0 (100)	85 (100)
14	0 (100)	1 (100)
15	0 (100)	0 (100)

* Refer to page 44 for details of storage and germination conditions
  and achene treatment, if any, in each test.

produced the only germination of *S. acutus* (test 11). The 2% rate

of germination of *S. acutus* was very poor in comparison with the 74%

rate shown by the *S. validus* achenes, however.

The addition of a period of freezing after storage (test 13)

produced the highest recorded rate for *S. validus* (85%), while no

S. acutus achenes germinated.

Freezing in distilled water without mud as a medium for

storage (test 12) resulted in reduced germination of *S. validus*.

The results of the first tests indicate that a period of

storage of at least 120 days is required for germination of

S. validus. Best results were obtained for both types of achenes

when mud was used as a storage medium. Freezing does not enhance

the germination of either *S. acutus* or *S. validus*. Tests 14 and 15

suggest that the period of storage should be conducted at low temp-

eratures, probably without light.

Examination of the embryos at the completion of the tests

indicated that they had not been damaged by the test conditions, as

they appeared normally developed and healthy upon excision. It

seems unlikely then that the low germination rate, particularly of

S. acutus, is due to an inherently poor ability to germinate, but

rather that there are precise requirements for germination which

were not provided in the experiments. This is supported by a 92%

germination rate of *S. acutus* achenes that resulted from 95 days

storage at approximately $2^{o}C$. During this time the achenes underwent

a period of fermentation sufficient to crack the stoppered vial in

which they were stored. This indicates that the achenes of *S. acutus*

are capable of high germination rates, probably after a combination
of storage at cool temperatures, bacterial action, and anaerobic
conditions.

(d) Biomass estimates

The biomass of aerial shoots which results from one growing
season is presented for 12 sites in Table IV. The values given in
Table IV represent the means of five samples, or 5 m^2 surface area.
The samples were collected at the end of the growing season and
represent approximate estimates of net primary shoot production.
Mean values for the six *S. acutus* stands range from 83 g/m^2 at
site 42 (The Pas study area) to 365 g/m^2 at site 2 (Langruth study
area). The data for *S. validus* sites in this table shows an even
greater range from 60 g/m^2 at site 34 (The Pas) to 570 g/m^2 at site
4 (Netley Marsh).

The standard deviations associated with the means are very
large, in almost all cases equal to or greater than 50% of the mean.
This variability makes comparison between *S. acutus* and *S. validus*
production impossible.

Table V compartmentalizes the standing crop attributable to
the various plant components. The data indicate that the total
standing crop of the above- and below-ground components of *S. acutus*
(site 102) is 2,366 g/m^2, while that of *S. validus* (site 103) is
1,687 g/m^2. The above-ground components represent only 20% of the
total biomass in *S. acutus*, but is considerably more in the *S. validus*
stand (51%). Again, however, the great variation indicated by the

TABLE IV.   AERIAL BIOMASS OF *S. ACUTUS* AND *S. VALIDUS*
(AUGUST 1-11, 1972)

	Site Number	Number of Samples	Biomass (g/m^2)	
			mean	s.d.
S. acutus				
	1	5	290	146
	2	5	365	289
	35	3	323	161
	36	5	349	295
	41	5	164	30
	42	5	83	55
S. validus				
	4	5	570	160
	17	5	94	104
	18	5	331	144
	24	5	491	209
	31	5	394	217
	34	5	60	39

TABLE V. BIOMASS OF AERIAL AND SUBTERRANEAN COMPONENTS OF *SCIRPUS ACUTUS* (SITE 102, JULY 27, 1972) AND *S. VALIDUS* (SITE 103, AUGUST 1, 1972). ALL WEIGHTS EXPRESSED AS G/M^2

	Inflorescence	Culm	Root	Rhizome	TOTAL Above	TOTAL Below	Whole Plant
S. acutus							
Site 102 n = 10							
$\overline{x}$	34.7	389.5	322.8	1614.5	438.5	1937.0	2366.0
s.d.	12.3	160.6	321.1	792.5	175	1001	1021.3
Mean % of total biomass	1.6	18.8	15.8	63.8	20	79.5	
S. validus							
Site 103 n = 10							
$\overline{x}$	84.0	714.4	45.3	842.0	798.3	88.8	1686.7
s.d.	58.3	205.6	26.6	541	224	547	707.1
Mean % of total biomass	4.7	47.2	3.1	61.4	50.6	46.8	

standard deviations makes comparisons unreliable.

B. Community relationships

1. Plant species associated with *S. acutus* and *S. validus*

      A difference in the species composition of plants associated with *S. acutus* and *S. validus* stands suggests a markedly different environment occupied by each of these bulrushes. Table VI lists the 51 species of rooted plants which were found associated with 27 stands of *S. acutus* and 16 stands of *S. validus*. The data represent stands from all five study areas. Although there is no statistical difference in the mean number of species in stands of each type (*S. acutus* $\bar{x}$ = 4.5; *S. validus* $\bar{x}$ = 6.7; t = 1.46; p < 0.1), there is a significant difference in the species associated with them (rank correlation coefficient = 0.76; n = 51; p < 0.01).

      Table VII lists the ten most frequent associates of *S. acutus* and *S. validus*. The occurrence of submerged hydrophytes (*Myriophyllum exalbescens* and *Utricularia vulgaris*) in the *S. acutus* stands indicates a deep, relatively stable water depth in the *S. acutus* habitat. In contrast, *Beckmannia syzigachne*, *Bidens cernua*, *Galium septentrionale* and *Ranunculus cymbalaria* are more characteristically found in moist habitats or shallow water and were frequent associates of *S. validus*. The more frequent occurrence of *Eleocharis palustris* and *Typha latifolia*, both shallow-water emergents, in *S. validus* stands similarly reflects this habitat difference. The equal ranking of *Sonchus asper* in both *S. acutus* and *S. validus* is due to the frequent occurrence of this species in the vegetation zone adjacent to the shallow-water end of the vegetation transects in *S. acutus* stands; in *S. validus* stands it occurred with a higher frequency

TABLE VI.   ASSOCIATED SPECIES OF PLANTS AND THEIR
FREQUENCY OF OCCURRENCE IN 19 *S. ACUTUS*
AND 13 *S. VALIDUS* STANDS
(AUGUST 1-31, 1972)

| Species | Number of Occurrences | OCCURRENCES IN STANDS OF | | | |
| | | *S. acutus* | | *S. validus* | |
		No.	%	No.	%
Typha latifolia	14	7	24	7	47
T. angustifolia	1	1	3.5	0	0
Sparganium eurycarpum	6	3	10.5	3	20
Potamogeton vaginatus	3	3	10.5	0	0
P. pectinatus	2	2	6.9	0	0
P. zosteriformis	2	2	6.9	0	0
P. richardsonii	1	1	3.5	0	0
Alisma triviale	5	0	0	5	33
Sagittaria cuneata	6	2	6.9	4	26
Glyceria grandis	2	0	0	2	13
Scolochloa festucacea	18	12	41	6	40
Poa palustris	2	0	0	2	13
Agropyron repens	2	0	0	2	13
Calamagrostis neglecta	3	2	6.9	1	6.7
Hordeum jubatum	3	2	.6.9	1	6.7
Beckmannia syzigachne	6	2	6.9	4	26
Spartina gracilis	1	1	3.5	0	0
Zizania aquatica	1	0	0	1	6.7
Phragmites communis	11	11	38	0	0
Eleocharis palustris	19	9	31	10	67
E. acicularis	5	2	6.9	3	20
Scirpus fluviatilis	6	4	14	2	13
S. paludosus	1	0	0	1	6.7
Carex sp.	16	10	35	6	40
C. lasiocarpa	1	0	0	1	6.7
C. atherodes	18	14	48	4	26

TABLE VI (continued)

Species	Number of Occurrences	OCCURRENCES IN STANDS OF			
		S. acutus		S. validus	
		No.	%	No.	%
Juncus sp.	3	0	0	3	20
J. balticus	2	2	6.9	0	0
J. bufonius	1	1	35	0	0
Polygonum amphibium	3	1	3.5	2	13
P. lapathifolium	1	0	0	1	6.7
Rumex maritimus	3	0	0	3	20
Chenopodium sp.	4	2	6.9	2	13
Nuphar variegatum	2	2	6.9	0	0
Ranunculus cymbalaria	3	0	0	3	20
Anemone canadensis	1	0	0	1	6.7
Potentilla anserina	2	2	6.9	0	0
Geum rivale	1	0	0	1	6.7
Myriophyllum exalbescens	9	7	24	2	13
Cicuta maculata	1	0	0	1	6.7
Sium suave	5	0	0	5	33
Lycopus asper	4	2	6.9	2	13
Mentha arvensis	4	2	6.9	2	13
Utricularia vulgaris	5	4	14	1	6.7
Galium septentrionale	3	0	0	3	20
Bidens cernua	4	0	0	4	26
Aster sp.	4	4	14	2	13
A. puniceus	1	0	0	1	6.7
Sonchus asper	9	5	17	4	26
Cirsium arvense	2	0	0	2	13
Artemisia sp.	2	0	0	2	13

TABLE VII. THE TEN MOST FREQUENTLY ASSOCIATED SPECIES
OF PLANTS IN 19 *S. ACUTUS* AND 13 *S. VALIDUS*
STANDS, LISTED IN DESCENDING ORDER OF
IMPORTANCE
(AUGUST 1-31, 1972)

S. acutus		*S. validus*	
Carex atherodes		*Eleocharis palustris*	
Scolochloa festucacea		*Typha latifolia*	
Phragmites communis	equal	*Scolochloa festucacea*	equal
Carex sp.		*Carex* sp.	
Eleocharis palustris		*Beckmannia syzigachne*	
Typha latifolia	equal	*Carex atherodes*	equal
Myriophyllum exalbescens		*Bidens cernua*	
Sonchus asper		*Sonchus asper*	
Utricularia vulgaris	equal	*Galium septentrionale*	equal
Scirpus fluviatilis		*Ranunculus cymbalaria*	

throughout the length of the transects. Although the ubiquitous
Phragmites communis has been found associated with *S. validus*, its
absence from this sample is thought to be significant, indicating a
drier, less stable habitat than this reed normally occupies.

2. Wildlife utilization of bulrushes

Scirpus acutus stands provide favored nesting sites for a
number of waterfowl and other wetland species of birds. From Table
VIII it is apparent that the canvasback duck (*Aythya valisineria*),
the American coot (*Fulica americana*), the redwinged and yellow-
headed blackbirds (*Agelaius phoeniceus* and *Xanthocephalus
xanthocephalus*) and the marsh wrens (*Telmatodytes palustris* and
Cistothorus platensis stellaris) make the greatest use of *S. acutus*
stands as a source of nesting cover. Amongst the relatively few
nests found in *S. validus* stands, the predominance of upland-nesting
species (mallard, pintail, baldpate, blue-winged teal, shoveller,
and killdeer) reflects the habitat most characteristically occupied
by *S. validus*. Stands of this species are probably unsuitable as
nesting sites in many cases because of the unstable water levels
early in the growing season.

The main function of bulrushes for nesting waterfowl was ob-
served to be as a source of cover, with the actual nesting material
being other than bulrush culms. Some species of birds do, however,
employ the culms of bulrushes, *S. acutus* in particular, in actual
nest construction.

The function of bulrush stems in nest construction is differ-

TABLE VIII.   SPECIES OF BIRDS AND NUMBERS OF NESTS WITH EGGS
OR YOUNG IN 69 *S. ACUTUS* AND 45 *S. VALIDUS* STANDS
(MAY–JUNE 1970–1972)

Species[1]	NUMBER OF NESTS IN		
	S. acutus	*S. validus*	TOTAL
Western grebe	4	0	4
Pied-billed grebe	3	0	3
American bittern	1	0	1
Mallard	1	2	3
Pintail	0	1	1
Baldpate	1	3	4
Blue-winged teal	0	4	4
Shoveller	0	1	1
Canvasback	8	0	8
Redhead	1	0	1
Ruddy duck	1	0	1
Sora rail	0	1	1
American coot	14	1	15
Killdeer	0	1	1
Forster's tern	4	0	4
Black tern	4	0	4
Marsh wrens[2]	5	1	6
Yellow-headed blackbird	7	0	7
Red-winged blackbird	8	1	9
TOTAL	62	16	78

[1] See Appendix III for scientific names.

[2] Long-billed and short-billed marsh wrens not distinguished.

TABLE IX.   SPECIES OF WATERFOWL UTILIZING *S. ACUTUS*
OR *S. VALIDUS* ACHENES[1] AS A FOOD SOURCE

Species[2]	Number of Samples	NUMBER OF DIGESTIVE TRACTS[3] WITH			
		Scirpus Only	Scirpus and Other	Other Food	Empty
Mallard	11	1	2	7	1
Gadwall	1	0	1	0	0
Baldpate	4	2	0	1	1
Blue-winged teal	4	2	0	0	1
Shoveller	5	3	0	1	1
Redhead	4	2	0	2	0
Lesser scaup	5	2	0	3	1
TOTAL	34	12	3	14	5

[1] Although the achenes of these two species are readily distinguished from those of other Cyperaceae occurring in Manitoba, they cannot be distinguished with certainty from each other.

[2] See Appendix III for scientific names.

[3] Esophagus, proventriculus and ventriculus.

ent with different species of birds, but three common patterns were observed. The blackbirds and marsh wrens utilize the culms for support of an aerial nest, the actual nest material being cattail or grass leaves. These are interwoven among several bulrush culms, effectively tying the culms into a loose ring. The nest is then constructed around these culms. The coots and grebes build a floating nest, and utilize living and dead bulrush culms merely for flotation. The nest itself is composed of grasses or other fine material, or in the case of the grebes, debris picked from the bottom of the marsh (Figure 38). The Forster's tern, however, utilizes the dead culms of the previous year both for flotation and as the 'nest' material. The eggs are laid on floating mats of the previous year's culms which have been broken and piled by the wind, with little attempt to form an actual nest (Figure 39). When diving ducks (mainly the redhead, canvasback and ruddy ducks) utilize bulrushes to build floating nests, they use the culms both for flotation and nesting material, although the nest is usually lined with finer material and feathers.

In addition to using bulrushes for nesting, several species of waterfowl feed on the achenes of *S. acutus* and *S. validus*. Table IX lists the species of ducks which were examined in late fall from the Delta Marsh. Although the sample size is too small to draw many meaningful conclusions, it seems significant that those birds which had eaten bulrush achenes had little or no food material of any other type, suggesting that these birds were selectively feeding on bulrushes. It is not clear whether the achenes were being removed from the inflorescences or being selectively sought once they had

Figure 38. Nest of Western grebe (*Aechmorphorus occidentalis*), illustrating the use of bulrush culms (*S. acutus*) for flotation; the actual nest material is debris picked from the lake bottom. (Murphy Lake, The Pas study area, June 11, 1972)

Figure 39. Forster's tern (*Sterna forsteri*) nest on floating mat of dead bulrush culms. The culms provide flotation as well as the material for the 'nest'.

dropped from the plant. The fact that diving ducks appeared to be selecting them would suggest the latter explanation. The absence of scales or whole spikelets from the samples would also support this explanation.

During the study period, 46 stands of bulrushes harbored one or more active muskrat houses (Figure 40). These structures if found in bulrush stands are invariably constructed partially or completely from the culms and rhizomes of these plants. The animals forage in the area surrounding the house, heaping cut culms and rhizomes with adhering mud onto the top of the mound. This eventually results in a circular area around the house which is devoid of vegetation.

In addition to the houses, numerous 'feeding platforms' were found in those stands occupied by muskrats. These feeding sites are the result of the muskrat bringing culms to a central area, feeding on the basal meristematic tissue, then abandoning the rest of the culm, which becomes incorporated into the platform. The shredded material on the feeding platform in Figure 41 is the discarded leaf sheaths from the bases of the culms; these are not generally eaten.

Of the 46 muskrat houses found in bulrush stands, 42 were associated with *S. acutus*, only four with *S. validus*. The preference for *S. acutus* does not seem to be based on the quality of the plants, since those *S. validus* stands which were occupied were being utilized extensively.

Figure 40. Muskrat (*Ondatra zibethica*) 'house'
constructed from bulrush (*S. acutus*)
culms. (Site 42, Murphy Lake,
August 16, 1972)

Figure 41. Muskrat (*Ondatra zibethica*) feeding
platform. Basal portions of *S. acutus*
culms have been eaten, the white
strips of plant material are the leaf
sheaths. Upper portions of culms form
the floating platform. (Site 52,
Delta study area, July 26, 1971)

C. Stand performance

      The response of *S. acutus* and *S. validus* to the different environmental conditions in the five study areas was measured by a stand performance factor. This factor was calculated for each stand from the mean density and the fertility rate. The density and fertility data, as well as their product, stand performance, is presented for sites 1 - 60 in Table X.

      The culm density ranged from 5.6 culms/m^2 (site 37) to 257.6 culms/m^2 for site 56. Fertility varied from 16.6% at site 19 to a maximum of 88.4 at site 22. The highest stand performance value (144) was calculated for site 56, the lowest (4.0) for sites 34 and 37. There is little correlation between density and fertility rates when individual stands are considered, or when stands are grouped on the basis of study areas. The highest density and fertility were recorded at Delta sites, for example, but the lowest density was recorded at The Pas and the lowest fertility at Langruth.

TABLE X. CALCULATION OF STAND PERFORMANCE FROM
DENSITY AND FERTILITY FOR SITES 1 to 60

Site Number	Density (culms/m^2) (a)	Fertility % (b)	Stand Performance (a x b)	Site Number	Density (culms/m^2) (a)	Fertility % (b)	Stand Performance (a x b)
1	65.2	31.3	20.2	31	112.0	77.1	86.2
2	76.8	33.2	25.3	32	56.4	73.3	41.2
3	48	52.1	25	33	76.8	85.5	65.3
4	86.4	48.0	41.5	34	30.4	13.3	4
5	105.6	23.2	24.3	35	75.2	29.3	21.8
6	117.6	66.7	77.6	36	81.6	28.3	22.8
7	93.2	32.3	29.8	37	5.6	72.3	4
8	96	37.4	35.5	38	88	30.8	26.4
9	75.6	45.8	34	39	30.5	85.2	103.7
10	47.2	21.6	9.9	40	79.2	29.6	23
11	36.8	34.6	12.5	41	61.6	39.2	24
12	72.8	29.2	21.1	42	26.8	37.7	9.9
13	56.8	44.7	25	43	80.4	22.2	11.1
14	58	51.4	29.6	44	75.2	60.9	45.1
15	68	46.6	31.3	45	77.6	69	53.5
16	56	18.3	10.1	46	87.2	79.7	68.9
17	34.4	87.5	29.9	47	71.2	37.7	26.3
18	114.8	35	40.2	48	52.4	87.6	45.6
19	61.6	16.6	10	49	72.8	74.2	53.9
20	116.4	68.3	79.5	50	134.4	52.8	69.9
21	88.4	62.7	54.8	51	55.6	32.1	17.8
22	51.2	88.4	45.1	52	76.8	55.2	42.2
23	66.4	57.2	37.8	53	50.7	72.7	36.6
24	132	79.7	104.3	54	90	69.4	62.1
25	75.6	56.8	42.3	55	134.8	50.7	67.4
26	49.2	26.5	12.8	56	257.6	56.9	144.3
27	82.8	58.8	48	57	37.6	48.5	18
28	124.8	60.4	74.9	58	92	69.1	63.5
29	54	27	14.6	59	108	53.7	57.2
30	84	84	70.6	60	63.2	74.1	46.8

D. Taxonomic assessment

   1. Character selection

        Thirteen morphological characters were employed in a factor

analysis to determine if there were one or more groups of charact-

ers which showed covariation. Such groups would appear in the analy-

sis as clusters of characters contributing to the definition of

individual factors.

        The first portion of output from the factor analysis program

is a matrix of simple correlation coefficients (Table XI). Three

characters show a highly significant ($p < 0.005$) correlation with

inflorescence length (1). The number of primary rays (10) varies

with the inflorescence length, indicating that specimens with large

inflorescences also have many primary rays. A similar relationship

holds for inflorescence length and the number of secondary, tertiary,

and quaternary rays (11). Thus, large inflorescences show a greater

elaboration of the pattern of ray branching.

        Inflorescence length is also highly correlated with the

number of spikelet clusters composed of one or two spikelets. This

correlation refers to the tendency for larger inflorescences to have

greater absolute numbers of single or double spikelets. The lack of

correlation between inflorescence length and the number of spikelet

clusters of three or more spikelets is due to the tendency for short-

inflorescence specimens (of the *S. acutus* form) to have a large

proportion of the clusters of this multiple-spikelet composition,

with absolute numbers of clusters being relatively small. The large-

inflorescence specimens of the *S. validus* form tend to have propor-

1. Inflorescence length

2. Involucral bract length

3. Spikelet length

4. Spikelet width

5. Scale length

6. Scale width

7. Awn length

8. Achene length

9. Achene width

10. Number of primary rays

11. Number of secondary, tertiary and
    quaternary rays combined

12. Number of spikelet clusters composed
    of one or two spikelets

13. Number of spikelet clusters composed
    of five or more spikelets

TABLE XI. SIMPLE CORRELATION COEFFICIENTS OF 13 MORPHOLOGICAL CHARACTERS[1] (n = 1,500)

Morphological Characters	1	2	3	4	5	6	7	8	9	10	11	12	13
1	1.00												
2	0.08	1.00											
3	-0.32	0.08	1.00										
4	0.19	0.06	0.31	1.00									
5	-0.35	0.028	0.26	-0.01	1.00								
6	-0.32	0.03	0.27	0.09	0.26	1.00							
7	-0.23	0.00	0.19	-0.00	0.18	0.10	1.00						
8	-0.10	-0.03	0.06	-0.04	0.23	0.11	0.04	1.00					
9	-0.20	0.05	0.13	0.01	0.16	0.27	0.07	0.76*	1.00				
10	0.82*	-0.01	-0.36	0.09	-0.31	-0.34	-0.25	-0.07	-0.21	1.00			
11	0.81*	-0.01	-0.41	0.09	-0.34	-0.38	-0.22	-0.10	-0.23	0.86*	1.00		
12	0.74*	-0.03	-0.42	0.12	-0.29	-0.32	-0.27	-0.09	-0.19	0.77	0.81*	1.00	
13	-0.15	0.00	0.13	-0.14	0.07	0.09	0.11	0.04	0.03	-0.15	-0.27	-0.19	1.00

[1] See facing page for description of characters corresponding to numbers 1 to 13.

* Denotes characters showing a correlation greater than p=.01

tionately far fewer multiple-spikelet clusters.

The shape of the achenes is relatively constant in the spec-
imens examined; the achene length (8) and the achene width (9) show
a high positive correlation, indicating that size may vary, but that
the length and width vary in proportion to one another.

As indicated in the consideration of inflorescence length,
the number of primary rays, the number of secondary, tertiary and
quaternary rays, and the number of single- or double-spikelet
clusters all were positively correlated with inflorescence length.
It is expected, then that these characters will also be correlated
with one another. This is the case, as indicated by the high cor-
relation coefficients for characters 10 and 11, 10 and 12, and 11
and 12.

The second portion of the program's output is the factor
loadings matrix shown in Table XII. High factor loadings (positive
or negative) for a character on a particular factor indicate a sig-
nificant contribution of that character to the definition of the
factor. These are indicated by asterisks in Table XII. The com-
munality associated with each character indicates the proportion
of the variance of the measurements of each character which is ac-
counted for by the factors; values significantly less than one
indicate that a portion of the variance is due to error or some
unique quality of the character which is unaccounted for by the
factors. The high communality associated with each character indi-
cates that virtually all of the variance can be attributed to the
12 factors. The slightly lower communality associated with ray

1. Inflorescence length

2. Involucral bract length

3. Spikelet length

4. Spikelet width

5. Scale length

6. Scale width

7. Awn length

8. Achene length

9. Achene width

10. Number of primary rays

11. Number of secondary, tertiary and
    quaternary rays combined

12. Number of spikelet clusters composed
    of one or two spikelets

13. Number of spikelet clusters composed
    of five or more spikelets

TABLE XII. ROTATED FACTOR MATRIX OF LOADINGS ON 12 FACTORS
FOR 13 MORPHOLOGICAL CHARACTERS[1] (n = 1,500)

Morphological Characters	Factors												Communality
	1	2	3	4	5	6	7	8	9	10	11	12	
1	0.87*	-0.06	0.12	0.07	-0.02	-0.08	0.14	-0.09	-0.08	-0.02	0.002	-0.43*	0.99
2	0.01	0.01	0.02	0.99*	0.00	-0.00	-0.01	0.01	0.03	-0.00	0.005	-0.008	0.99
3	-0.28	0.04	0.20	0.04	0.06	0.07	-0.10	0.10	0.92*	0.03	0.00	0.01	0.99
4	0.10	-0.01	0.97*	0.02	-0.07	0.00	0.00	0.05	0.16	0.00	0.00	-0.01	0.99
5	-0.21	0.11	-0.00	0.01	0.02	0.07	-0.95*	0.09	0.09	-0.01	-0.00	0.01	0.99
6	-0.24	0.10	0.05	0.01	0.03	0.02	-0.10	0.95*	0.09	-0.02	0.01	0.01	0.99
7	-0.16	0.02	0.00	-0.00	0.05	0.98*	-0.06	0.02	0.06	-0.01	0.00	0.00	0.99
8	-0.01	0.95*	-0.03	-0.03	0.01	0.01	-0.12	-0.00	0.01	-0.02	-0.27*	0.00	0.99
9	-0.15	0.90*	0.02	0.04	-0.00	0.02	-0.02	0.15	0.03	0.01	0.37*	0.00	0.99
10	0.94*	-0.04	0.01	-0.01	-0.00	-0.09	0.07	-0.10	-0.09	-0.12	-0.006	0.10	0.96
11	0.91*	-0.07	0.01	-0.01	-0.15	-0.05	0.11	-0.14	-0.12	0.03	-0.03	0.06	0.92
12	0.82*	-0.06	0.05	-0.03	-0.06	-0.11	0.06	-0.09	-0.16	0.50*	0.01	0.01	0.99
13	-0.12	0.01	-0.07	0.00	0.98*	0.05	-0.02	0.03	0.04	-0.01	-0.00	0.00	0.99

[1] See facing page for description of characters corresponding to numbers 1 to 13.

development (characters 10 and 11) cannot be accounted for.

The percent of the variability attributed to each factor and a summary of the characters involved in each factor is presented in Table XIII. The same four characters which showed high correlation in Table XI appear in Factor 1. This factor is interpreted as a general 'inflorescence form' factor, describing the variation in inflorescence composition and the morphological characters which contribute to the variation. This factor accounts for the largest single proportion of the total variance in the data (33%).

The second factor is clearly an achene size factor, indicated by the high factor loadings on characters eight and nine. Thirteen percent of the variability is attributable to this factor.

The third factor involves a single character, spikelet width, and accounts for 10% of the total variance. Similarly, the remaining nine factors involve one character each (two for Factor 11) and account for progressively less of the data variance. The most important characters for distinguishing the groups, then, would be those involved in factors accounting for the largest portions of the total variance.

The previously described method of defining the character states to be associated with each of the hybrid index scores is based upon a bimodal frequency histogram of individual measurements for a character. The histograms of inflorescence length and the number of primary rays, the first two characters in Factor 1 (Table XII), are shown in Figures 42 and 43. Both characters displayed bimodal distributions indicating two modal types for each

TABLE XIII. SUMMARY OF FACTORS 1 to 12, THE %
VARIABILITY ATTRIBUTED TO EACH, AND
THE CHARACTERS WITH HIGH LOADING ON
EACH FACTOR

Factor	% Variability Attributed to Each Factor	Characters With High Loadings on Each Factor
1	33.2	inflorescence length number of 1° rays number of 2°, 3°, 4° rays number of 1- and 2-spikelet clusters
2	13.3	achene length achene width
3	10.4	spikelet width
4	7.8	bract length
5	7.4	number of clusters of 5 or more spikelets
6	6.7	awn length
7	6.2	scale length
8	5.4	scale width
9	3.5	spikelet length
10	3.0	number of 1- and 2-spikelet clusters
11	1.5	achene length achene width
12	1.2	inflorescence length

Figure 42. Histogram of inflorescence lengths of
            specimens from sites 1 to 60 (n = 1,500);
            abscissa intervals 2 mm, ordinate inter-
            vals 5.

Figure 43. Histogram of numbers of primary rays
            of specimens from sites 1 to 60
            (n = 1,550); abscissa intervals 2 mm,
            ordinate intervals 10.

FREQUENCY

80

40

0

0   60   120

INFLORESCENCE   LENGTH   (mm)

FREQUENCY

260

130

0

0   10   20   30

NUMBER OF PRIMARY RAYS
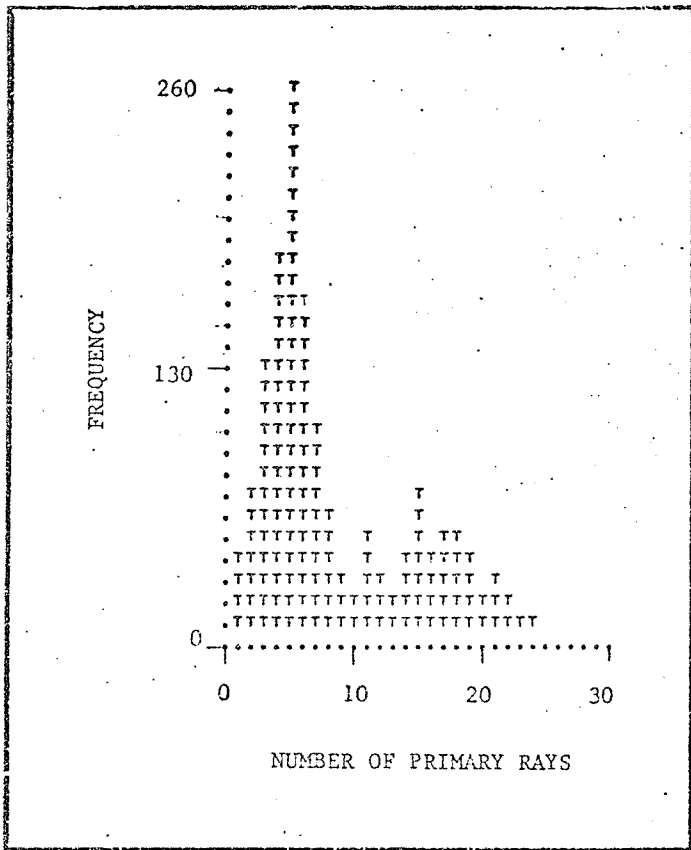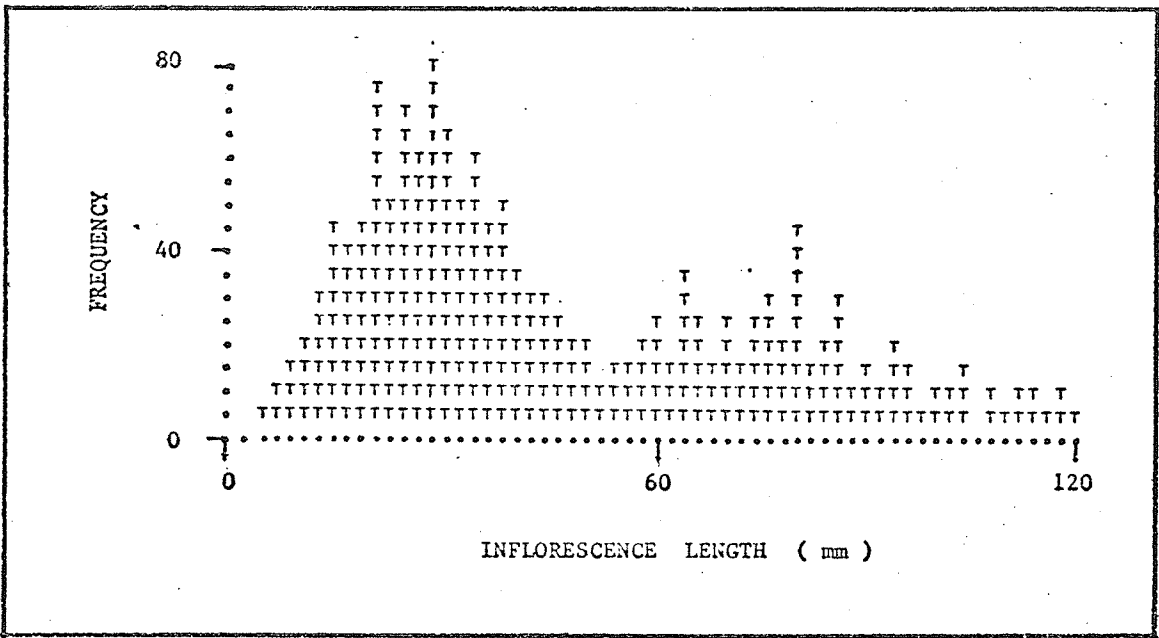
character.

Applying Riley's (1938) technique to the inflorescence
lengths (Figure 42): those greater than 80.5 mm were assigned the
value of 0; lengths of 47.1 - 80.4 were intermediate (1); and those
less than 47 mm were scored as 2. Similarly, from Figure 43,
specimens with 13 or more primary rays were scored 0; those with 7 -
13 rays were scored 1; inflorescences with less than 7 rays were
scored as 2.

The occurrence in Factor 1 of the number of primary rays,
the total number of secondary, tertiary and quaternary rays, and
the number of single- and double-spikelet clusters suggested a pos-
sible mathematical relationship between these three; the number of
primary rays would logically have some influence on the possible
number of branches, and these in turn would determine the possible
number of spikelets. Heslop-Harrison (1952) and Davis and Heywood
(1963) caution against using empirically related characters.

In order to eliminate the possible influence of a mathemat-
ical relationship and still retain the correlation with inflores-
cence length, qualitative expressions of ray branching and spikelet
clustering were used. The presence or absence of branches (second-
ary, tertiary, quaternary rays) replaced the related quantitative
character. To describe the pattern of spikelet clustering, the
presence or absence of clusters of five or more spikelets showed
the greatest correlation with inflorescence length. A preliminary
analysis of 300 inflorescences chosen randomly showed perfect agree-
ment between inflorescence length and presence or absence of clusters

of five or more spikelets; none of the inflorescences longer than 80.5 mm had spikelet clusters exceeding four spikelets, while all those inflorescences less than 47 mm long had at least one such cluster.

In order to obtain the required minimum of five characters, the histograms of achene length and width (Factor 2) were plotted (Figures 44 and 45). The distributions were unimodal and therefore could not be included in the analysis.

Although it was unlikely that characters involved in Factors 3 - 12 would prove more useful, histograms of these were plotted for verification. Figures 46 - 51 indicate the unimodal distributions displayed by spikelet length and width (Figures 46 and 47), bract length (Figure 48), awn length (Figure 49), and floral scale length and width (Figures 50 and 51). Because these characters showed no evidence of bimodality, they could not be divided into the necessary three character states; they were all therefore dropped from further consideration.

From the factor analysis, four of thirteen characters were selected as being of potential use in constructing the hybrid index; all four characters were associated with the general inflorescence form Factor (Factor 1).

Two additional characters were considered for possible inclusion. Lacunar diameter and culm color were measured in the field and had shown some correlation; light green or glaucous stems were associated with large lacunae, while dark green stems had much smaller, more numerous lacunae (Figure 52). Lacunar diameters of 1,500

111

Figure 44. Frequency histogram of achene lengths
            of specimens from sites 1 to 60
            (n = 1,500); abscissa intervals 0.05 mm,
            ordinate intervals 5.

Figure 45. Frequency histogram of achene widths
            of specimens from sites 1 to 60
            (n = 1,500); abscissa intervals 0.04 mm,
            ordinate intervals 5.

FREQUENCY

85

40

0

1.50   2.50   3.5

ACHENE LENGTH (mm.)

FREQUENCY

75

50

25

0

1.5   2.0   2.5   2.8

ACHENE WIDTH (mm.)

112
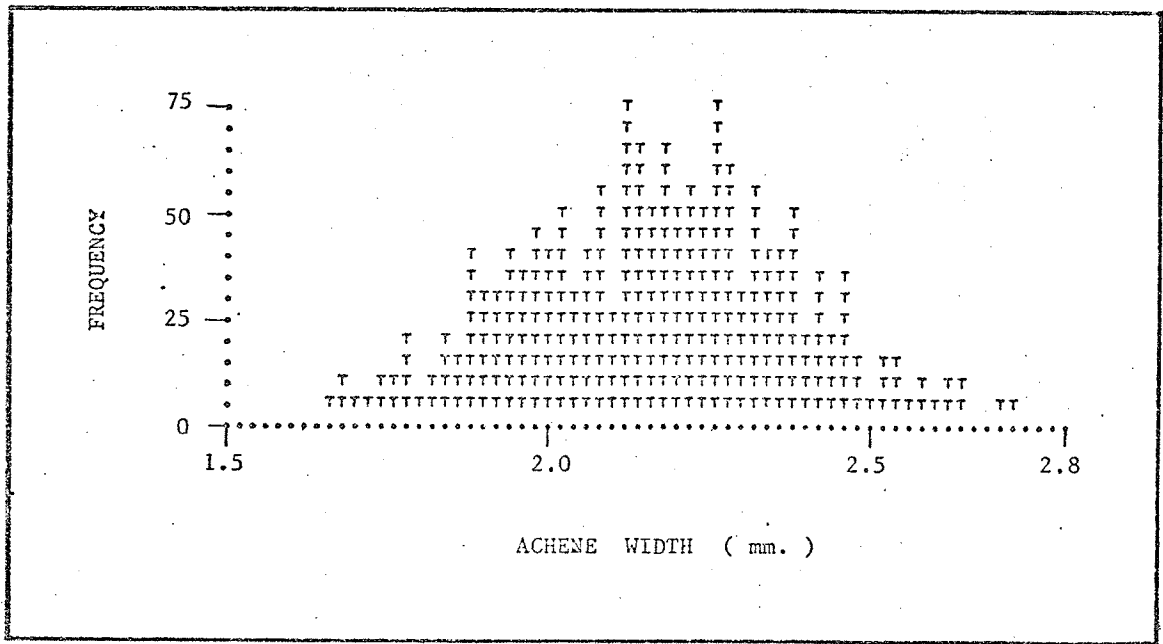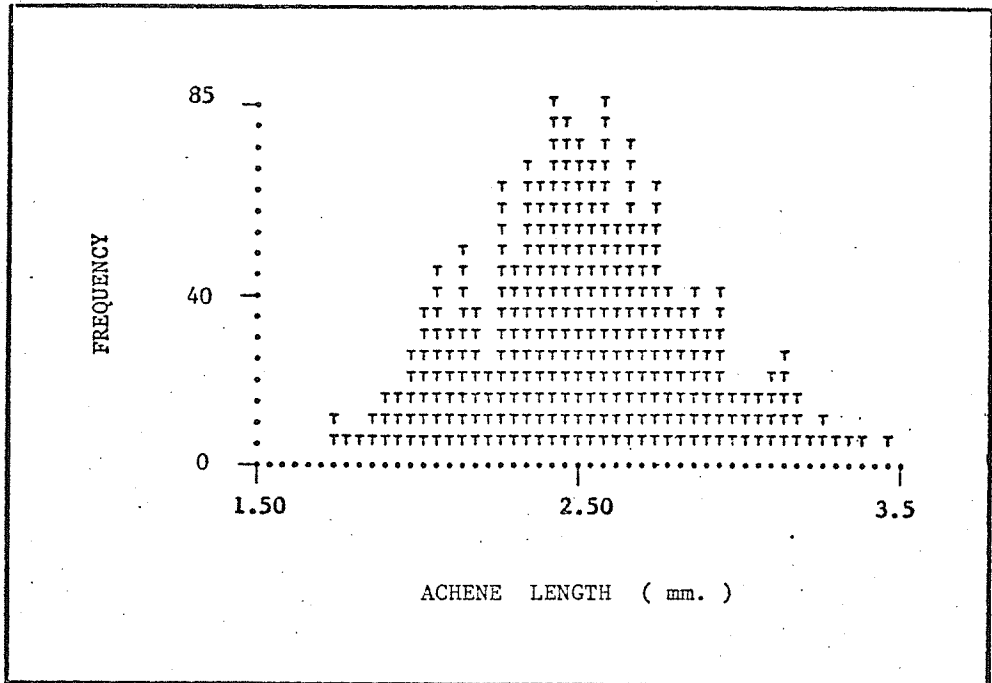
Figure 46.　Frequency histogram of spikelet lengths
of specimens from sites 1 to 60
(n = 1,500); abscissa intervals 0.2 mm,
ordinate intervals 5.

Figure 47.　Frequency histogram of spikelet widths
of specimens from sites 1 to 60
(n = 1,500); abscissa intervals 0.1 mm,
ordinate intervals 5.

FREQUENCY

90

45

0

2.0   8.75   15.5

SPIKELET   LENGTH   (mm.)

FREQUENCY

90

45

0

1.5   4.0   6.5

SPIKELET   WIDTH   (mm.)

113
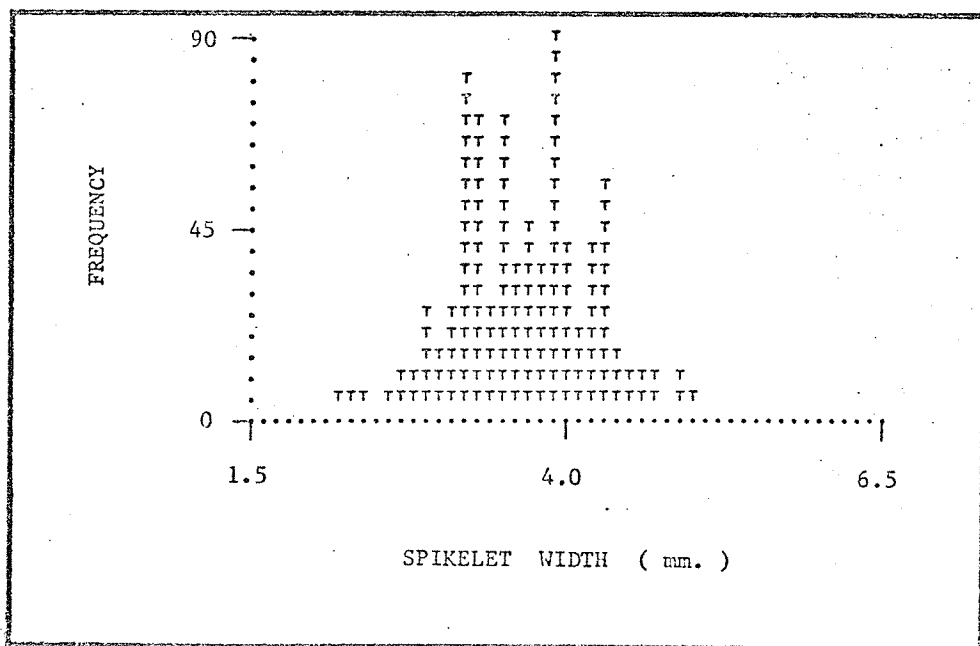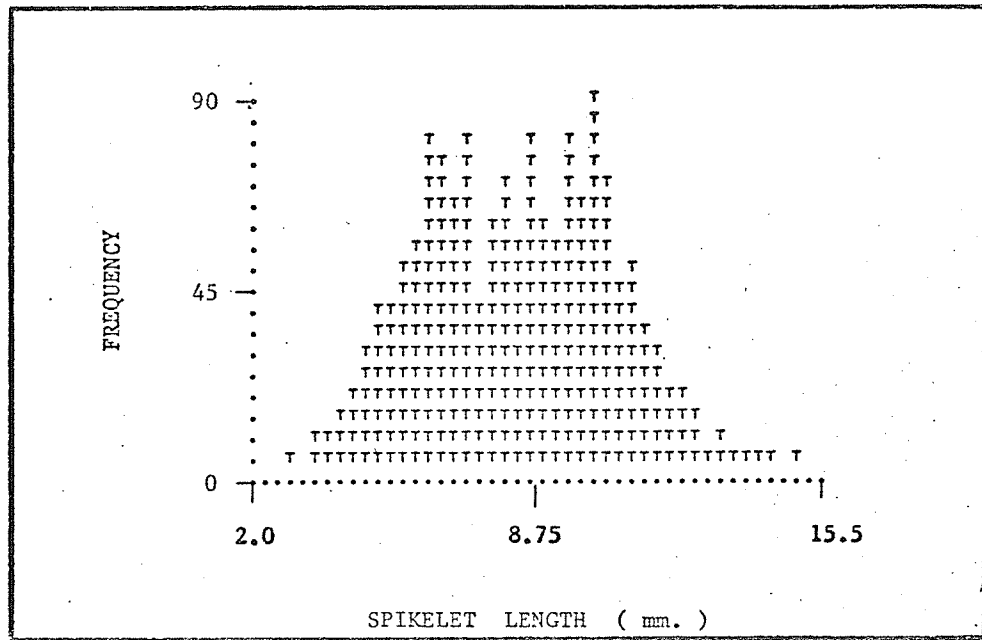
Figure 48.   Frequency histogram of involucral bract
             lengths of specimens from sites 1 to 60
             (n = 1,500); abscissa intervals 1 mm,
             ordinate intervals 5.

Figure 49.   Frequency histogram of awn lengths of
             specimens from sites 1 to 60 (n = 1,500);
             abscissa intervals 0.05 mm, ordinate
             intervals 5.

FREQUENCY

75 —

50 —

25 —

0 —

0   20   40   60

INVOLUCRAL   BRACT   LENGTH   (mm.)

FREQUENCY

95 —

50 —

0 —

0   1.0   2.0

AWN   LENGTH   (mm.)
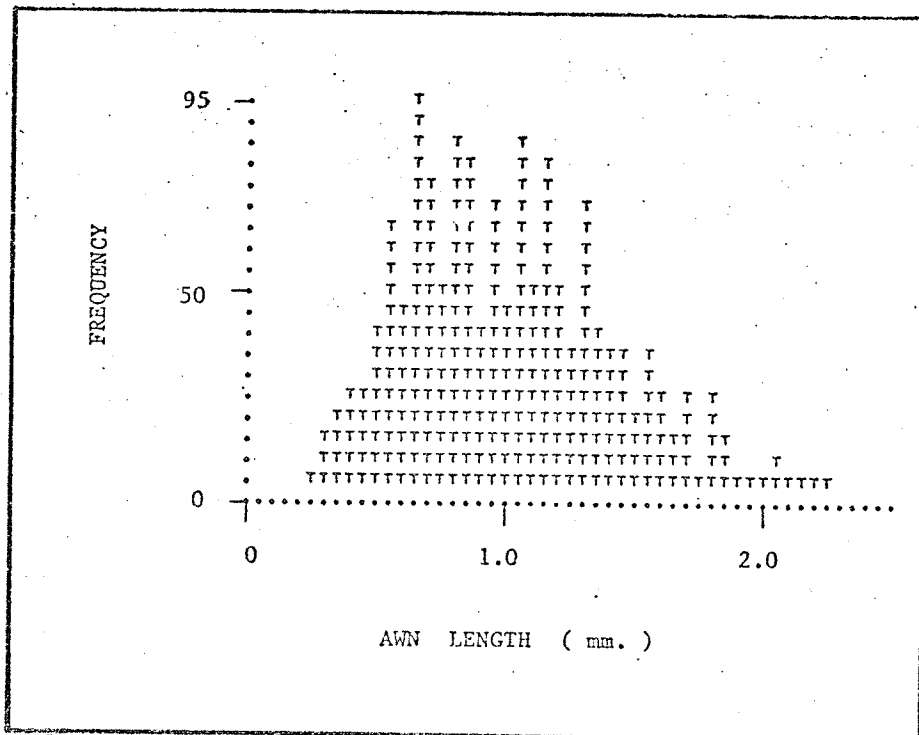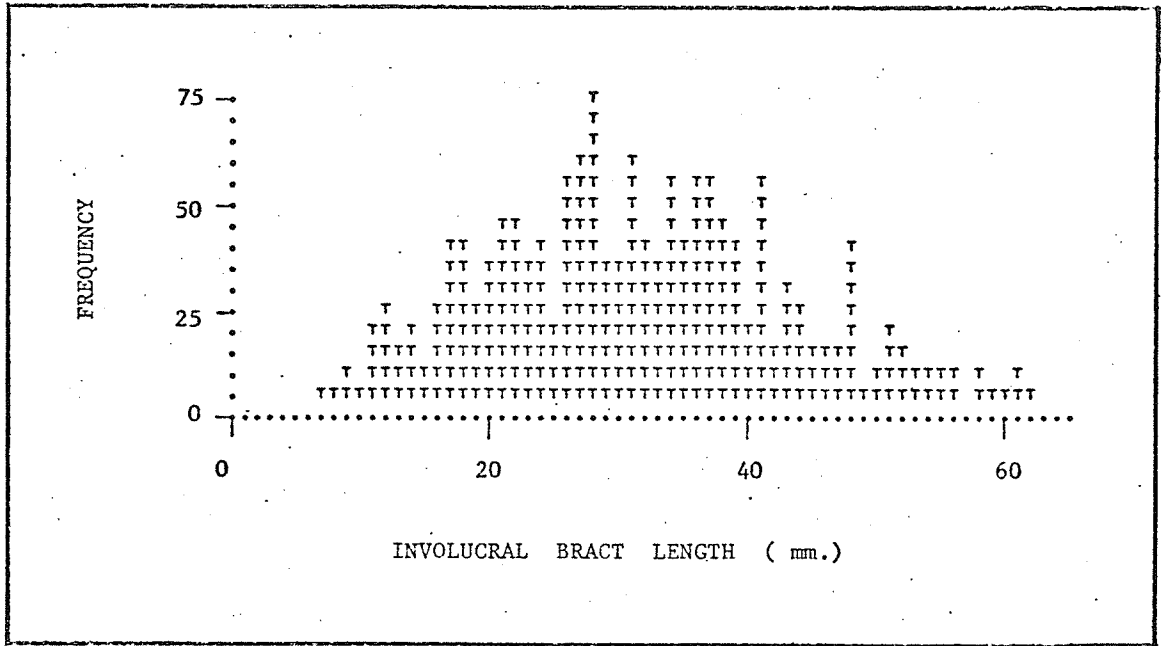
Figure 50. Frequency histogram of floral scale
lengths of specimens from sites 1 to 60
(n = 1,500); abscissa intervals 0.05 mm,
ordinate intervals 5.

Figure 51. Frequency histogram of floral scale widths
of specimens fror sites 1 to 60 (n = 1,500);
abscissa intervals 0.05 mm, ordinate inter-
vals 5.

FREQUENCY

110 —

55 —

0 —

1.0   2.0   3.0   4.0

FLORAL   SCALE   LENGTH (mm.)

FREQUENCY

115 —

60 —

0 —

1.0   2.0   3.0

FLORAL SCALE WIDTH (mm.)

115
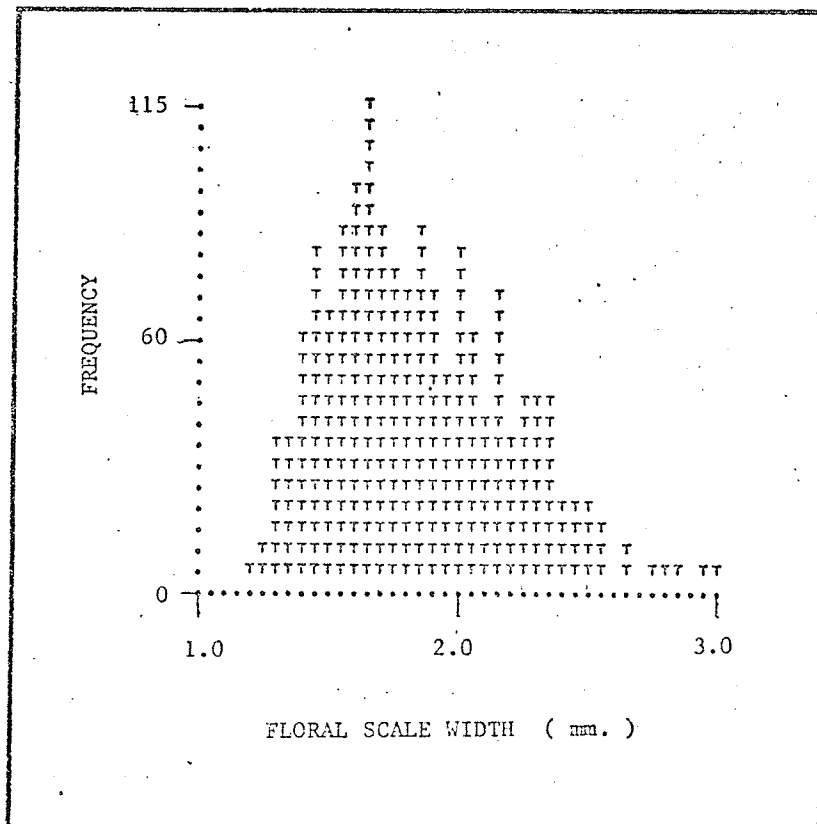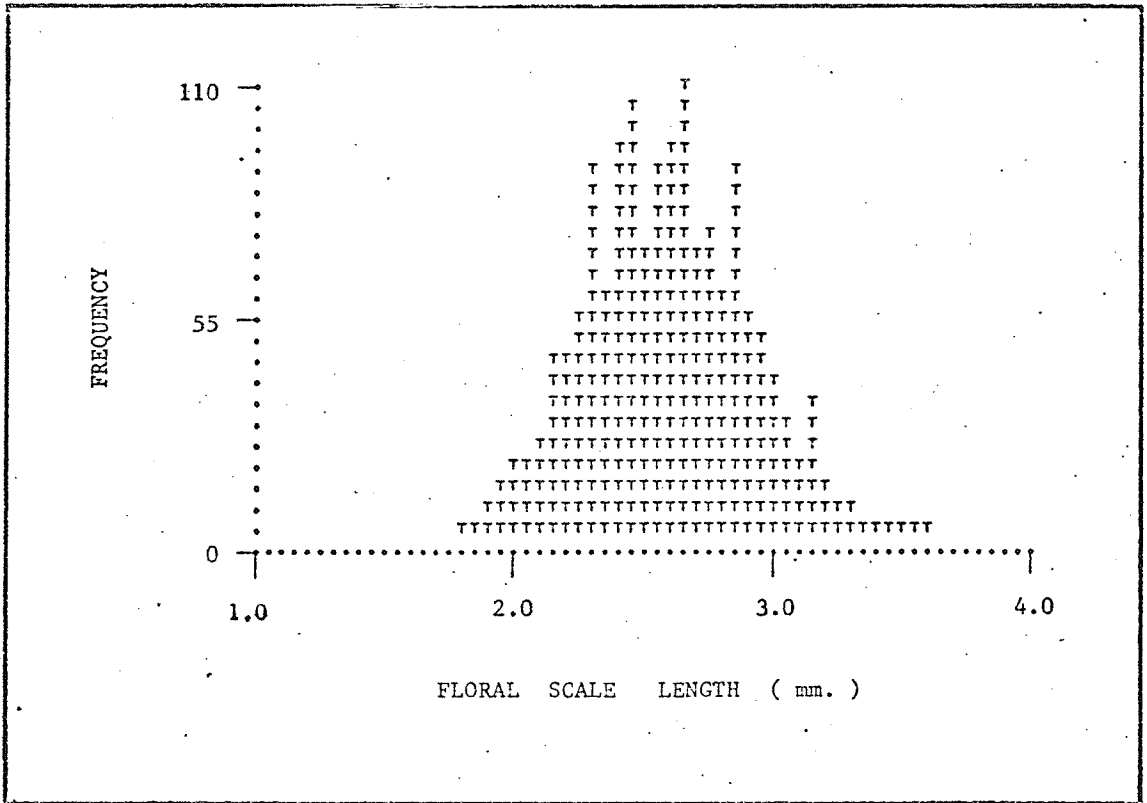
Figure 52.   Scatter diagram of culm diameter and
             number of lacunae. Each circle repre-
             sents the mean of 25 measurements.
             Open circles indicate mean culm color
             scores between 2 and 3 (dark green),
             closed circles represent culm color
             scores between 1 and 2 (glaucous or
             light green).

Figure 53.   Frequency histogram of lacunar diameters
             of specimens from sites 1 to 60
             (n = 1,500); abscissa intervals 0.05 mm,
             ordinate intervals 5.

Top plot:

NUMBER OF LACUNAE (y-axis)

12.0

8.5

5.0

4.5 8.25 12.0

CULM DIAMETER (mm.)

Bottom plot:

FREQUENCY (y-axis)

135

65

0

0.2 1.2 2.2

LACUNAR DIAMETER (mm.)
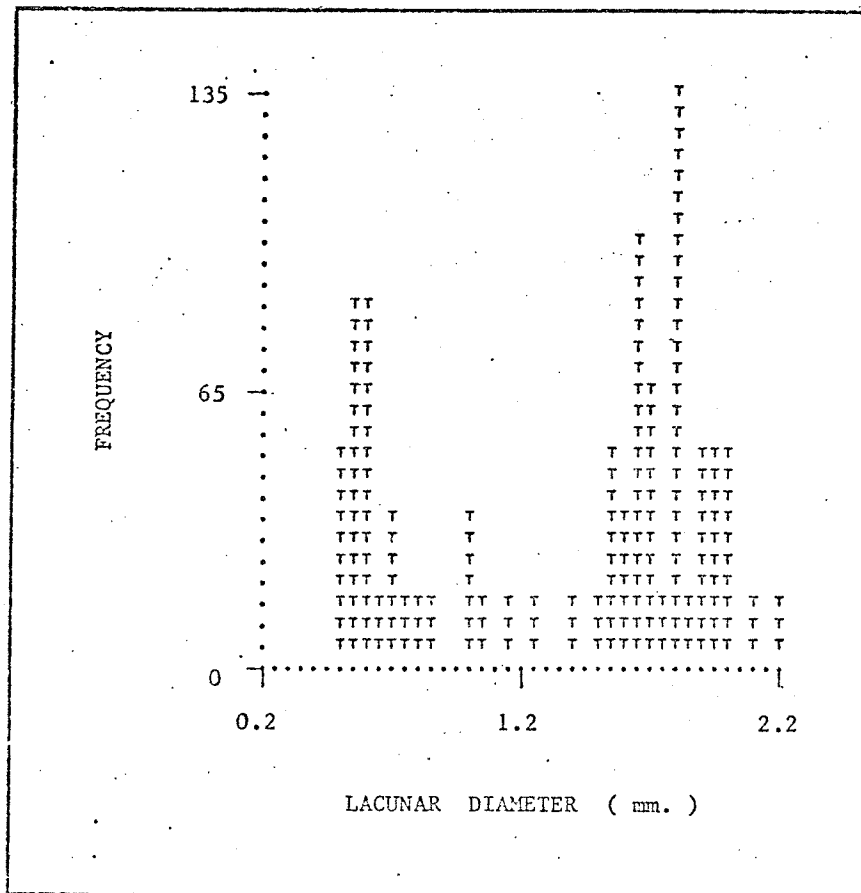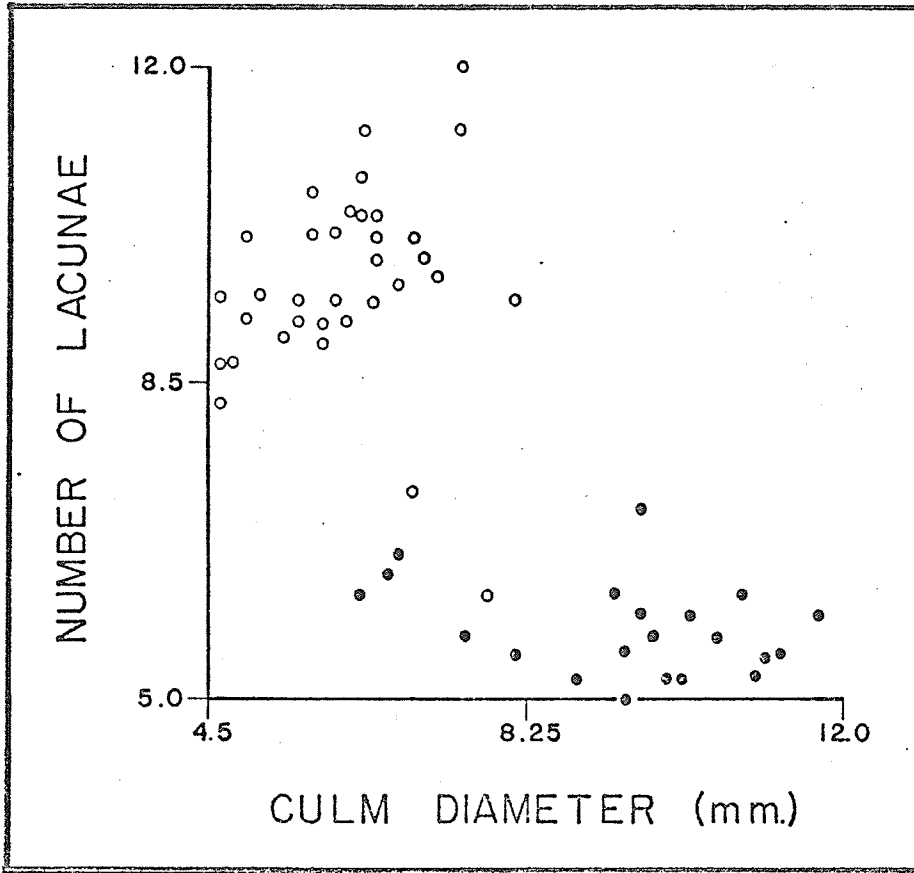
Figure 54.   Cross-section of *S. acutus* culm (x10) showing the numerous, small aerenchymal lacunae.

Figure 55:   Cross-section of *S. validus* culm (x10) showing the large aerenchymal lacunae.

specimens were plotted in a frequency histogram (Figure 53) and showed a strongly bimodal distribution. The previously used technique of defining the three character states was employed to assign the hybrid index score of '0' to lacunar diameters greater than 1.51 mm, '1' to diameters between 0.87 and 1.50 mm, and '2' to diameters less than 0.87 mm. The difference in the size of lacunae between the *S. validus* and *S. acutus* states is indicated in Figures 54 and 55. The more numerous lacunae in the *S. acutus* culm are also much smaller than those of *S. validus*.

The apparent correlation between lacunar diameter and culm color shown in Figure 52 was the basis for assigning the hybrid index values of 0, 1, and 2 to color scores representing the pale green (0), intermediate (1), and olive green (2) shades, as defined on page 53.

A summary of the character states and the hybrid index scores assigned to each is given in Table XIV.

TABLE XIV. SCORES USED TO COMPUTE HYBRID INDEX

Character	Character States		
	S. validus (0)	Intermediate (1)	*S. acutus* (2)
1. Culm color	color scores of 0	color scores of 1	color scores of 2
2. Inflorescence length	> 80.5 mm	47.1–80.4 mm	< 47 mm
3. No. of primary rays	> 13	7–13	< 7
4. Secondary rays	present	--	absent
5. Lacunar diameter	> 1.5 mm	0.9–1.5 mm	< 0.9 mm
6. Clusters of 5 or more spikelets	absent	--	present

2. The hybrid index

The agreement between these six characters in scoring 25 specimens from 60 sites was then tested. The mean scores for 25 specimens from sites 1 - 60 and the hybrid index values assigned to these stands on the basis of the six characters are given in Table XV. All six characters show good agreement in assessing the hybrid index of the stands. For any single stand, the range between hybrid index scores for single characters is always less than one, and usually less than 0.5. Standard deviations accompanying the mean score for each character indicate the variation of scores for individuals within each stand. Culm color, the presence of secondary rays and the lacunar diameter show the highest agreement for scoring individuals within stands; inflorescence length, number of primary rays and the presence or absence of clusters of five or more spikelets show greater variability, as indicated by the higher standard deviations. Two explanations are possible for this variability in agreement. The most obvious cause is that some of the characters are more reliable than others because of inaccuracy in defining the character states to be associated with each of the hybrid index scores. The other possibility is that some characters are intrinsically more variable than others. Because two of the three characters which show high variability are quantitative characters, the former explanation is more likely.

The correlation between scores of individual characters was tested by means of their rank correlation coefficients (Hoel, 1960, p. 255). A matrix of the rank correlation coefficients between all

TABLE XV. MEAN HYBRID INDEX SCORES FOR SIX MORPHOLOGICAL CHARACTERS
AND HYBRID INDEX VALUES ASSIGNED TO SITES 1 to 60

Stand Number	1 $\overline{x}$	1 s.d.	2 $\overline{x}$	2 s.d.	3 $\overline{x}$	3 s.d.	4 $\overline{x}$	4 s.d.	5 $\overline{x}$	5 s.d.	6 $\overline{x}$	6 s.d.	Hybrid Index
1	2	0	1.84	0.37	1.84	0.37	2	0	2	0	2	0	11.7
2	2	0	1.84	0.28	1.92	0.27	2	0	1.76	0.66	2	0	11.5
3	1.76	0.44	1.56	0.51	1.64	0.49	2	0	1.68	0.75	2	0	10.6
4	0	0	0.24	0.44	0.28	0.61	0.16	0.55	0.56	0.92	0	0	1.26
5	2	0	1.76	0.44	1.88	0.33	2	0	1.52	0.87	2	0	11.16
6	2	0	1.68	0.48	1.76	0.44	2	0	2	0	2	0	11.46
7	0.24	0.44	0.08	0.28	0.52	0.51	0	0	0	0	0	0	0.84
8	0	0	0.44	0.51	0.32	0.56	0.16	0.55	0.16	0.55	0	0	1.08
9	2	0	2	0	2	0	2	0	1.68	0.75	2	0	11.64
10	2	0	1.88	0.33	1.88	0.33	2	0	1.89	0.55	2	0	11.64
11	2	0	1.48	0.51	1.68	0.48	2	0	2	0	2	0	11.16
12	0	0	0.6	0.58	1.16	0.69	0.48	0.87	0.4	0.82	0	0	2.64
13	2	0	1.76	0.44	1.84	0.37	1.92	0.40	1.92	0.40	2	0	11.46
14	2	0	1.96	0.20	1.92	0.28	2	0	1.92	0.40	2	0	11.76
15	2	0	1.96	0.20	1.88	0.33	2	0	1.44	0.92	2	0	11.28

1. culm color

2. inflorescence length

3. number of primary rays

4. presence or absence of secondary rays

5. lacunar diameter

6. presence or absence of clusters of five or more spikelets

TABLE XV (continued)

Stand Number	1 $\overline{x}$	1 s.d.	2 $\overline{x}$	2 s.d.	3 $\overline{x}$	3 s.d.	4 $\overline{x}$	4 s.d.	5 $\overline{x}$	5 s.d.	6 $\overline{x}$	6 s.d.	Hybrid Index
16	2	0	1.80	0.41	1.96	0.20	2	0	1.92	0.40	2	0	11.7
17	0	0	0.16	0.37	0.32	0.48	0	0	0.64	0.95	0	0	1.14
18	0	0	0.76	0.66	0.44	0.65	0.64	0.95	0.64	0.95	0	0	2.46
19	0.16	0.47	0.72	0.46	0.76	0.83	0.48	0.87	0.08	0.40	0	0	2.22
20	1.43	0.877	1.80	0.41	1.96	0.20	2	0	1.92	0.40	1.49	0.74	10.62
21	2	0	1.88	0.33	1.84	0.37	1.68	0.75	1.84	0.55	2	0	11.22
22	0.187	0.40	0.04	0.2	0	0	0	0	0	0	0.96	0.60	1.2
23	0.32	0.63	0.6	0.71	0.72	0.74	0.32	0.75	0.08	0.40	0.56	0.77	2.54
24	0	0	0	0	0.08	0.28	0	0	0.08	0.40	0	0	0.16
25	2	0	1.8	0.41	1.8	0.41	2	0	1.84	0.55	1.96	0.20	11.4
26	2	0	1.92	0.28	1.88	0.33	2	0	2	0	1.91	0.29	11.46
27	1.92	0.28	1.80	0.41	1.92	0.28	1.92	0.40	1.68	0.75	1.92	0.28	11.16
28	0.90	0.83	0.76	0.72	0.60	0.76	0.64	0.95	1.52	0.87	1.25	0.85	5.7
29	2	0	1.92	0.28	1.92	0.28	2	0	1.92	0.40	2	0	11.76
30	0.12	0.33	0.28	0.46	0.20	0.41	0	0	0.24	0.66	0.16	0.38	1.02

1. culm color

2. inflorescence length

3. number of primary rays

4. presence or absence of secondary rays

5. lacunar diameter

6. presence or absence of clusters of five or more spikelets

TABLE XV (continued)

Stand	1		2		3		4		5		6		Hybrid
Number	$\overline{x}$	s.d.	$\overline{x}$	s.d.	$\overline{x}$	s.d.	$\overline{x}$	s.d.	$\overline{x}$	s.d.	$\overline{x}$	s.d.	Index
31	0	0	0.40	0.5	0.44	0.58	0	0	0.08	0.40	0	0	0.90
32	0.28	0.54	0.16	0.37	0.04	0.20	0	0	0.24	0.66	0	0	0.72
33	0.17	0.49	0.44	0.58	0.32	0.48	0.24	0.66	0.48	0.87	0.36	0.64	2.04
34	0.96	0.76	1.48	0.65	1.32	0.75	1.44	0.92	1.84	0.55	1.04	0.74	8.1
35	2	0	1.76	0.44	1.80	0.41	2	0	2	0	2	0	11.58
36	2	0	1.76	0.44	1.80	0.41	2	0	2	0	2	0	11.58
37	1.96	0.20	0.52	0.71	0.40	0.71	0.24	0.66	0.32	0.75	0	0	3.42
38	2	0	2	0	1.88	0.33	2	0	1.84	0.55	2	0	11.7
39	0.52	0.51	0.44	0.51	0	0	0	0	0.32	0.75	0.84	0.37	2.1
40	0	0	0.56	0.58	0.28	0.54	0.48	0.87	0.32	0.75	0	0	1.62
41	2	0	2	0	1.76	0.44	2	0	2	0	2	0	11.76
42	2	0	2	0	1.88	0.33	2	0	2	0	1.91	0.29	11.82
43	2	0	1.72	0.46	2	0	2	0	2	0	2	0	11.76
44	2	0	1.92	0.28	1.68	0.48	2	0	2	0	2	0	11.58
45	2	0	1.56	0.51	1.80	0.41	2	0	2	0	2	0	11.34

1. culm color

2. inflorescence length

3. number of primary rays

4. presence or absence of secondary rays

5. lacunar diameter

6. presence or absence of clusters of five or more spikelets

TABLE XV (continued)

Stand	1		2		3		4		5		6		Hybrid
Number	$\overline{x}$	s.d.	$\overline{x}$	s.d.	$\overline{x}$	s.d.	$\overline{x}$	s.d.	$\overline{x}$	s.d.	$\overline{x}$	s.d.	Index
46	1.12	0.33	1.84	0.37	1.92	0.28	2	0	2	0	1.96	0.19	10.86
47	2	0	2	0	2	0	2	0	2	0	1.27	0.45	11.28
48	0.17	0.48	0.64	0.57	0.32	0.56	0	0	0.08	0.40	0.58	0.64	1.8
49	2	0	1.92	0.28	1.92	0.28	2	0	2	0	2	0	11.82
50	2	0	1.84	0.37	1.84	0.37	2	0	2	0	2	0	11.76
51	2	0	1.64	0.49	1.76	0.44	2	0	2	0	2	0	11.4
52	1.56	0.51	1.72	0.46	1.80	0.41	2	0	1.8	0.55	1.92	0.28	10.8
53	0.83	0.65	1.52	0.65	1.44	0.77	1.20	1	1.6	0.82	0.96	0.71	7.56
54	2	0	1.80	0.41	1.80	0.41	1.92	0.40	2	0	2	0	11.52
55	0	0	0.24	0.44	0.08	0.28	0	0	0.4	0.82	0.64	0.49	1.38
56	2	0	1.92	0.28	1.88	0.33	2	0	2	0	2	0	11.82
57	2	0	1.80	0.41	1.92	0.28	2	0	1.92	0.40	2	0	11.64
58	2	0	1.64	0.57	1.88	0.33	2	0	2	0	2	0	11.52
59	1.52	0.51	1.96	0.20	2	0	1.76	0.66	2	0	2	0	11.22
60	1.16	0.37	2	0	1.80	0.41	2	0	2	0	2	0	10.98

1. culm color

2. inflorescence length

3. number of primary rays

4. presence or absence of secondary rays

5. lacunar diameter

6. presence or absence of clusters of five or more spikelets

pairs of the six characters is presented in Table XVI. The high correlation between all pairs of characters supports the choice of characters and the definition of the character states. It also indicates that the characters chosen from the factor analysis are in agreement with the additional characters, lacunar diameter and culm color.

The mean hybrid index values for each stand (the last column of Table XII) are based on the hybrid index scores of 25 specimens for the six characters. The scores of the specimens were summed and divided by 25 to give the mean value for the stand. Thus, a pure stand of *S. acutus* would be represented by 25 specimens scoring '2' for each character, or summing the scores, 25 specimens each with a hybrid index of 12. The resulting hybrid index value for the stand would then be: 25 x 12 ÷ 25 = 12. Pure stands of *S. validus* would have hybrid index values of '0'. From Table XII, hybrid index values for sites 1 to 60 ranged from 0.84 (site 7) to 11.82 (sites 42, 49, and 56). These stands represent the extreme ends of the scale of morphological variability. The remaining 56 stands fall between these extremes, but tend to be clustered towards either end of the scale, with only three stands having hybrid index values near the center (sites 28, 34, and 53).

The distribution of these stands on the hybrid index scale of zero to twelve is depicted in Figure 56. With the exception of the three intermediate stands, there is complete discontinuity in the distribution.

The intermediate values for sites 28, 34, and 53 could arise

TABLE XVI. MATRIX OF RANK CORRELATION
COEFFICIENTS OF MEAN HYBRID
INDEX SCORES OF 60 STANDS FOR
SIX MORPHOLOGICAL CHARACTERS

(p < 0.01 for r > 0.475)

* characters	1	2	3	4	5	6
1		0.85	0.91	0.89	0.94	0.82
2			0.84	0.87	0.87	0.79
3				0.92	0.83	0.88
4					0.95	0.91
5						0.88
6						

*

1. culm color
2. inflorescence length
3. number of primary rays
4. presence or absence of secondary rays
5. lacunar diameter
6. presence or absence of clusters of five or more spikelets

125

Figure 56. Frequency histogram of hybrid index
scores for sites 1 to 60. The inter-
mediate stands (sites 28, 34, and 53)
are mixtures of the two morphological
types.
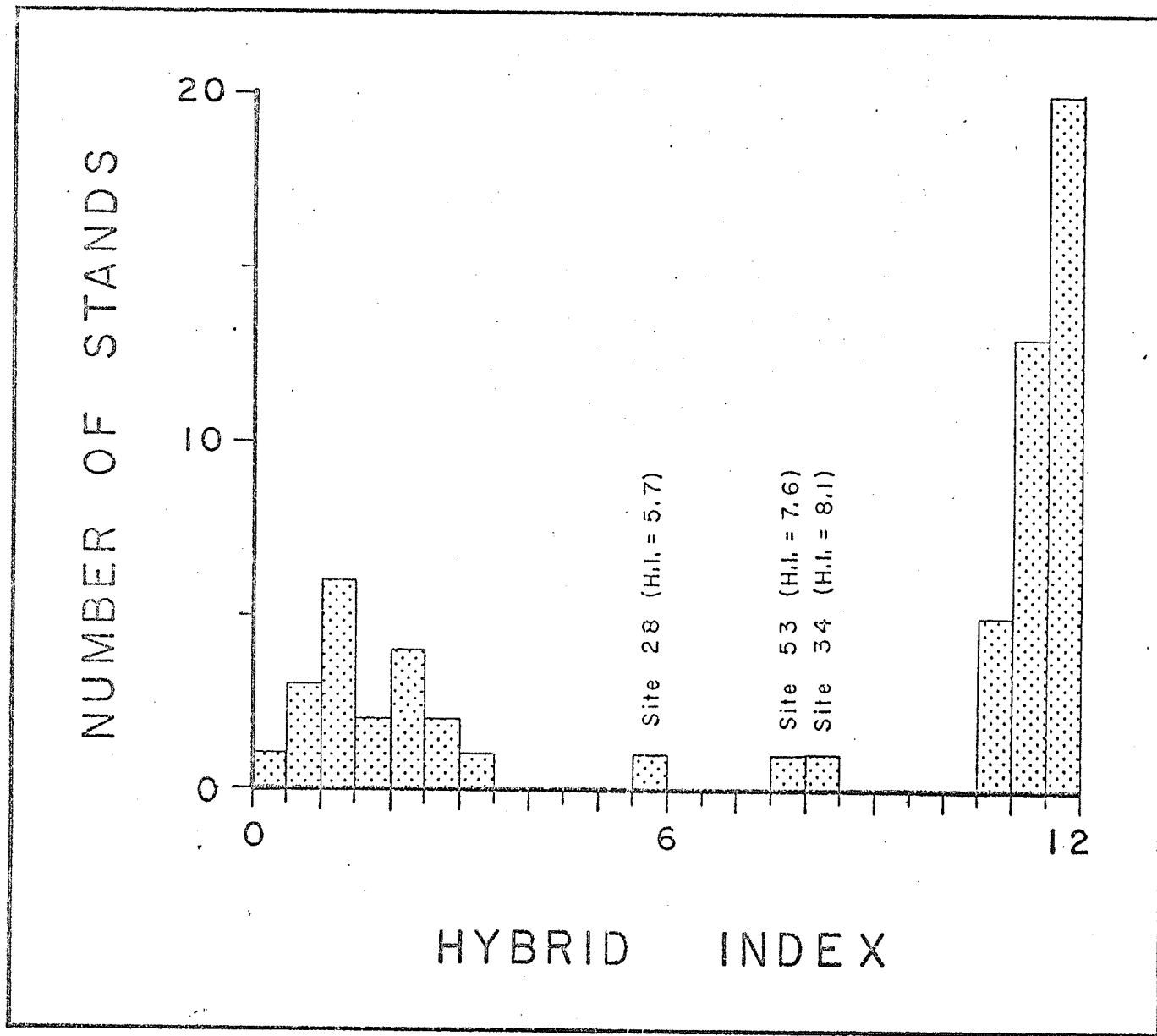
from one of two sources; either the specimens examined are all morphologically intermediate or they represent mixtures of the two morphological types.

Returning to Table XII, the standard deviations for scores on all characters for these three sites are high, even for those characters that show little or no variation for the other stands (characters 1, 4, and 6). This suggests a mixed population of the two morphological types. This is verified if the hybrid index scores for the individual specimens of the three stands are plotted. Figure 57 indicates the complete discontinuity between the two groups in each case. No morphologically intermediate specimens were found in any of these stands, suggesting that little or no hybridization was occurring.

One additional mixed stand was found at site 20 (Figure 58); however it did contain a small number of morphologically intermediate individuals. Although the hybrid index score (10.6) indicates a *Scirpus acutus* stand, there was a narrow band of *S. validus* along the open water margin, with a few scattered individuals showing intermediate morphological characters. Because the *S. validus* and the putative hybrids were in small numbers at one edge of the stand, a systematic sampling procedure resulted in their presence being masked by the predominant numbers of *S. acutus* specimens (Figure 59). A special collection was made from this site in order to collect specimens showing the complete range of variation. The range in inflorescence form and the hybrid index scores of each specimen are shown in Figure 60. It is evident that some specimens are morpho-

Figure 57. Frequency histograms of the hybrid index
scores of individual specimens from
sites 28, 34, and 53 indicating the mor-
phologically mixed nature of these stands.
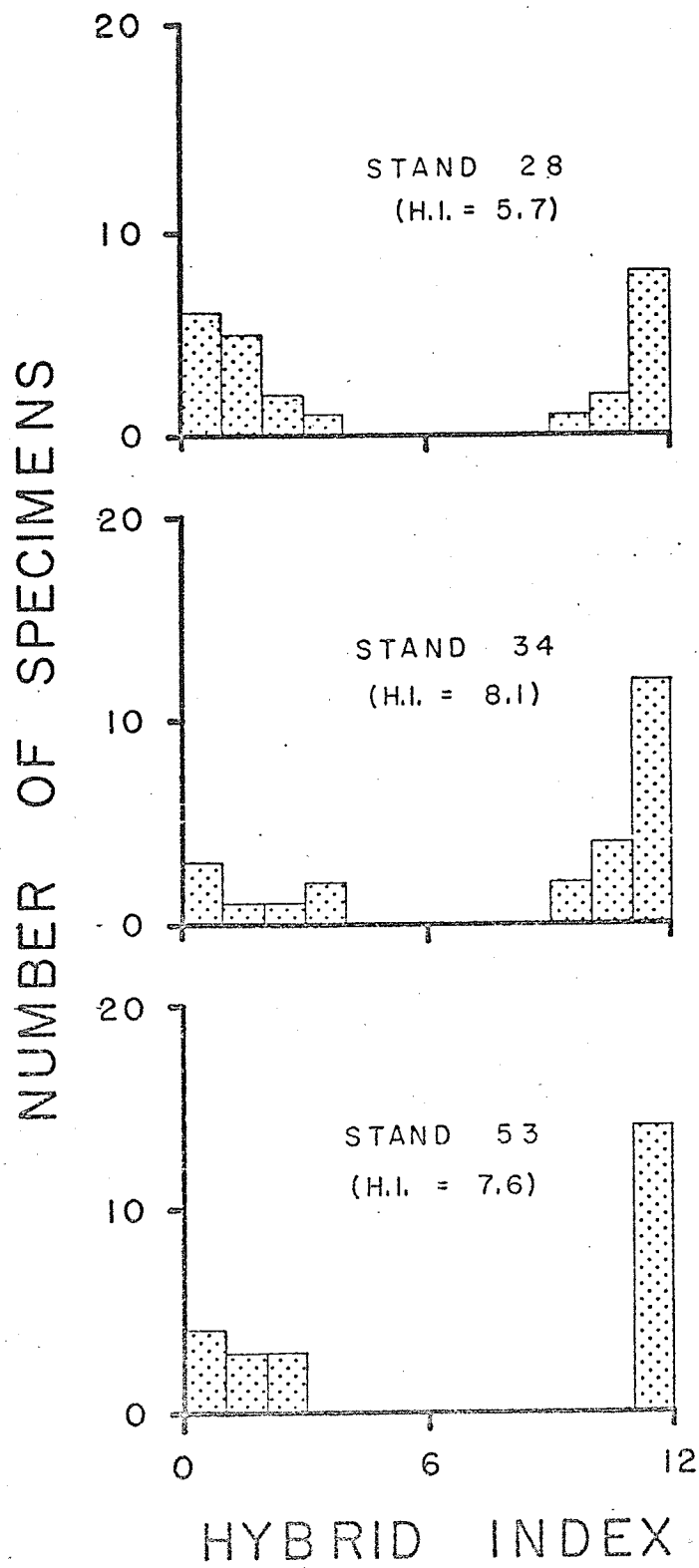
Figure 58. Site 20, Portage Creek. *S. validus*
            growing on the open-water margin of
            the creek, with *S. acutus* in shallower
            water in the background. At the time
            photo was taken (September 2, 1972),
            the water in the creek was very low,
            exposing the mud bar on which this
            S. validus had germinated during a
            previous low-water period in 1965.

Figure 59. Frequency histogram of hybrid index
            scores of individual specimens from
            site 20. The large proportion of
            S. acutus specimens and the relatively
            small number of *S. validus* specimens
            created a high hybrid index score which
            masked the mixed nature of the stand.

STAND 20
(H.I. = 10.6)
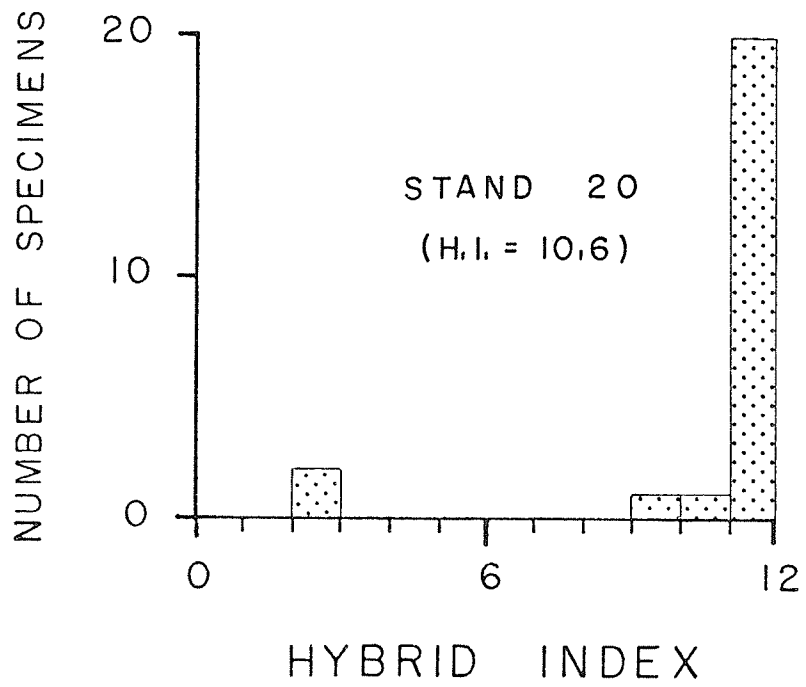
Figure 60. Six inflorescences collected from site 20
showing the range in inflorescence form.
Typical *S. validus* (a) has a hybrid index
score of zero, typical *S. acutus* (f) has
a score of 12, and specimens b, c, d, e
have intermediate scores. The abnormally
narrow spikelets of these latter speci-
mens is due to the absence of developing
achenes.
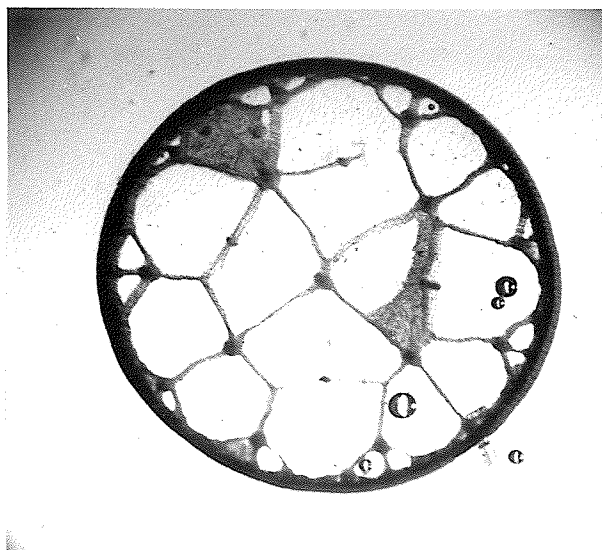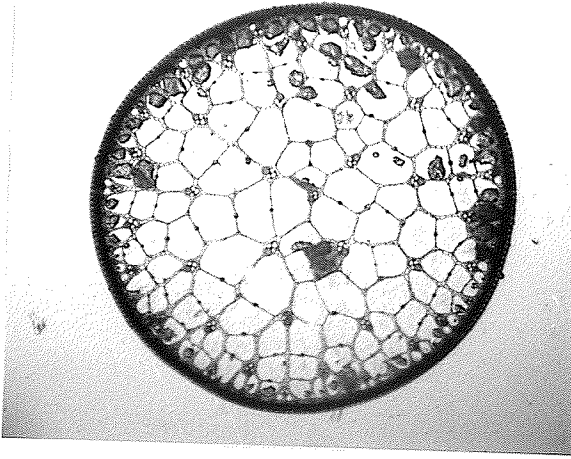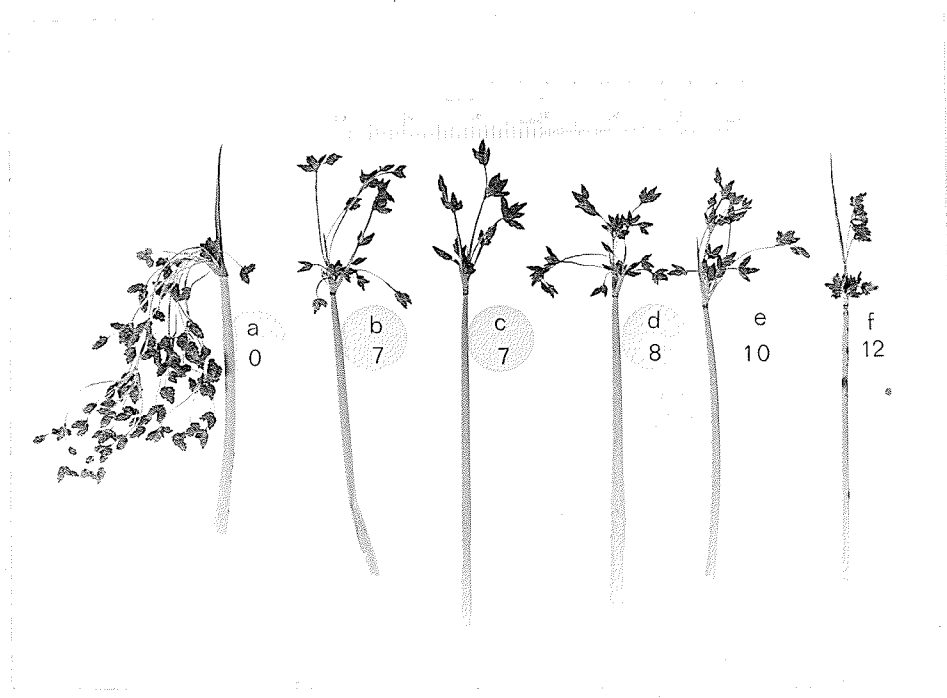
logically intermediate, and it is probably significant that the spikelets of these individuals bear only one or two apparently normal, although immature achenes each, which accounts for their narrow appearance.

3. Additional morphological characters

Three additional characters were examined because of their prominence in the literature as diagnostic characters. The results of analysis and comparison with the hybrid index assessment are presented here for subsequent discussion.

Floral scale color has been used to distinguish *S. validus* from *S. acutus* by numerous authors (Beetle, 1941; Smith, 1969; Dabbs, 1971). An examination of herbarium specimens and some of the author's material indicated that, in general, three character states existed. Material resembling *S. validus* in other characters tended to have floral scales which were suffused with a rusty brown throughout; *S. acutus* specimens showed the opposite state, with a pale grey to tan background color with variable numbers of linear red dots. Between the two extremes, many scales show a partial suffusion with red, usually near the tip, or very dense red spotting. These three states were arbitrarily defined and assigned values of 1 (suffused with red), 2 (red near tip or very dense red spotting), and 3 (dominantly tan or grey, with some red spotting).

Figure 61 represents the correlation of mean scale color scores of 25 scales for sites 1 - 60 when plotted against the hybrid index values of the stands (identical values represented by only one

Figure 61. Scatter diagram of the mean floral scale
color scores of 25 specimens for sites
1 to 60 plotted against the hybrid index
score of the stand. Scales suffused
with red (scores near 1) are associated
with stands diagnosed as *S. validus* by
the hybrid index (H.I. < 4.0); scales
with a tan or grey color (scores near 3)
are associated with stands diagnosed as
S. acutus (H.I. > 10).

circle). Two groups are apparent, one at mean scale colors near '1', with low hybrid index values, and the second at hybrid index values near 12, with much higher mean scale color scores. The position of the mixed stands at hybrid index values of 5.7, 7.6 and 8.1 are also intermediate in scale color. Thus, these three arbitrarily defined color states do show a correlation with the hybrid index assessment.

A second character, the scale length to achene length ratio, was initially examined by plotting its frequency histogram (Figure 62). This shows a unimodal distribution of 1,500 measurements indicating that there is no discontinuity between groups. When the means of 25 scale lengths and achene lengths for sites 1 - 60 were plotted with the hybrid index assessment for each site indicated, a general trend is apparent (Figure 63). The longest scales were associated with *S. acutus* stands (open circles), while *S. validus* stands occupied the lower to mid-range of the scale. Because of the wide range in variation, however, a t test (Klugh, 1970, p. 181) of the means of the two groups was not significant (t = 1.87; df = 1,498; p < 0.01).

The third character examined, spikelet shape and size, was compared for the two groups defined by the hybrid index. A scatter diagram of the mean spikelet lengths and widths of 25 specimens from sites 1 - 60 is presented in Figure 64. Spikelet widths show complete overlap for the two groups defined by the hybrid index; the longest spikelets (greater than 7 mm) are associated with the *S. acutus* group (open circles), but in the range from 5 - 7 mm, both *S. acutus* and *S. validus* stands show complete overlap. Again

Figure 62.   Frequency histogram of the ratio of
floral scale length to achene length
for specimens from sites 1 to 60
(n = 1,500); abscissa intervals 0.02 mm,
ordinate intervals 5.

Figure 63.   Scatter diagram of mean scale length
and mean achene length for specimens
from sites 1 to 60. Open circles rep-
resent stands with hybrid index scores
greater than 10 (*S. acutus*), closed
circles represent stands with hybrid
index scores less than 4. Half-closed
circles indicate the three mixed
stands.

RATIO OF ACHENE TO SCALE LENGTHS

MEAN SCALE LENGTH
(mm.)
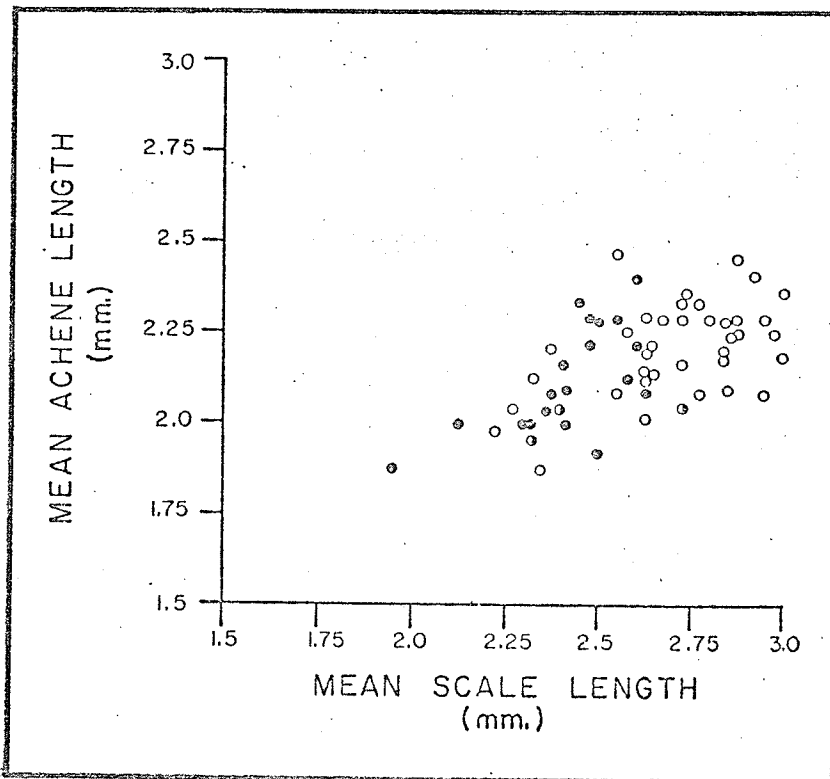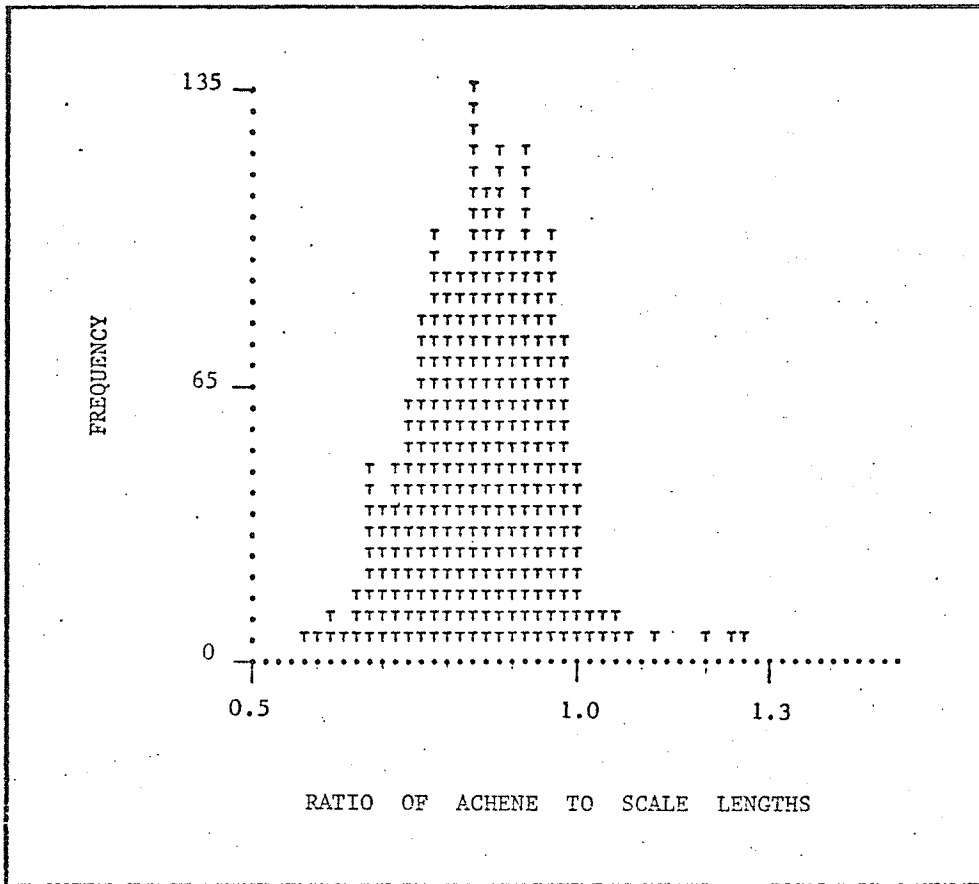
Figure 64. Scatter diagram of spikelet lengths and
widths of specimens from sites 1 to 60,
each circle representing the mean of 25
measurements. Open circles represent
the stands with hybrid index scores
greater than 10 (*S. acutus*), closed
circles represent hybrid index scores
less than 4 (*S. validus*). Half-open
circles represent mixed stands.
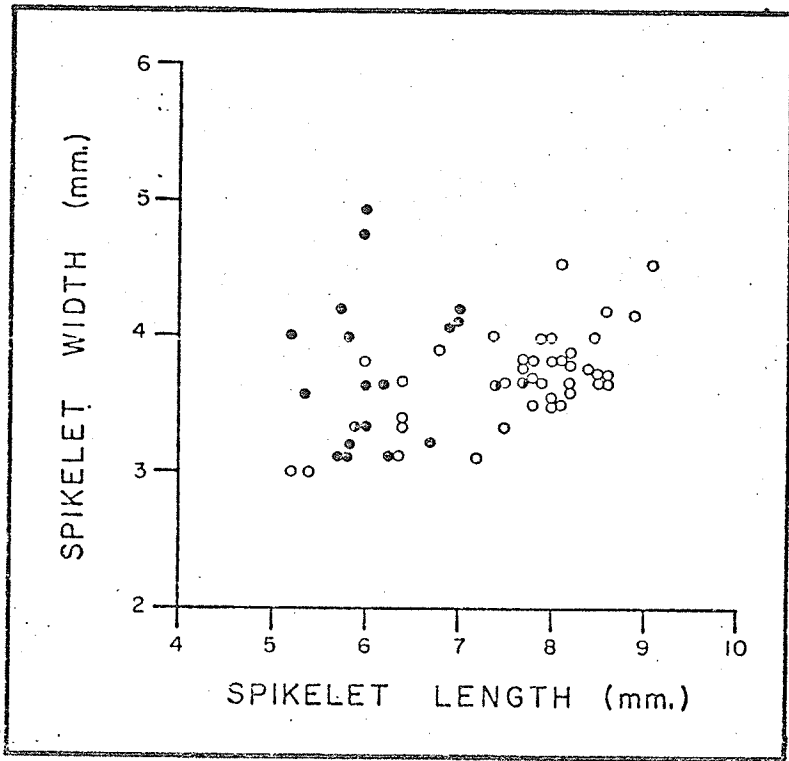
no statistical difference exists between the group means ($t = 2.0$,

$df = 1,498$; $p < 0.01$).

E. Environmental parameters

In this section, a number of environmental parameters measured in the five study areas are related to differences of stand performance of the two morphological types diagnosed by the hybrid index.

1. Substrate texture

Considerable variation of substrate texture was encountered, not only between the five study areas but also between sites within one area. Sites from the Langruth study area had the coarsest 'soils', the dominant fraction being sand. The proportion of sand varied from 60% at site 13 to 85% at site 15. The silt fraction was consistently low, 4% at site 4 to 11% at site 38; clay varied from 10% at site 2 to 32% at site 13.

The mud samples from the Minnedosa sites were also dominated by sands, but tended to be more variable than those from Langruth. The sand fraction varied from 15 - 89%, silt from 1 - 35%, and clay from 10 - 62%.

The variability in sites at The Pas reflects the variation in the parent materials. Sites 24 - 31 west of The Pas showed high silt and clay fractions, sand representing only 17% at both sites. In the Murphy Lake-Murphy Extension samples, sites 41 and 46 were predominantly sand and clay, while 34 and 42 were high in both silt and clay fractions. Samples from site 36 on Grace Lake were almost pure silt (81%). Data were not available for site 43, but the substrate was observed to be a coarse sand with numerous boulders.

The Netley sites were uniformly high in sand (38 - 69%) and clay (25 - 42%), silt-sized particles comprising 20% or less of the samples.

Delta samples were also clay-dominated, with the exception of site 33, which was located in an old creek channel (Figure 14) and had a high sand content, 43%. Table XVII summarizes these substrate particle size distributions for sites 1 - 60.

No difference in substrate textures between the *S. validus* and *S. acutus* stands was found. Figure 65 positions stands 1 - 60 with respect to the proportions of sand, silt and clay in the substrate of each site. The closed circles represent stands determined to be *S. acutus* on the basis of hybrid index values; open circles indicate *S. validus* stands. The distributions of both *S. acutus* and *S. validus* are completely overlapping, although *S. acutus* stands tend to have a wider distribution with respect to proportion of clay. This is probably a reflection of the wider range of habitats occupied by this form.

2. Water depth and water level fluctuations

The mean depth of water at sites 1 to 60 was calculated from 25 measurements obtained by systematic sampling along the water-depth gradient. The growth response of the two morphological types to different water depths is presented in Figure 66 and accompanying Table XVIII. The vertical axis represents the stand performance parameter; the hybrid index and mean water depths of each stand are plotted on the horizontal axes. Each of the stakes represents a

TABLE XVII. SOIL PARTICLE SIZE DISTRIBUTION OF SITES 1 to 60

Stand Number	% Sand	% Silt	% Clay	Stand Number	% Sand	% Silt	% Clay
1	69	6	25	31	17	41	42
2	83	7	10	32	10	38	52
3	21	32	47	33	43	19	38
4	47	12	41	34	20	28	52
5	81	8	11	35	41	23	36
6	75	10	15	36	8	81	11
7	38	20	42	37	14	28	58
8	45	14	41	38	71	11	18
9	69	7	24	39	19	11	60
10	65	12	23	40	50	14	36
11	57	6	31	41	46	4	33
12	52	16	32	42	15	38	47
13	60	8	32	43	ND	ND	ND
14	71	10	19	44	36	17	47
15	85	4	11	45	0	58	42
16	64	9	27	46	0	37	63
17	69	6	25	47	10	28	62
18	60	22	18	48	4	29	67
19	53	16	32	49	23	41	36
20	15	48	37	50	11	29	60
21	26	35	39	51	19	12	69
22	11	36	53	52	23	38	39
23	19	21	60	53	12	31	57
24	17	11	72	54	13	27	60
25	15	23	62	55	12	31	57
26	60	19	21	56	38	25	47
27	89	1	10	57	9	38	53
28	19	28	53	58	0	38	62
29	70	8	22	59	11	29	60
30	28	19	53	60	22	31	48
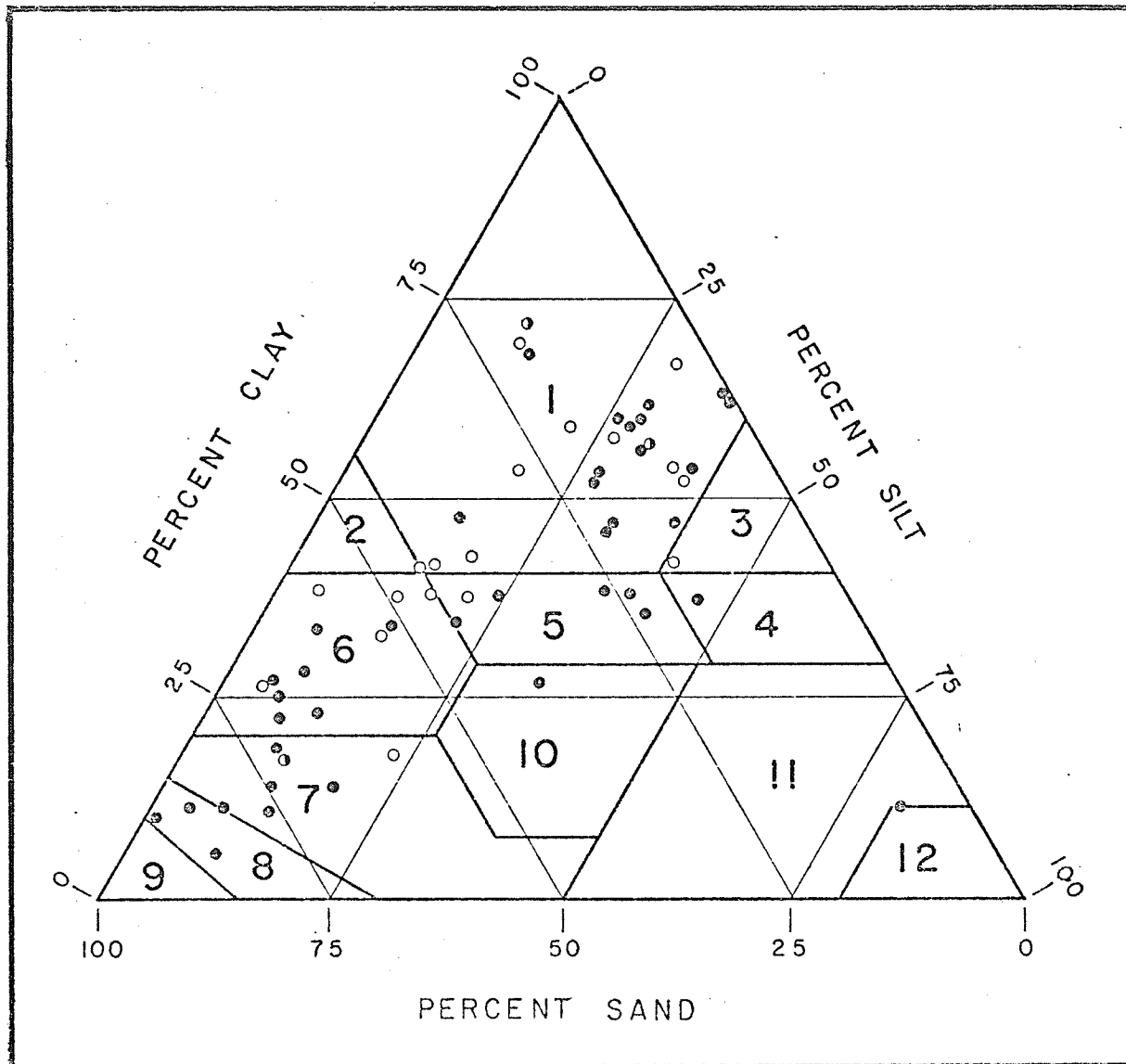
Figure 65. Distribution of sites 1 to 60 on a 'soil texture triangle' (Buckman and Brady, 1960). *S. acutus* stands represented by closed circles, *S. validus* by open circles. See facing table for actual percentages for each site. Numbers refer to textural names as follows:

1. clay	5. clay loam	9. sand
2. sandy clay	6. sandy clay loam	10. loam
3. silty clay	7. sandy loam	11. silt loam
4. silty clay loam	8. loamy sand	12. silt

TABLE XVIII.   MEAN WATER DEPTH, HYBRID INDEX, AND STAND PERFORMANCE

Site Number	Hybrid Index	Stand Performance	Mean Water Depth (cm)	Site Number	Hybrid Index	Stand Performance	Mean Water Depth (cm)
1	11.7	20.2	25	31	0.9	86.2	13.2
2	11.5	25.3	10.7	32	0.7	41.2	25.9
3	10.6	25.0	0.3	33	2	65.3	0
4	1.3	41.5	0	34	8.1	4	45.8
5	11.2	24.3	27.1	35	11.6	21.8	41.8
6	11.5	77.6	11.6	36	11.6	22.8	70
7	0.8	29.8	4	37	3.4	4	48.3
8	1.1	35.5	22	38	11.7	26.4	0
9	11.6	34	0	39	2.1	103.7	0
10	11.6	9.9	0	40	1.6	23	6.2
11	11.2	12.5	37.1	41	11.8	24	18.4
12	2.6	21.1	23.3	42	11.8	9.9	11.9
13	11.5	25	27.6	43	11.8	11.1	42.4
14	11.8	29.6	19	44	11.6	45.1	12.1
15	11.3	31.3	2.5	45	11.3	53.5	18.1
16	11.7	10.1	42.5	46	10.9	68.9	27
17	1.1	29.9	0.5	47	11.3	26.3	81.8
18	2.5	40.2	13.3	48	1.8	45.6	0
19	2.2	10	18.3	49	11.8	53.9	29.8
20	10.6	79.5	16.6	50	11.8	69.9	21.2
21	11.2	54.8	0.2	51	11.4	17.8	16.9
22	1.2	45.1	0	52	10.8	42.2	37.5
23	2.5	37.8	0	53	7.6	36.6	0
24	0.2	104.3	0	54	11.5	62.1	16.2
25	11.4	42.3	12.8	55	1.38	67.4	0
26	11.5	12.8	38.4	56	11.8	144.3	26.5
27	11.2	48	4.7	57	11.6	18	72.4
28	5.7	74.9	17.1	58	11.5	63.5	39.9
29	11.8	14.6	23.3	59	11.2	57.2	13.6
30	1	70.6	21.5	60	11	46.8	27.6
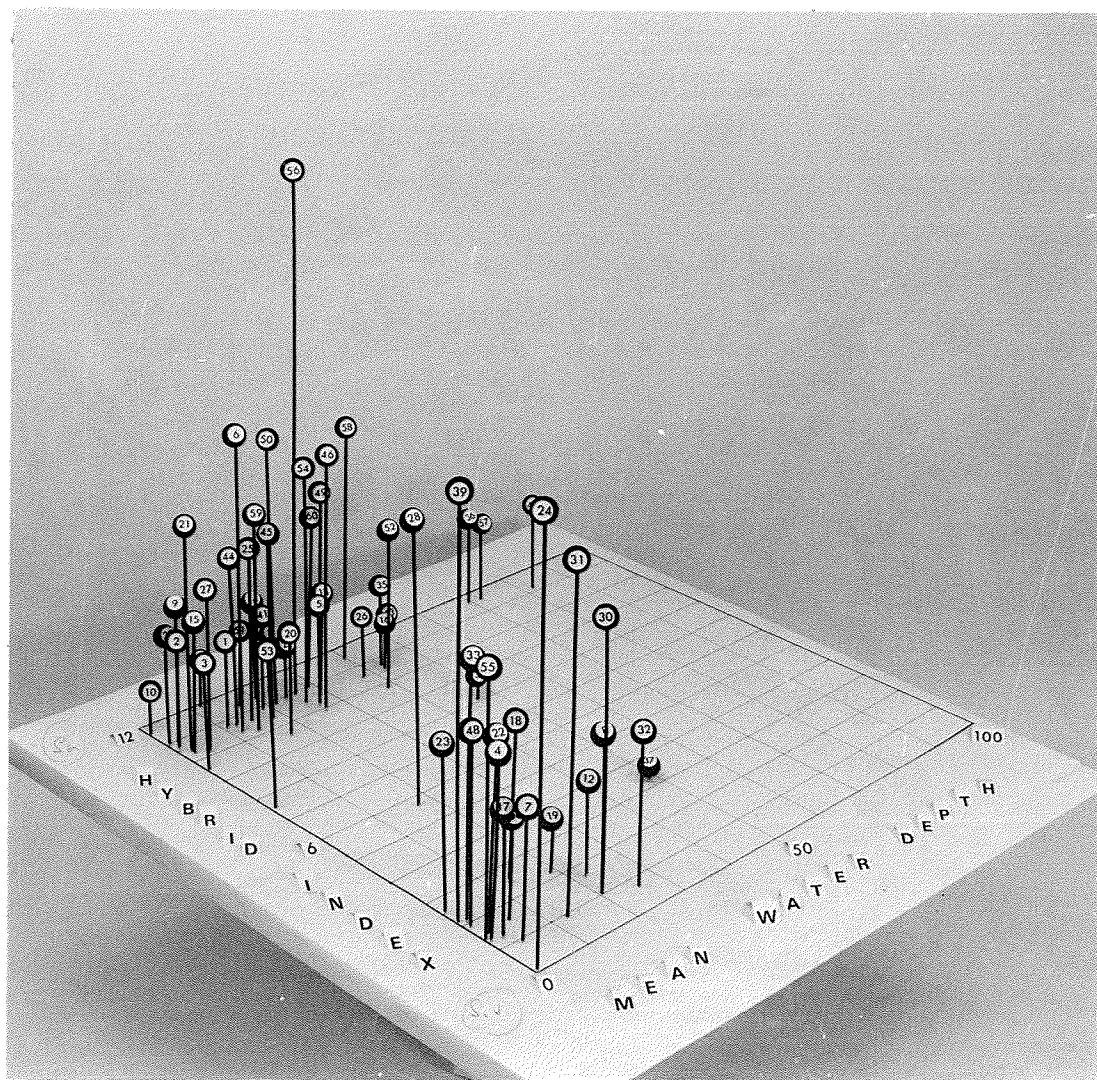
Figure 66. The relationship between mean water depth, the hybrid index and stand performance (vertical axis) at sites 1 to 60. The numbers on the spheres identify the stands. The height of the spheres above the horizontal plane indicates the stand performance values; see facing table for actual values. Intervals on the water depth scale are 10 cm, intervals on the hybrid index scale are 1.

stand, identified by the site number at the top.

The *S. validus* group at the low end of the hybrid index scale is restricted to mean water depths of less than 50 cm. The highest stand performance values, sites 39, 24 and 31 are associated with depths less than 20 cm; stands growing in mean water depths greater than this show reduced stand performance. Site 37, growing at a mean depth of 48.3 cm shows the lowest stand performance of the group of stands.

The *S. acutus* stands clustered at the upper end of the hybrid index scale show a considerably wider range of mean depths, from 0 - 82 cm (site 47, partially hidden). The stand performance of those stands near 0 cm is very low (site 10 = 9.9), but stands in progressively deeper water show increased stand performance, to an optimum in the range of 15 - 40 cm. Those stands at depths greater than 40 cm again show reduced stand performance, indicating an optimum mean depth range from 15 - 40 cm. Although depths in this range produce the greatest stand performance values, *S. acutus* is frequently observed growing at depths of 1.5 - 2 m. Under such circumstances, however, the culms rarely bear inflorescences and grow very sparsely. Such a stand is illustrated in Figure 67, growing at a depth of 160 cm.

The mixed stands, sites 28, 34, and 53, are positioned near the middle of the hybrid index scale at depths of 17.1, 45.8, and 0 cm, respectively. As would be expected of a mixed stand, site 28 at the intermediate depth showed the highest stand performance.

The relationship portrayed visually in Figure 66 indicates a

Figure 67.   Stand of *S. acutus* growing in water 160 cm
             deep. Note the low density of culms and
             the absence of inflorescences. (Simpson
             Bay, Delta Marsh, August 6, 1971)

significantly different response of the two groups to different water
depths. The relationship is also statistically significant (t = 3.53,
df = 58, p < 0.01), *S. acutus* occupying deeper water than *S. validus*.

Field observations on the effect of changing water levels
indicate that *S. validus* is unable to tolerate sustained water depths
greater than 30 cm. Five stands of *S. validus* which volunteered on
the Ducks Unlimited Murphy Extension project following a drawdown
were observed in 1970 and again in 1972. After establishment of
the *S. validus* stands, the water level was raised 40 cm and held at
that level in 1971. By 1972 two of the five stands had died out
completely, and the remaining three were reduced 51, 68, and 73% in
density; all were sterile, while the fertility rates had been as
high as 84% in 1970. Conversely, a reduction in mean water depths
from 32 cm to mud surface on the Delta Waterfowl Research Station's
'Back Marsh' in 1972 resulted in a 70% increase in fertility and a
15% increase in density over the previous year.

The data of Table XVIII were obtained at the end of the
growing season; a considerably different situation would result if
the data were obtained earlier in the summer. *S. validus* is most
typically found in temporary water situations where the water may
be 55 cm deep in spring but drops to or below the mud surface by mid-
summer.

Figure 68 summarizes the continuous water level records of
17 sites monitored in 1971 and 1972 with Stephens water level re-
corders. The sites are arranged according to their hybrid index
scores. Five of the seven *S. validus* stands (H.I.<4) experienced

Figure 68. The pattern of water depth fluctuations
experienced by 17 stands. Stands are
arranged from left to right and top to
bottom in ascending order of their
hybrid index scores.

WATER DEPTH (cm)

WATER DEPTH (cm)

WATER DEPTH (cm)

TIME (months, May – Sept.)

STAND NUMBER
—————————
STAND PERFORMANCE
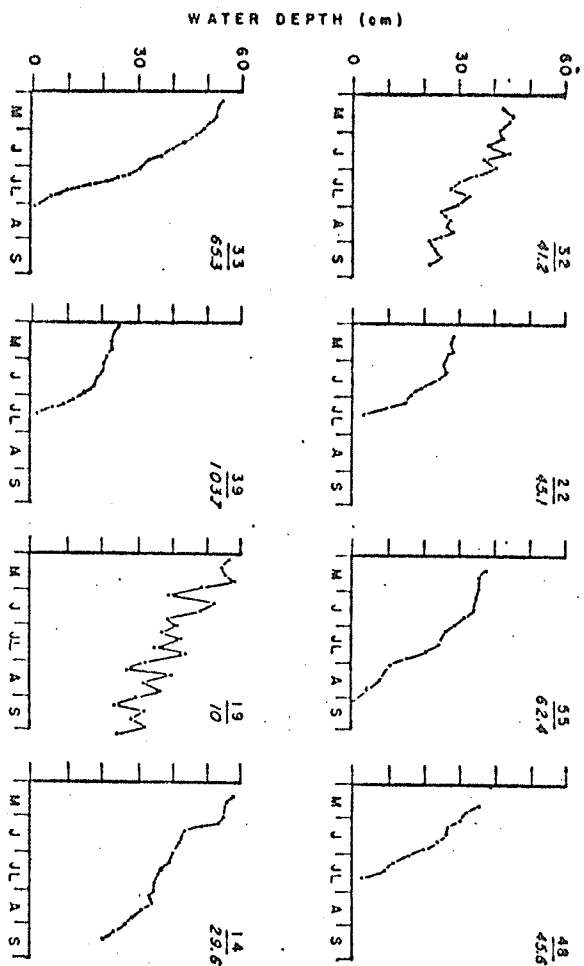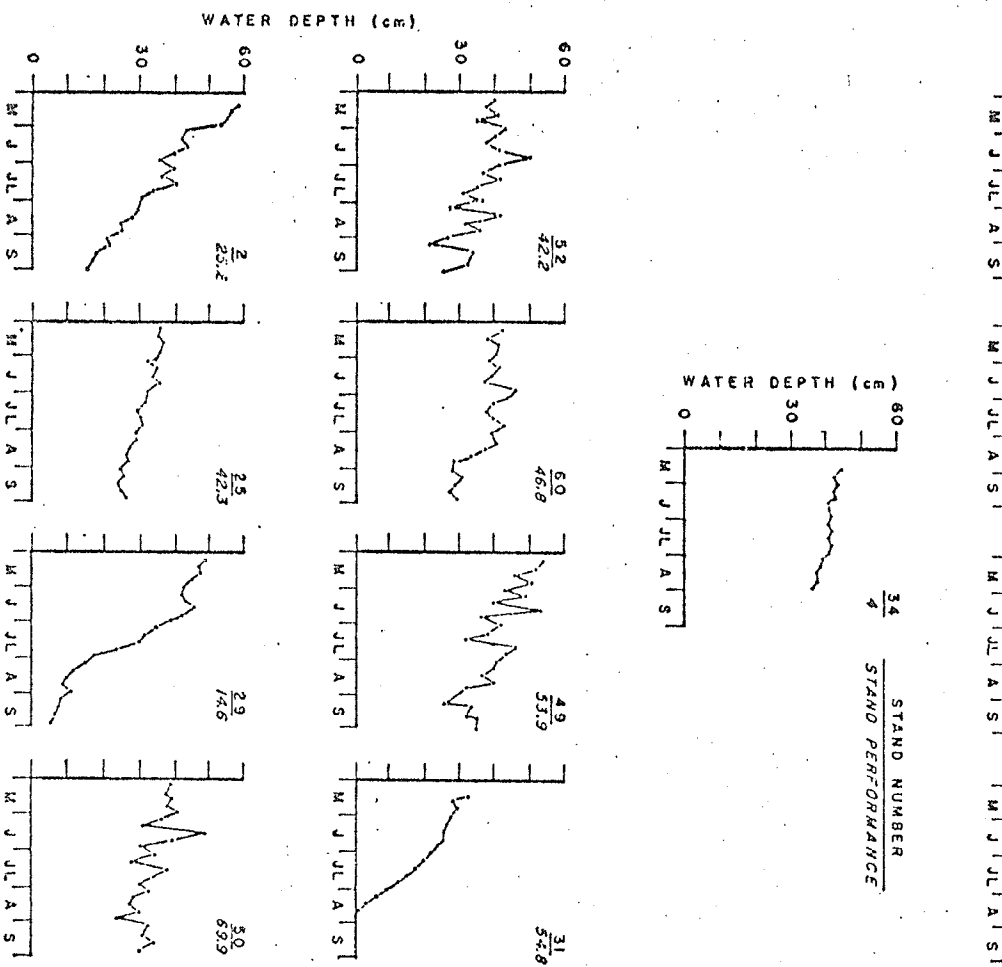
S. acutus

S. validus

high water in the spring which dropped rapidly below the soil surface
by mid-August. Sites 32 and 19 do not show this pattern; the lowest
stand performance of the *S. validus* group is found in these two
stands.

The mixed stand at site 34 (H.I. = 8.1) was growing under
stable water level conditions at a mean depth of 45.8 cm (Table
XVIII); the extremely low stand performance is attributed to the
reduced vigor of both the *S. acutus* and *S. validus* plants, the
former as a result of the severe drawdown in 1968 and the latter in
response to the deep water conditions at the time of sampling.

The pattern of water level fluctuations of the *S. acutus*
group in Figure 68 shows a greater tendency towards stable water
levels. Five of the eight water level records for this group show
a fluctuation of the water levels but a less pronounced drop from
spring to fall. Site 52, for example, shows an amplitude of 29 cm
in the fluctuation of the water level, but the water depth never
dropped below 22 cm. Three sites deviated from this pattern,
sites 21, 2 and 29. The stands at site 2 and site 29 had the
lowest stand performance values (26.2 and 14.6 respectively) of
the *S. acutus* group, but the high stand performance of the site 21
stand (54.8) indicates that water depth fluctuation *per se* is not
the causal factor in reduced stand performance at sites 2 and 29.

Of 27 additional *S. validus* sites visited in August or
September, 23 were completely dry with no surface water; thus, of
a total of 47 stands of *S. validus* for which August data are avail-
able, 33 or 71% were completely dry, compared with 7 of 88 *S. acutus*

stands (9%) which were completely dry.

The nature of the unstable water levels in habitats occupied by *S. validus* is shown in Table XIX which is a comparison of the habitat types in which *S. acutus* and *S. validus* were found.

TABLE XIX.   HABITAT TYPES OCCUPIED BY *S. ACUTUS* AND *S. VALIDUS*

Habitat Type	Number of Stands	
	S. acutus	*S. validus*
Roadside ditches	3	19
Temporary ponds or creek beds	0	48
Borrow pits	0	14
Unstable marsh or lake	38	19
Stable marsh or lake	122	7
	213	107

The category unstable marsh or lakes includes water bodies which are known to have undergone a drawdown, artificially or naturally, and the borders of marshes which are known to become dry by fall. *S. validus* more frequently occupies habitat that is disturbed (such as borrow pits) or has unstable or temporary waters.

3. Water chemistry parameters

Six water chemistry parameters were measured at sites 1 - 60. Parameters were chosen which would be associated with the more calcareous parent materials of the Langruth and Minnedosa study areas. As mentioned previously (Figure 26), *S. validus* was not found in

association with material high in limestone.

A summary of the hydroxide, carbonate and bicarbonate alkalinities, as well as conductivity and pH values for sites 1 - 60 is given in Table XX.

The alkalinity of waters in the Langruth study area was chiefly due to bicarbonates, which ranged from 215 - 360 ppm. Conductivity readings were relatively low, 290 - 411 micromhos/cm^2. The range of pH was 8.0 - 8.9.

Carbonates made a more important contribution to the alkalinity of the Minnedosa sites. Carbonate concentrations varied from 100 - 240 ppm, while bicarbonates varied from 90 - 465 ppm. An anomalously high hydroxide alkalinity was obtained for site 57; no explanation can be made for this isolated occurrence of hydroxide alkalinity. Conductivities were among the highest recorded, ranging from 925 - 1,375 micromhos/cm^2. High pH values of 8.7 - 9.4 were recorded for The Pas sites. Alkalinity of sites in The Pas study area were dominated by bicarbonate ions, carbonates never exceeding 50 ppm. Conductivities varied from 175 to 980 micromhos/cm^2. The pH also showed a wide range, from 7.9 - 9.1.

Sites in the Netley study area can be characterized as being of bicarbonate-dominated alkalinity (160 - 205 ppm), moderately low conductivity (250 - 750 micromhos/cm^2), and pH readings from 8.2 - 8.6.

The bicarbonate ion was also most conspicuous at Delta, ranging from 80 - 190 ppm. Conductivity varied greatly at different sites, ranging from 427 micromhos/cm^2 at site 30 to 2,580 microm-

TABLE XX. ALKALINITY, pH, AND CONDUCTIVITY OF SURFACE WATER,
SITES 1 to 60 (AUGUST, 1971 and 1972)

Site Number	OH$^-$	CO$_3^=$	HCO$_3^-$	Conductivity (μ mhos/cm^2)	pH	Site Number	OH$^-$	CO$_3^=$	HCO$_3^-$	Conductivity (μ mhos/cm^2)	pH
1	0	10	200	290	8.5	31	0	20	250	980	8.2
2	0	0	205	315	8.7	32	0	0	380	1150	7.9
3	ND	ND	ND	ND	ND	33	0	0	148	350	6.9
4	0	10	220	280	8.5	34	0	0	155	480	7.2
5	0	0	260	350	8.7	35	0	50	140	380	9.1
6	0	160	240	1250	8.9	36	0	0	465	230	9.0
7	0	60	160	281	8.6	37	0	0	280	494	8.4
8	0	20	205	252	8.3	38	ND	ND	ND	ND	ND
9	0	0	250	345	8.6	39	ND	ND	ND	ND	ND
10	0	40	330	382	8.6	40	0	40	180	266	8.6
11	130	240	0	1085	8.7	41	0	0	130	225	8.3
12	0	10	205	337	8.6	42	0	10	125	240	8.4
13	0	0	215	324	8.0	43	0	50	150	175	8.9
14	0	0	360	363	8.2	44	0	160	80	2580	9.6
15	0	50	230	411	8.9	45	0	160	80	1950	9.6
16	0	140	90	1050	9.4	46	0	110	160	950	9.3
17	0	0	260	270	8.2	47	0	0	190	750	8.6
18	0	40	180	275	8.6	48	ND	ND	ND	ND	ND
19	0	20	195	314	8.5	49	0	60	30	1580	9.2
20	0	120	240	1375	9.1	50	0	160	80	1760	9.6
21	0	120	110	1375	8.7	51	ND	ND	ND	ND	ND
22	0	0	190	279	7.9	52	0	110	160	910	9.3
23	0	150	275	800	8.2	53	ND	ND	ND	ND	ND
24	0	0	195	281	7.9	54	0	50	230	720	8.6
25	0	100	245	1190	8.8	55	ND	ND	ND	ND	ND
26	0	110	330	925	8.7	56	0	60	30	1580	9.2
27	ND	ND	ND	ND	ND	57	0	100	160	740	9.0
28	0	100	295	950	8.9	58	0	100	160	740	9.0
29	0	0	465	1300	8.4	59	0	80	150	810	8.8
30	0	5	145	427	8.0	60	0	200	100	1210	9.5

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hos/cm^2 at site 44. The pH values also showed a wide range, 6.9 -

10.0, the latter at site 44 again. The only marked difference in

the five study areas was the carbonate domination of the Minnedosa

sites. No statistical difference exists for any of the other para-

meters between sites.

The stands diagnosed as *S. validus* were not found in waters

with carbonate concentrations in excess of 150 ppm; *S. acutus* stands

were found in waters ranging from 0 - 240 ppm carbonate concentration.

There was no statistical difference between the means for the two

groups, however. Similarly, no significant difference was found

with respect to bicarbonate concentrations.

The mean conductivity values for the *S. acutus* group

($\overline{x}$ = 877 micromhos/cm^2) and the *S. validus* group ($\overline{x}$ = 439 micromhos/

cm^2) differed significantly (t = 3.5; df = 48; p < 0.01). The con-

ductivity is a measure of the total dissolved solids in the water,

and indicates here that the *S. acutus* stands were found in waters

with a higher total concentration of salts.

The highest pH readings (9.6) were associated with *S. acutus*

stands, but there was no significant difference between the means

for the groups.

In addition to the three anions mentioned in relation to

alkalinity, sulfate concentrations were also measured at sites 1 - 60.

Minnedosa sites showed the highest concentrations of sulfates, 1,900

ppm. The Langruth sites ranged from 170 - 700 ppm. A similar range

occurred in sites at Delta, although sites 22, 23, 32 and 33 had con-

centrations below 100 ppm. Sulfate concentrations at Netley did not

exceed 180 ppm except at site 17, where 300 ppm was found. The Pas study area had the lowest concentrations of sulfates, generally ranging from 0 - 30 ppm, with site 31 giving a value of 110 ppm.

A comparison of the mean sulfate concentrations associated with *S. acutus* and *S. validus* stands gave a highly significant result ($t = 5.5$, df = 52, $p < 0.01$). This indicates that the mean sulfate concentrations for the two groups was different; the distribution of individual stands with respect to their hybrid index values, sulfate concentrations, and stand performance is indicated in Figure 69. The comparable tabular data are given in Table XXI. The *S. validus* stands are clustered at the low end of the hybrid index scale at sulfate concentrations less than 700 ppm. Stand performance is progressively reduced from low to high sulfate concentrations. The *S. acutus* stands associated with the higher hybrid index values appear to show an optimum stand performance at approximately 250 ppm sulfate; but stand performance is not severely affected by this parameter even at concentrations as high as 1,900 ppm.

The concentrations of two cations, calcium and magnesium, were measured in all study areas. The highest calcium levels were found at Delta at sites 28 and 53 (Table XXII). With the exception of these two sites, calcium concentrations ranged between 185 and 390 ppm. Minnedosa sites ranged from 210 - 630 ppm calcium, only sites 6 and 16 being below 500 ppm. The Langruth sites did not show the high calcium concentrations expected; three sites were below 200 ppm, the remaining four sites showed a range of 200 - 270 ppm. The

TABLE XXI. SULFATE CONCENTRATIONS, HYBRID INDEX, AND STAND PERFORMANCE

Site Number	Hybrid Index	Stand Performance	Sulfate Concentration (Mg/1)	Site Number	Hybrid Index	Stand Performance	Sulfate Concentration (Mg/1)
1	11.7	20.2	170	31	0.9	86.2	110
2	11.5	25.3	170	32	0.7	41.2	35
3	10.6	25	225	33	2	65.3	45
4	1.3	41.5	140	34	8.1	4	10
5	11.2	24.3	160	35	11.6	21.8	0
6	11.5	77.6	1900	36	11.6	22.8	7
7	0.8	29.8	140	37	3.4	4	700
8	1.1	35.5	110	38	11.7	26.4	700
9	11.6	34	425	39	2.1	103.7	ND
10	11.6	9.9	225	40	1.6	23	140
11	11.2	12.5	1250	41	11.8	24	0
12	2.6	21.1	180	42	11.8	9.9	4
13	11.5	25	210	43	11.8	11.1	11
14	11.8	29.6	250	44	11.6	45.1	225
15	11.3	31.3	27	45	11.3	53.5	220
16	11.7	10.1	1500	46	10.9	68.9	225
17	1.1	29.9	300	47	11.3	26.3	6
18	2.5	40.2	170	48	1.8	45.6	ND
19	2.2	10	140	49	11.8	53.9	180
20	10.6	79.5	300	50	11.8	69.9	250
21	11.2	54.8	1400	51	11.4	17.8	ND
22	1.2	45.1	70	52	10.8	42.2	225
23	2.5	37.8	20	53	7.6	36.6	300
24	0.2	104.3	30	54	11.5	62.1	180
25	11.4	42.3	175	55	1.38	67.4	200
26	11.5	12.8	1600	56	11.8	144.3	200
27	11.2	48	1500	57	11.6	18	250
28	5.7	74.9	500	58	11.5	63.5	225
29	11.8	14.6	1350	59	11.2	57.2	200
30	1	70.6	600	60	11	46.8	250

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Figure 69. The relationship between sulphate concentration, the hybrid
index, and stand performance (vertical axis) at sites 1 to
60. The numbers on the spheres identify the stands. The
height of the spheres above the horizontal plane indicates
the stand performance values; see facing table for actual
values. Intervals on the sulphate axis are 200 ppm, in-
tervals on the hybrid index axis are 1.

highest level of calcium recorded for The Pas was 220 ppm at site 24;
the remaining sites varied from 45 - 125 ppm. At Netley all sites
except site 17 were found at concentrations of 130 - 150 ppm. Site
17 had a calcium concentration of 240 ppm.

There is no significant difference statistically between the
calcium concentrations of *S. validus* and *S. acutus* stands; however,
the graphical representation of the stands in Figure 70 has two
interesting features. The *S. acutus* group (hybrid index values near
12) display an apparent optimum for calcium concentrations at approx-
imately 300 ppm. The small number of *S. validus* stands do not permit
such interpretation. The second significant feature is the high
values of calcium in which the mixed stand (sites 28 and 53) are
found well beyond the observed range of either group. Rather than
illustrating the hybrid quality of transgressive variation (Clausen
and Hiesey, 1958), as these stands superficially appear to, they
must be viewed as mixed stands (not hybrids) which serve to extend
the observed range of tolerance of both *S. acutus* and *S. validus*
beyond that which is illustrated by the pure stands.

The second cation measured, magnesium, was found at highest
concentrations at Minnedosa. Site 25 had 2,180 ppm magnesium; the
other sites within the study area ranged from 350 to 1,155 ppm mag-
nesium. The concentration of this ion at Langruth sites was ex-
tremely variable, from 0 ppm at site 15 to 405 ppm at site 38. At
The Pas, concentrations were also quite variable, from 45 to 200 ppm.
In contrast, a narrow range was exhibited by sites at Netley, from
95 to 110 ppm. Delta sites tended to be higher than either The Pas

TABLE XXII. CALCIUM CONCENTRATIONS, HYBRID INDEX, AND STAND PERFORMANCE

Site Number	Hybrid Index	Stand Performance	Calcium Concentration (Mg/1)	Site Number	Hybrid Index	Stand Performance	Calcium Concentration (Mg/1)
1	11.7	20.2	150	31	0.9	86.2	125
2	11.5	25.3	150	32	0.7	41.2	245
3	10.6	25	425	33	2	65.3	210
4	1.3	41.5	150	34	8.1	4	80
5	11.2	24.3	240	35	11.6	21.8	75
6	11.5	77.6	260	36	11.6	22.8	45
7	0.8	29.8	150	37	3.4	4	1200
8	1.1	35.5	150	38	11.7	26.4	245
9	11.6	34	245	39	2.1	103.7	ND
10	11.6	9.9	270	40	1.6	23	145
11	11.2	12.5	530	41	11.8	24	75
12	2.6	21.1	150	42	11.8	9.9	65
13	11.5	25	90	43	11.8	11.1	70
14	11.8	29.6	200	44	11.6	45.1	310
15	11.3	31.3	270	45	11.3	53.5	280
16	11.7	10.1	210	46	10.9	68.9	270
17	1.1	29.9	240	47	11.3	26.3	50
18	2.5	40.2	150	48	1.8	45.6	ND
19	2.2	10	130	49	11.8	53.9	390
20	10.6	79.5	260	50	11.8	69.9	300
21	11.2	54.8	520	51	11.4	17.8	ND
22	1.2	45.1	185	52	10.8	42.2	360
23	2.5	37.8	200	53	7.6	36.6	1300
24	0.2	104.3	220	54	11.5	62.1	345
25	11.4	42.3	600	55	1.38	67.4	380
26	11.5	12.8	630	56	11.8	144.3	380
27	11.2	48	565	57	11.6	18	310
28	5.7	74.9	1990	58	11.5	63.5	360
29	11.8	14.6	505	59	11.2	57.2	380
30	1	70.6	460	60	11	46.8	300
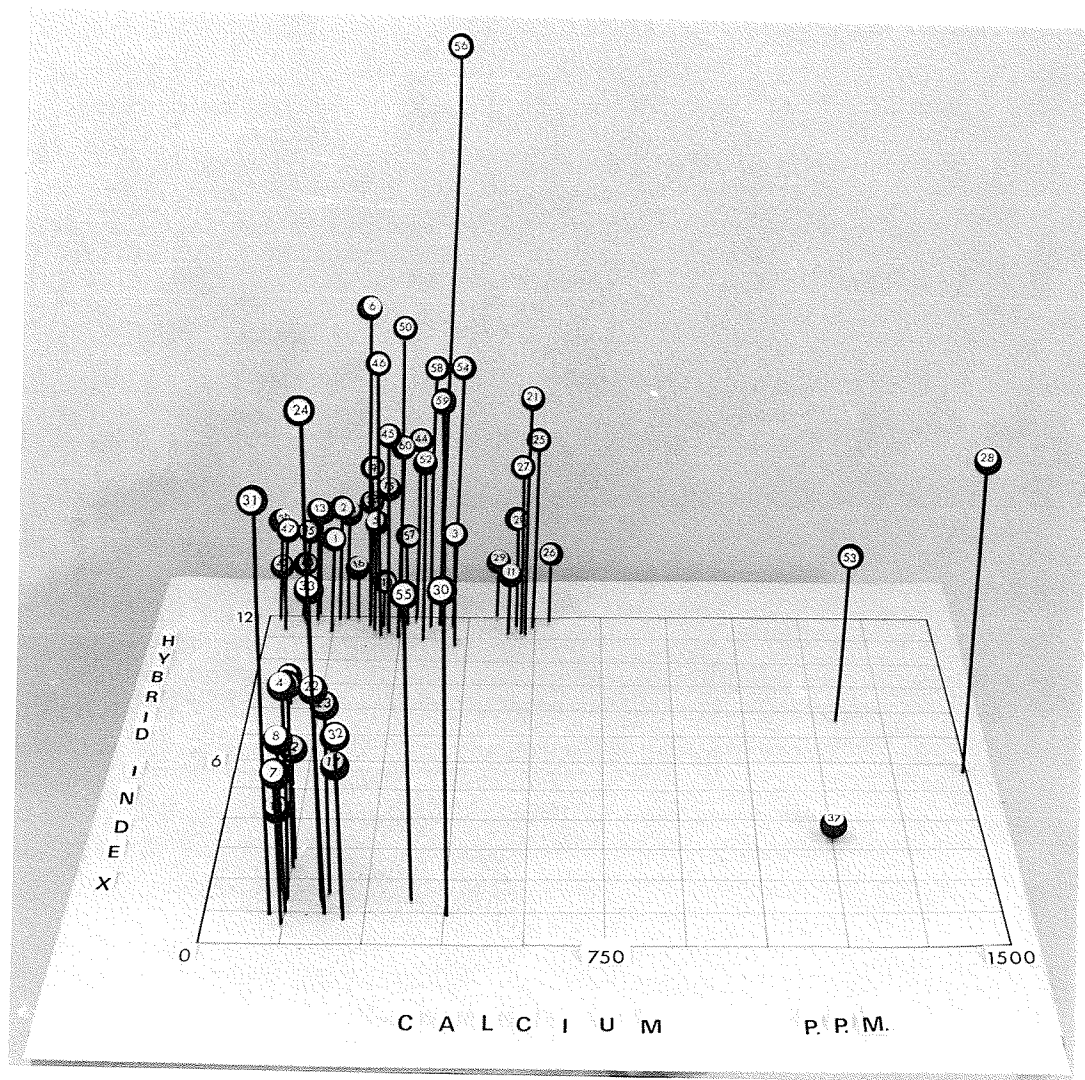
Figure 70. The relationship between calcium concentration, the hybrid
index, and stand performance (vertical axis) at sites 1 to
60. The numbers on the spheres identify the stands. The
height of the spheres above the horizontal plane indicates
the stand performance value; see facing table for actual
values. Intervals on the calcium axis are 150 ppm, inter-
vals on the hybrid index axis are 1. The calcium concen-
tration for stand 28 is off the scale at 1,990 ppm.

or Netley, but there was a marked difference between sites. Site 53 had the highest concentration (990 mg/l), but other sites ranged between 40 and 600 mg/l (Table XXIII).

Accompanying this table is Figure 71 which depicts the relationship between magnesium concentrations, the hybrid index, and stand performance. There is a highly significant difference (t=4.0; df=52; p less than 0.01) between the *S. validus* and *S. acutus* groups. The figure illustrates the very narrow range of magnesium concentrations exhibited by the *S. validus* group; none of the *S. validus* stands were found at magnesium concentrations above 230 mg/l. The *S. acutus* shows, by its consistently high stand performance values, that magnesium concentrations as high as 1,990 mg/l do not severely reduce stand performance. The tolerance of *S. validus* to magnesium concentrations may be higher than indicated in Figure 71, since the two mixed stands (sites 28 and 53) were found at concentrations greater than indicated by the pure stands. Those of *S. validus* individuals in the mixed populations are capable, temporarily at least, of withstanding such high magnesium concentrations.

The statistical difference between the *S. validus* and *S. acutus* stands with respect to magnesium and sulfate concentrations could be an artifact of the data. In both cases, a few relatively high values (e.g. 2,180 mg/l magnesium for site 25) occur in the *S. acutus* group which greatly increase the means and tend to create artificially high t-statistics. In order to eliminate the effect of these few high values, the much less powerful 'median test' (Klugh, 1970) was employed for comparison (Table XXIV). The agree-

TABLE XXIII. MAGNESIUM CONCENTRATIONS, HYBRID INDEX, AND STAND PERFORMANCE

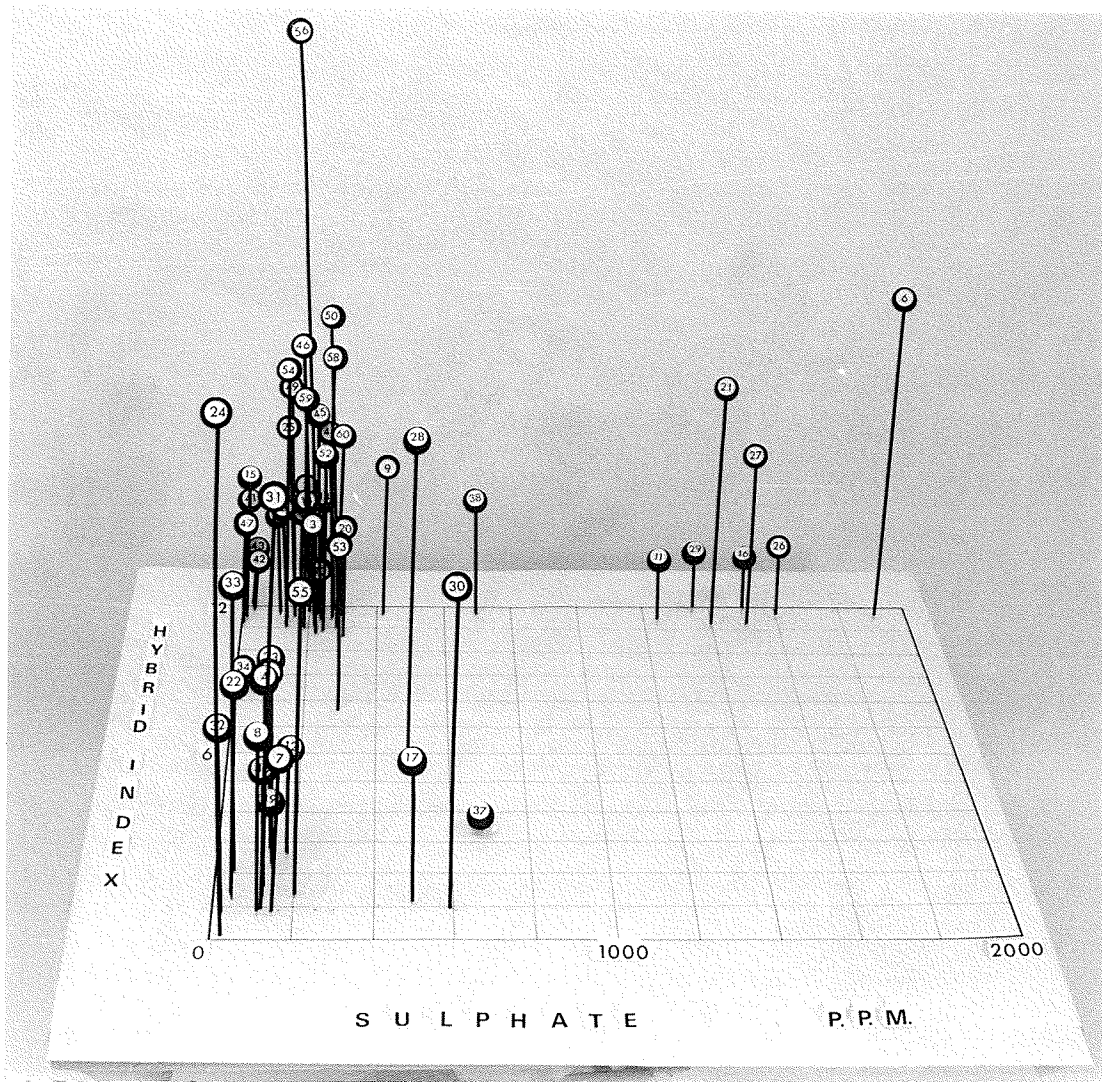| Site Number	Hybrid Index	Stand Performance	Magnesium Concentration (Mg/l)	Site Number	Hybrid Index	Stand Performance	Magnesium Concentration (Mg/l)
1	11.7	20.2	125	31	0.9	86.2	105
2	11.5	25.3	125	32	0.7	41.2	230
3	10.6	25	640	33	2	65.3	190
4	1.3	41.5	90	34	8.1	4	45
5	11.2	24.3	60	35	11.6	21.8	145
6	11.5	77.6	1155	36	11.6	22.8	115
7	0.8	29.8	90	37	3.4	4	140
8	1.1	35.5	100	38	11.7	26.4	405
9	11.6	34	80	39	2.1	103.7	ND
10	11.6	9.9	400	40	1.6	23	95
11	11.2	12.5	705	41	11.8	24	145
12	2.6	21.1	95	42	11.8	9.9	140
13	11.5	25	155	43	11.8	11.1	110
14	11.8	29.6	240	44	11.6	45.1	640
15	11.3	31.3	0	45	11.3	53.5	610
16	11.7	10.1	840	46	10.9	68.9	700
17	1.1	29.9	100	47	11.3	26.3	125
18	2.5	40.2	90	48	1.8	45.6	ND
19	2.2	10	110	49	11.8	53.9	20
20	10.6	79.5	310	50	11.8	69.9	580
21	11.2	54.8	350	51	11.4	17.8	ND
22	1.2	45.1	160	52	10.8	42.2	540
23	2.5	37.8	180	53	7.6	36.6	990
24	0.2	104.3	200	54	11.5	62.1	65
25	11.4	42.3	2180	55	1.38	67.4	40
26	11.5	12.8	670	56	11.8	144.3	40
27	11.2	48	396	57	11.6	18	560
28	5.7	74.9	720	58	11.5	63.5	630
29	11.8	14.6	625	59	11.2	57.2	40
30	1	70.6	225	60	11	46.8	363
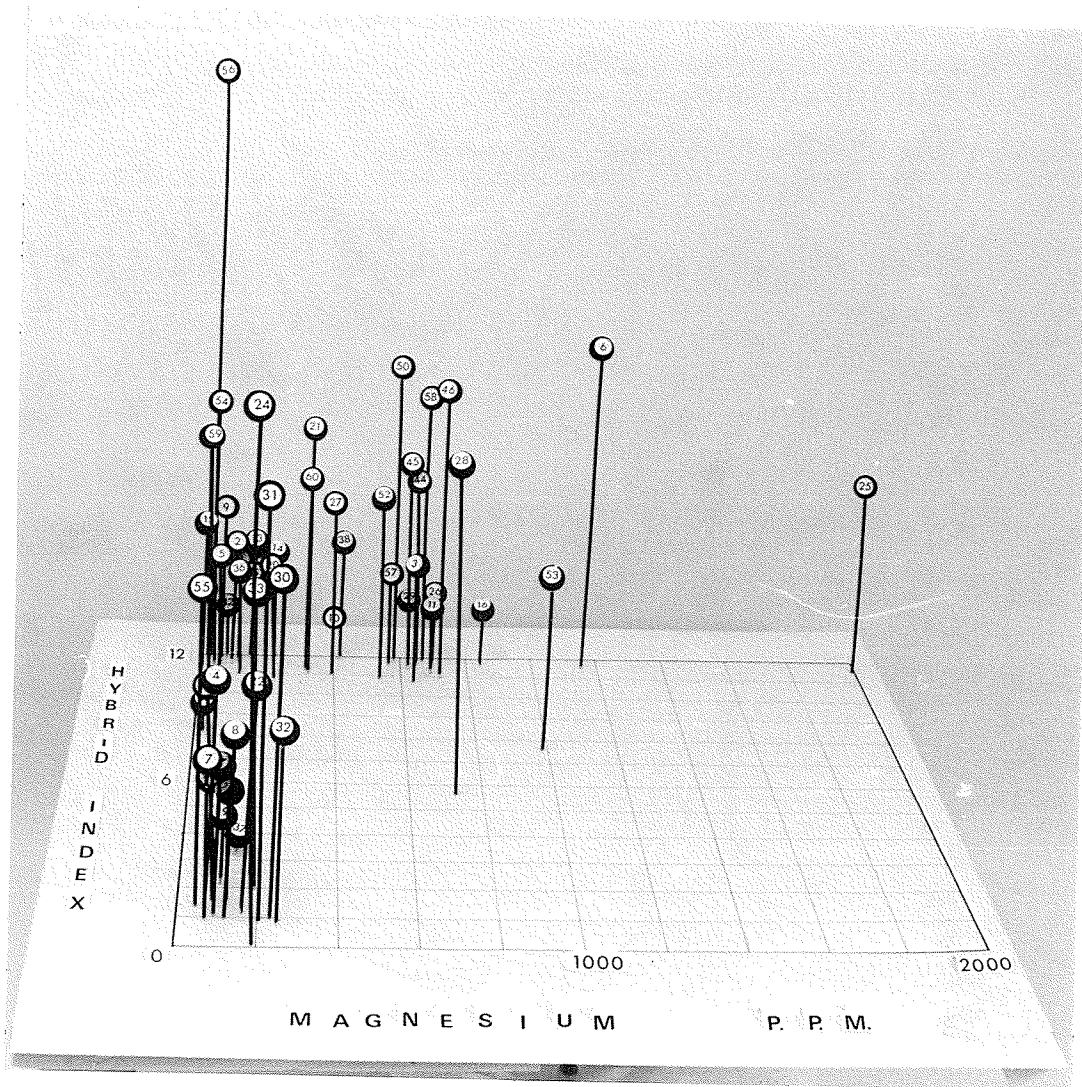
Figure 71. The relationship between magnesium concentration, the
hybrid index, and stand performance (vertical axis) at
sites 1 to 60. The numbers on the spheres identify the
stands. The height of the spheres above the horizontal
plane indicates the stand performance values; see facing
table for actual values. Intervals on the magnesium
scale are 200 ppm, intervals on the hybrid index axis
are 1. The magnesium concentration for stand 25 is off
the scale at 2,180 ppm.

ment between the tests is good, verifying the validity of the t-test.

TABLE XXIV. A COMPARISON OF 't' STATISTICS AND x^2
(MEDIAN TEST) VALUES FOR MAGNESIUM
AND SULFATE CONCENTRATIONS

(*Significant at $p < 0.01$)

	Magnesium	Sulfate
t (df = 52)	4.0*	5.5*
x^2 (df = 1)	11.1*	8.8*

4. Nutrient culture experiment

The response of *S. acutus* and *S. validus* to varying concen-
trations of calcium, magnesium, and sulfate ions was measured in
nutrient culture experiments. The dry weight of culms, percent
fertility of culms, and the percent of transplanted rhizomes which
produced shoots in response to four different concentrations of each
ion are presented in Table XXV. *S. acutus* rhizomes in both controls
did not survive, and erratic behavior in the enriched solutions
prevents one from drawing any meaningful conclusions. *S. validus*
produced culms in all experimental and control tanks, including the
nutrient-free culture solution. Culm dry weights, percent culm
fertility, and percent of rhizomes sprouting were consistently
higher in *S. validus*, but the ability of the rhizomes to produce
abundant fertile culms in a nutrient-free medium makes any more
meaningful conclusions questionable.

Two observations are possible, however. The rhizomes of

TABLE XXV. THE GROWTH OF *S. ACUTUS* AND *S. VALIDUS* IN RESPONSE TO VARYING CONCENTRATIONS OF CALCIUM, MAGNESIUM AND SULFATE IONS IN NUTRIENT CULTURE. ACTUAL NUMBERS IN PARENTHESES. (FEBRUARY 25 to APRIL 18, 1971)

Ion Concentrations (ppm)	Culm Dry Weight (g)		% Fertile Culms		% Rhizomes Sprouting	
	S. acutus	*S. validus*	*S. acutus*	*S. validus*	*S. acutus*	*S. validus*
Calcium						
Controls 0	0	25	0	70 (14)	0	100 (6)
234	0	31	0	10 (4)	0	100 (5)
400	9	61	0	42 (21)	33 (2)	100 (5)
600	0	49	0	25 (10)	0	50 (3)
Magnesium						
Controls 0	0	25	0	70 (14)	0	100 (6)
60	0	31	0	10 (4)	0	100 (5)
400	20	34	0	85 (17)	33 (2)	50 (3)
800	21	51	0	42 (19)	67	67 (4)
Sulfate						
Controls 0	0	25	0	70 (14)	0	100 (6)
18	0	31	0	10 (4)	0	100 (5)
300	21	69	0	45 (15)	25 (1)	50 (3)
900	0	31	0	27 (6)	0	25 (2)

S. acutus are apparently less able to withstand the shock of the experimental conditions than are those of *S. validus*. The ability of *S. validus* rhizomes to produce healthy, fertile culms despite the lack of nutrients suggests that nutrients for the growth of new culms are stored in the rhizome, and growth may, initially at least, be independent of external nutrient sources.

CHAPTER IV

DISCUSSION

A. Morphological

Complete morphological discontinuity exists between *S. acutus* and *S. validus* based on six characters (Figure 72): inflorescence length, the number of primary rays, the presence of secondary or higher levels of branching, the presence or absence of spikelet clusters composed of five or more spikelets, the size of aerenchymal lacunae, and the color of the culms. Additional characters which show some agreement with the hybrid index diagnosis are the scale color, spikelet length, and floral scale length to achene length ratio; these latter two characters, however, do not show a statistically significant difference between the means for the two groups.

The inflorescence length and number of primary rays have not previously been used to distinguish *S. acutus* from *S. validus*. Both of these characters show a continuous range of variation between the two extreme states, with *S. validus* specimens exhibiting a wider range of variation for both characters than *S. acutus*. This is indicated by the flatter, broader peaks of the *S. validus* group in Figures 42 and 43. This variation exists both within and between stands of *S. validus*, and observations in the field indicate that both characters as well as the branching of the primary rays may be modified by environmental conditions. Specimens with short inflorescences, few primary and secondary rays, and no tertiary rays occur (Figure 22) which superficially resemble *S. acutus*; the inflorescence length in such specimens is greater than 47 mm, however, and the pattern of spikelet clustering and light green culms with large

Figure 72. The range of inflorescence forms
shown in Figure 22 can be separated
into two distinct groups on the
basis of six morphological characters.
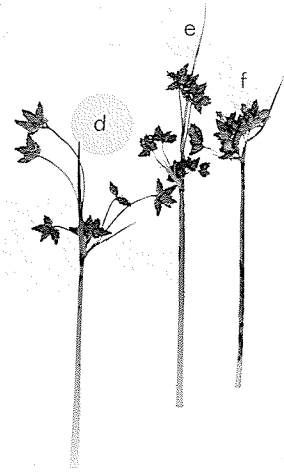
lacunae indicate the *S. validus* affinity. Similar observations were made by Dabbs (1971).

The ray development (branching of the inflorescence) has been used previously by Beetle (1941) and Dabbs(1971) with conflicting interpretations. The data presented here support the treatment by Dabbs (*op. cit.*). *S. acutus* rarely shows the development of secondary rays and never do these rebranch to produce tertiary or quaternary rays. *S. validus* however has secondary and usually tertiary rays; quaternary rays are occasionally present.

The pattern of spikelet clustering was used by Smith (1969) ("the number of solitary spikelets out of ten"), but this is a character which is difficult to interpret; which group of ten should be counted? The presence of spikelet clusters composed of five or more spikelets, which diagnoses *S. acutus*, is an unequivocal, easily measured field character. *S. acutus* inflorescences examined in this study have most of the spikelets arranged in clusters of three to eight, whereas *S. validus* most commonly shows single spikelets and clusters of two or three.

The aerenchymal lacunae of *S. acutus* are smaller and more numerous in a culm cross section than those of *S. validus*. In a cross section midway from the base to the tip of the culm, *S. acutus* usually shows 8 to 15 lacunae, with an average diameter less than 0.9 mm; *S. validus* culms, however have four to six lacunae, averaging more than 1 mm, and often greater than 1.5 mm. Smith (*op. cit.*) used the number of lacunae in cross section; *S. acutus* showed more than nine and *S. validus* less than four. Very large culms of *S. validus*,

of red protruberances justifies the cautious use of the character, however.

Differences in the size of spikelets, scales, and achenes are mentioned by many authors as characteristic of these taxa (Chase, 1904; Beetle, 1941; Fernald, 1950; Gleason, 1952; and Dabbs *op. cit.*). For all of these characters, the extremes of the size range may occur in the two taxa (the largest spikelets, scales, and achenes in *S. acutus*, the smallest in *S. validus*), but all show such a high degree of overlap in most specimens that they are not useful. Similarly, the ratio of scale length to achene length has been used to describe the more open nature of the ripe spikelet in *S. validus* (Dabbs *op. cit.*). The histogram of 1,500 measurements (Figure 62) indicates the unimodal distribution of this character. When the mean scale lengths and mean achene lengths of 25 measurements for 60 stands are plotted (Figure 63) complete overlap is shown, with scale lengths exceeding achene lengths in all cases. Dabbs (*op. cit.* p. 148) found that ten measurements of these characters for each of 29 collections resulted in two "distinct clusters". However, if the standard deviations given for the means (incorrectly referred to as standard error) were indicated, the "distinct clusters" became a continuous range of variation with complete overlap.

This raises the question of the reliability of scatter diagrams when mean values are plotted with no indication of the variability of the measurements involved. Such diagrams are useful to suggest trends, but if they are to be used as evidence of discontinuity between groups, the range of variation must be taken into

consideration. The range of variation is much more clearly portrayed in scatter diagrams or frequency histograms of individual measurements; evidence for discontinuity is most validly obtained from such data.

The method of character selection used in this study is *a posteriori* or correlation weighting, which Davis and Heywood (1963, p. 48) state is the only theoretically sound method of character selection. Correlation weighting is the selection of those characters which show maximum covariation within the taxa under consideration. This is essentially the intuitive process employed by taxonomists in defining the facies of a taxon; from a number of characters, those which covary and together define the 'concept' of a taxon are subconsciously selected and used for subsequent identification. The technique of factor analysis mimics this mental process by operating on a correlation matrix and separating (as factors) those characters which covary. The factors which account for the greatest portions of the variability represent the facies by which a taxon is most easily recognized.

The factor analysis employed in this study was of limited use; of the most important characters selected by the technique, only two could be utilized in their original form (inflorescence length and number of primary rays). The two remaining characters in Factor 1 had to be changed to qualitative characters (presence or absence of branching, presence or absence of clusters of five or more spikelets). Characters involved in Factors 2 to 12 could not be used since they showed unimodal frequency distributions from which

the character states of the hybrid index could not be defined.

This study has, however, illustrated the value of factor
analysis in selecting the most important characters by which one or
more groups may be described. Once these characters are selected,
the use of factor analysis or any of the other clustering techniques
(see Sokal and Sneath, 1963) may be employed to examine the relation-
ship between taxa. In the present study, the hybrid index was em-
ployed because of its simplicity and adaptability to rapid field
assessment of taxonomic relationships (Davis and Heywood, 1963,
p. 479).

The discontinuity displayed between the two taxa when
the six characters are used allows the construction of the following
diagnostic key:

1. Culms dark green (Munsell colors 10GY 5/4, 10GY 5/6,
   or 2.5GY 5/6); aerenchymal lacunae less than 0.9 mm
   in diameter; inflorescence length less than 47 mm;
   number of primary rays less than 7; secondary rays
   absent; clusters of 5 or more spikelets present .... *S. acutus*

1. Culms light green to glaucous (Munsell colors
   5GY 4/4, 5GY 4/6, 7.5GY 3/4, 7.5GY 4/4, 7.5GY 4/6,
   or 10GY 4/4); aerenchymal lacunae more than 1.5 mm
   in diameter; inflorescence length greater than
   80.5 mm; number of primary rays greater than 13;
   secondary, tertiary, and occasionally quaternary
   rays present; spikelets mostly borne singly, rarely
   in groups of more than 3 .... *S. validus*

B. Ecological

1. Water depth and water level fluctuations

The *S. acutus* and *S. validus* stands examined in this study occupy habitats which differ in water depth, the pattern of water level fluctuations, conductivity, and the concentrations of magnesium and sulfate ions in the water. These habitat differences are reflected in the distribution of the two taxa in southern Manitoba and the plants and animals found associated with stands of the two types.

The results of this study indicate that *S. acutus* occupies a much wider range of mean water depths than *S. validus*; *S. acutus* is found at mean depths from 0 to 80 cm, while *S. validus* occupies depths less than 50 cm (Figure 66). Furthermore, depths in excess of 20 cm result in reduced stand performance of *S. validus*. Sigler (1948), Smith (*op. cit.*) and Dabbs (*op. cit.*) found that *S. acutus* was characteristic of deeper water while *S. validus* was commonly found in shallow water or wet mud. The mere presence of a plant, however, gives no indication of the optimum range of water depths. The use of the stand performance index (density x fertility) in this study indicates that the optimum range of mean water depths for *S. acutus* is 15 to 40 cm, while that of *S. validus* is below 20 cm. From observations made during this study, *S. validus* is unable to withstand prolonged water depths beyond 30 cm; greater depths will eliminate it in four years. Harris and Marshall (1963) report similar findings, *S. validus* was killed in three years by depths of 15 inches (38 cm).

The measurement of mean water depth in a stand at one point

in time is not the best means of expressing the water depth toler-
ance or optimum of a plant since the water levels fluctuate markedly,
as shown by continuous water level recordings; however, because the
sites in this study were distributed over a wide geographical area,
more frequent measurements were impossible. Ideally, such informa-
tion should be obtained by the extensive use of water level record-
ers and water depths expressed as function of both depth and time.

The 17 water level recordings which are presented in Figure
68 indicate that the pattern of water depth fluctuations also is dif-
ferent for habitats occupied by *S. acutus* and *S. validus*. The habi-
tat typically occupied by *S. acutus* does not undergo the continuous
drop in water levels which the *S. validus* stands encounter; rather,
fluctuation occurs about a mean depth, with a smaller net drop in
levels. *S. validus* stands may encounter two distinct habitats in
one growing season, as the water depth drops from 50 cm or more in
spring to below the mud surface by fall. Smith (1969) notes a
similar tendency for *S. validus* to occur in unstable habitats.

Although optimum depths differ, *S. validus* and *S. acutus*
show a broad zone of overlap from 0 to 30 cm mean depth in which
the two are capable of persisting. It is within this depth range
that they are found growing in mixed stands (sites 28 and 53 for
example), although Dabbs (*op. cit.*) cites extreme depths of 100 cm
for mixed stands. From observations made during this study, mixed
stands usually result from a lowered water level in an area in which
S. acutus is established. As a result of these lowered water levels,
S. validus achenes germinate on the exposed mud and will become es-

tablished and persist for a variable period of time, depending upon the subsequent water levels. The result is a zonation of the two bulrushes, *S. validus* usually occupying the shallower zone; sites 28 and 53 showed this pattern, and Dabbs (*op. cit.*) reported such a mixed stand at Big Lake in the Saskatchewan River Delta.

A second pattern of dispersion occurs in which sparsely scattered culms of *S. validus* form a matrix in which denser clumps of *S. acutus* occur. This pattern was found by the author in the mixed stand of the Murphy Extension Project in the Saskatchewan River Delta (site 34). The pattern develops when a drawdown is sufficiently severe to cause the die-back of *S. acutus* plants until only isolated clumps remain. This response seems to be caused by excessive drying of the substrate or prolonged low water. Slightly wetter conditions must occur in order to allow *S. validus* achenes to germinate and subsequent return to previous water levels produces the pattern; it appears to be only temporary as the *S. validus* is gradually eliminated in the deeper water.

A third pattern was found during this study, illustrated by the zonation at site 20. Here the typical zonation pattern was reversed, with *S. validus* growing in a narrow zone on the deep-water side of the stand. Prior to 1965, this stand was composed only of *S. acutus* which grew to the edge of open water (J. M. Shay, pers. comm.). As a result of lower water levels in 1965, a mud shelf was exposed along the outer margin of the stand and *S. validus* achenes germinated and became established in a narrow zone (Figure 58). With the return of higher water levels, the *S. validus* persisted, although

it was undergoing a progressive reduction during the three years of this study. Water depth and changes in water level have a controlling influence on the distribution of these plants; where the two are found growing together, it is generally the result of contemporary or recent historical water level conditions.

2. Water chemistry

The water chemistry parameters examined reflect a greater tolerance of *S. acutus* for alkaline conditions. No statistically significant difference exists between the mean carbonate and bicarbonate ion concentrations of *S. acutus* and *S. validus* sites. Carbonate concentrations ranged from 0 to 200 mg/1 for *S. acutus* and 0 to 150 mg/1 for *S. validus*; bicarbonate concentrations ranged from 30 to 465 mg/1 for *S. acutus* and 180 to 380 mg/1 for *S. validus*.

The highest pH values are associated with *S. acutus* stands (9.6 compared with 8.7 for *S. validus*), although the means are not significantly different.

Significant differences between *S. acutus* and *S. validus* did exist for conductivity. *S. validus* was not found at conductivities above 494μ mhos/cm^2, whereas *S. acutus* occurred in waters with conductivity as high as 2580μ mhos/cm^2. Both taxa have been recorded at higher conductivities than encountered in this study, however (Stewart and Kantrud, 1969; Smith, 1969).

S. acutus tolerates magnesium ion concentrations as high as 2,000 mg/1 and sulfate concentrations as high as 1,900 mg/1. *S. validus* is not found at magnesium concentrations above 230 mg/1 and

sulfate concentrations above 700 mg/l. In the Minnedosa study area, where *S. validus* does not occur, water analysis of all sites examined (6, 11, 16, 21, 25, 26, 27, 29) showed the concentration of magnesium (396 to 2,180 mg/l) to be above the observed tolerance level of *S. validus*. Similarly the concentration of sulfates at these sites was, with the exception of site 25, greater than the observed maximum of 700 mg/l for *S. validus*.

Mean calcium concentrations did not differ statistically between the two groups, the ranges for *S. acutus* and *S. validus* being 50 to 630 mg/l and 125 to 455 mg/l. Mixed stands (sites 28 and 53) and one stand of *S. validus* (site 27) were found in waters with considerably higher concentrations, however, suggesting the tolerance of both taxa may be as high as 1,500 mg/l.

Thus, two of the major ions composing these calcareous soils, magnesium and/or sulfate, are implicated as limiting the distribution of *S. validus*.

Both of these ions have been found to be limiting to terrestrial vegetation (Jacob, 1958; Strogonov, 1964; Proctor, 1970; Levitt, 1972). Moyle (1956) indicated that sulfate in surface waters may be a limiting factor in the distribution of some aquatic plants in Minnesota. Although data relating magnesium concentrations to toxicity of agricultural crops (Strogonov *op. cit:* Proctor *op. cit.*) may not be applicable to aquatic environments, the 'semi-terrestrial' habitat typical of *S. validus* sites in late fall provides an aerobic rooting medium similar to that for terrestrial plants. In addition, the periodic reduction of the water level to

or below the soil surface could result in an increased concentration of salts in the rooting zone, augmenting the normal salt concentrations and creating salt toxicity.

The physiological basis for salt toxicity is either an increased osmotic potential of the external solution (the "soil solution" of terrestrial habitats), or a direct toxic effect of a particular ion (Strongonov *op. cit.*). Magnesium toxicity occurs only in the absence of calcium (Proctor *op. cit.*) and, since calcium ions were present in all samples measured, it is unlikely that magnesium toxicity is operating to limit *S. validus*. Sulfate salts also have a direct toxic effect on the metabolism of plants (Levitt, 1972), initially increasing the transpiration rate, then slowing it down; the activity of enzymes with copper as a cofactor are inhibited by high sulfate concentrations. Therefore, a physiological basis has been established for implicating magnesium and/or sulfate concentrations as limiting factors to the observed distribution of *S. validus*. Further work is required, however, to isolate the effects of each ion and determine more precisely the levels of toxicity. This information could be obtained from nutrient culture experiments with seedlings.

3. Substrate texture

The textural quality of the substrate does not appear to be a limiting factor for either *S. acutus* or *S. validus*. During this study, both species were found on substrates ranging from heavy clay to very coarse sand and gravel. Sigler (1948) described *S. acutus*

growing on a wide variety of substrates from "...rocky bottoms to deep mud...". Emerson (1961) found that *S. acutus* (in New York State) grew on a wide variety of substrates, but did not occur on clay soils. He attempted to establish *S. acutus* and *S. validus* rhizomes in man-made "marshes" which had a heavy clay mineral substrate. The failure of *S. acutus* while *S. validus* rapidly became established was attributed to this inability to grow in heavy clay. Similar experience during this study indicates that *S. acutus* may not be limited by the fine texture so much as the raw mineral condition of the substrate which is exposed after the solum is removed.

If texture were a limiting factor, it would probably be in relation to the substrate's ability to provide a suitable rooting medium. The combined factors of reduced friction in a submerged substrate (Williams and Barber, 1961), the greater erosional forces of the aquatic environment, and the increased physical stress of wind and waves, make the problem of secure anchorage greater for emergents than most terrestrial or submerged aquatic plants. The absence of emergent vegetation from sand beaches where wave action can be extremely severe illustrates the greatest substrate-related limiting factor for emergent vegetation.

In exposed situations where the substrate provides adequate rooting material, the absence of *S. validus* has been noted by the present author and also by Martin and Uhler (1939), Emerson (1961), and Walker (1965). The culms of *S. validus* cannot withstand breakage by wind and wave action and this may be related to the reduced aerenchymal tissue, which Williams and Barber (*op. cit.*) suggest is prim-

arily designed to withstand bending strain. This characteristic is also seen in the tendency for dead culms of *S. validus* to break upon drying, whereas those of *S. acutus* bend but do not break.

4. Stand performance as an index of plant response to the environment

An index of plant response to these environmental parameters was derived from the product of culm density and the fertility rate. These parameters were chosen to indicate the relative vigor and vitality of different stands (Daubenmire, 1968). Several alternative parameters were considered for vigor, including net primary production in one growing season, culm height, culm diameter and leaf area index. The distance between sites and the poor accessability of many sites required a field technique which could be employed with a minimum of equipment. The need for large sample sizes and adequate drying facilities eliminated production estimates. Culm diameter and height would not reflect optimum conditions since they are physically related to water depth. As an example, the culm mean height for the *S. acutus* stand in deepest water (site 47, Figure 66) was 254.6 cm (± 24.59), while that of a stand in shallow water (site 10) was 170.12 cm (± 16.57). The mean culm diameters varied with height, being 8.04± 0.93 at site 47 and 4.63± 0.66 at site 10. Similar relationships hold for depths as great as 2.5 m, as found at Lake Athapapuskow in 1970. At one site examined on this lake, culms were growing at maximum depths of 2.5 m, with maximum culm heights of 3.6 m. Therefore, rather than reflecting optimum

conditions, culm size varies to a maximum at maximum depths. Similar

criticisms of leaf area index can be made, since leaf (or culm) area

is a function of both height and culm diameter (Dykyjova, 1971).

5. The pioneering ability of *S. validus*

Several factors combined indicate that *S. validus* is a more

effective pioneer species than *S. acutus*. *S. validus* frequently oc-

cupies disturbed habitats such as roadside ditches, borrow pits and

sites with unstable water levels. In the Delta Marsh for example,

S. validus occurs commonly on the margins of depressions recently

created by earthmoving equipment, but *S. acutus* is never found in

such sites. The rapid establishment of *S. validus* from seedling

following a drawdown in the Cumberland Marshes is characteristic of

this plant; *S. acutus*, however has not been reported to successfully

establish from seed; under artificial conditions as well, *S. validus*

germinates more readily than *S. acutus*. The biomass data presented

in Table V support observations that *S. validus* produces more

seed than *S. acutus*. According to Low (1944), the actual volume of

seed produced by *S. validus* is 50% more than that produced by *S.*

acutus. The achenes produced by *S. validus* float longer than those

of *S. acutus* (Figures 31 and 32) and they have been observed to cling

more readily to clothing, suggesting a better dispersal mechanism.

The last two characteristics may be related to the slightly longer

barbs on the perianth bristles, which has been observed in some *S.*

validus specimens. These characteristics combined indicate a greater

pioneering ability of *S. validus*. Although the achenes of *S. acutus*

must serve a dispersal function, once this form is established it is

probably maintained by a greater emphasis on vegetative reproduction

in stable environments.

C. Taxonomic treatment

While there are a number of characters which agree in defining the overall facies of the two taxa, the data presented here indicate that none of the characters examined show a complete discontinuity in the range of variation exhibited. This problem raises the question of whether the traditional specific level of distinction between the taxa should be retained, as Chase (1904), Beetle (1941), Smith (1969) and Dabbs (1971) suggest, or should distinction be at the subspecific level as Koyama (1962) states.

In order to answer this question, it is necessary to consider the definition of the species category in both the traditional morphological-geographical sense and in the biosystematic concept, where species are defined by reproductive isolation. The criteria for making a decision which will agree with both concepts are stated by Valentine and Love (1958, p. 157):

> "When the morphological and ecological differences are
> slight, and experiment shows complete interfertility,
> then the populations concerned should not be given spec-
> ific rank. When these differences are considerable, and
> there are well-defined internal barriers to gene-exchange,
> then specific rank should be given."

The data presented indicate that there are a number of characters which distinguish the two taxa. While no single character is diagnostic in all cases, the sum total of a number of characters describes two morphologically distinct groups. Differences exist

in the tolerance range for water depth, conductivity, and concentrations of magnesium and/or sulfate ions. On both morphological and ecological grounds, then, two distinct groups are apparent.

The third criterion, that of reproductive isolation, is somewhat more difficult to assess, since no experimental attempt has been made to hybridize the two taxa. Regarding this problem, Davis and Heywood (1963, p. 82) offer the following suggestion:

> "Two plants growing in different areas (allopatric) may
> or may not be interfertile--only experimental evidence
> can show us that. But if they grow in the same area
> (sympatric), and particularly when they grow in the same
> habitat, the situation is different. If the two plants
> continue distinct, it is fair to assume that there is
> some reproductive barrier between them."

Smith (*op. cit.*) Dabbs (*op. cit.*) and the present author all found instances of the two taxa growing together in the same habitat. Smith found 20 mixed stands, 14 containing morphologically intermediate specimens he felt were hybrids. Ward (pers. comm., 1973) collected extensively in the same region, however, and found no morphological evidence of hybrids, and in addition could not demonstrate any abnormality in chromosome behavior in mitotic pollen mother cell material. Since he found a consistent difference in chromosome numbers, one would expect that hybrid pollen would show some evidence of chromosomal aberration. Dabbs (*op. cit.*) found five cases of suspected hybridization; these specimens were sterile.

The present work cites one example of morphologically intermediate specimens (which were also almost sterile) from a total of 60 stands examined.

The pattern of flowering of spikelets and the anemophilous pollination (Willis, 1955) both tend to promote outbreeding; when these factors are combined with the overlapping periods of initiation and growth of culms in *S. acutus* and *S. validus* (Figures 29 and 30), ideal conditions for hybridization exist. Under such conditions the scarcity of hybrids, even in mixed stands, indicates that a significant barrier to gene exchange must exist, although it may be slightly "leaky" in the terminology of Solbrig (1970, p. 108). Solbrig (*op. cit.*) suggests that there are relatively few species that do not have "leaky" isolation barriers and that new species can be formed and maintained even where no absolute barriers to gene flow exist. Sufficient evidence has been accumulated to indicate that within central North America the taxa here referred to as *S. acutus* Muhl. and *S. validus* Vahl (Figure 72) should be maintained as distinct species.

D. <u>Management application</u>

The uncertainty surrounding the taxonomic and ecological
status of *S. acutus* and *S. validus* has probably been encountered
most forcefully by persons attempting to manage marshes in which
these plants grow. Not only do these individuals encounter the
taxonomic problem, but they are also faced with the confusing re-
sponse (or lack of it) of these plants to habitat manipulation.
The results of this study should clarify many of the problems pre-
viously encountered in managing these two species.

1. <u>Management of *S. acutus*</u>

The greatest part of wetland management to date has been
concerned with improving marshes for waterfowl or muskrats, and
because of its habitat 'preference' for stable, deep water sites,
S. acutus is the more important species in such work. This study
has shown the utilization of *S. acutus* by waterfowl, diving ducks
in particular, which has been documented previously by Steenis
(1938), Wolf (1955), and Lokomen (1966). The achenes are eaten
by a variety of diving and dabbling ducks, as indicated in Table IX.
Martin *et al* (1951) found that *S. acutus* was the most important
bulrush in the diet of ducks in the United States, and Martin and
Uhler (1938) considered *S. acutus* to be the most common and valuable
marsh plant of central and western Canada.

During this study, muskrats were a common inhabitant of many
S. acutus stands. The importance of *S. acutus* in the diet of musk-
rats has been documented by Yeager (1945), Errington (1948, 1963),

Bellrose (1950), and others.

The widespread distribution of *S. acutus* in southern Manitoba contributes to its importance in wetland management, since it is found in most of the major marshes in the area.

Management of *S. acutus* usually involves one of two basic aims, to propagate or eliminate. Propagation of *S. acutus* has been largely unsuccessful, whether seed or rhizomes have been used.

The germination of *S. acutus* achenes in laboratory experiments during this study did not exceed 2%. Isley (1944) reported similar results.

A high rate (98%) of germination of *S. acutus* achenes which were inadvertently allowed to undergo a period of fermentation suggests that the achenes are capable of higher germination rates. Harris and Marshall (1960) reported germination rates of 53% for *S. acutus* achenes stored in natural waters for eight months prior to germination. While further work is needed, the results of this study and those of Harris and Marshall (1960) indicate that the achenes require one or a combination of low temperature (above freezing), anaerobic conditions and bacterial action. Seeding programs would be most successful if the achenes were bagged and stored in stagnant water for approximately eight months prior to actual seeding.

Even if the correct storage procedure produced high germination rates, however, the problem of establishment of the seedlings in the desired areas is not assured. During this study, no instances were found of seedling establishment of *S. acutus*. Harris

and Marshall (1960, 1963) found that seeding in the fall on mud exposed by a spring drawdown produced the best results. The achenes remained dormant until the following spring, when they germinated on the mud surface. Such a program probably would not be successful in areas such as Delta, Netley or parts of The Pas study area, where a drawdown produces germination of *S. validus* during the first summer. The seedlings become well-established by fall and would likely out-compete the *S. acutus* seedlings germinating the next spring. In areas where *S. validus* does not occur, such a program would be more successful. The propagation of *S. acutus* from rhizome cuttings, while more laborious, will probably give better results. Experience with the rhizomes of this species during nutrient culture experiments indicates that the rhizomes are susceptible to a transplanting 'shock', which has been confirmed by Fellows (1951) and Emerson (1961). These investigators found that the mortality rate was very high (98% and 80% respectively) when the rhizomes were removed from the mud, cut into smaller pieces and transplanted. The present author found that good growth could be produced by transplanting a block of soil with intact rhizomes, and similar findings have been reported by Gates (1948). Until the problems involved in germination and seedling establishment are solved, the propagation of *S. acutus* probably will be most successful if blocks of intact rhizomes are used.

The propagation of established stands of *S. acutus* can be accomplished by providing optimum habitat conditions. Often, the only practical habitat manipulation involves water levels. The

optimum water conditions for *S. acutus*, as determined in this study, are stable water levels with water depths between 15 and 40 cm. *S. acutus* will grow in water above or below this range, but will show reduced stand performance.

The second aspect of the management of *S. acutus*, its elimination, is encountered when stands are so extensive as to reduce "edge effect". Increased edge can be produced by breaking up a continuous stand into smaller 'islands' with open water between them. Effective reduction in areal cover can be achieved by flooding or a drawdown. In the author's experience, flooding is most effective when the substrate is composed of a thick, unconsolidated layer of organic matter. Water depths of 1.5 m will reduce the density of culms as well as cause clumps of rhizomes and the organic substrate to float to the surface, thereby creating holes which are not readily recolonized. Once the desired reduction in cover has occurred, usually after one year of flooding, water levels can be lowered for several years until regrowth has occurred and requires reflooding. Observations on moderate flooding (1.5 m) of areas with a well-consolidated substrate suggest that a reduction in culm density and fertility will occur, with effective eradication taking several years; sterile scattered culms may persist indefinitely, however, at depths between 1.5 and 2.5 m.

2. Management of *S. validus*

The habitat usually occupied by *S. validus* is not utilized extensively by muskrats or waterfowl because of the shallow water

and the unstable water levels characteristically associated with this species. There are, however, several characteristics of the biology of *S. validus* which are potentially valuable in wetland management.

S. validus is more amenable to propagation by seed or rhizome transplants than *S. acutus*. The higher germination rate produced by a period of cold treatment of achenes stored in water makes seed propagation a practical consideration. The greater tolerance of the rhizomes to transplanting similarly makes *S. validus* much easier to propagate than *S. acutus*.

The rapid development from seed of flowering culms and the greater volume of seed produced by *S. validus* make it of potential use as a source of food for both muskrats and ducks. Access to the culms may be provided by raising the water level in the fall to approximately 40 cm and draining the water back down to within 15 cm of the mud surface the following spring. This should provide sufficient water for muskrats and waterfowl to gain access to the stands in fall and winter and still provide optimum growing conditions the next summer. While such a program has not been attempted, it is suggested that it would be highly successful if the high water before and after the growing season did not affect the dormant rhizomes. This has not been determined, however.

Such a management plan would be of limited application, since it requires high water levels when runoff is least available (in the fall) and low water in the spring when runoff is maximum. In marshes where food supplies are limiting and there is an adequate

upstream water storage area and a good downstream gradient, such a program could be highly beneficial.

The ability of *S. validus* to pioneer on mineral soil makes it of potential value in colonizing either newly-created wetlands with a mineral substrate, or dikes and islands created for nesting waterfowl. The extensive root and rhizome system would effectively bind the soil and reduce erosion, and at the same time add organic matter to the substrate and thus prepare it for more desirable species, including *S. acutus*. In any such program, however, the inability of *S. validus* to withstand severe wind and wave action will determine its usefulness.

Attempts to utilize *S. validus* must be tempered with the fact that the limited distribution of this species, which this study indicates is due to high concentrations of magnesium and/or sulfate ions in the soil, will preclude its use in areas such as the Minnedosa study area where these ions occur in high concentrations.

The necessity to eradicate *S. validus* may be encountered in the management of wild rice (*Zizania aquatica* var. *interior*) paddies, where *S. validus* occasionally becomes established. This occurred at sites 24 and 31, where an uneven bottom and very shallow water had exposed the higher portions of the mud and *S. validus* seedlings volunteered. Such occurrences could be prevented by maintaining 50 cm or more of water on the mud during the summer; in the event of establishment, *S. validus* could be eliminated by flooding with 30 to 50 cm of water and maintaining this water depth for two years or more until culms fail to appear in the summer.

3. Additional uses for *S. acutus* and *S. validus*

In addition to their usefulness in management programs
oriented to wildlife, several other possible uses are suggested.
The planting of *S. validus* in sewage lagoons is recommended as a
possible means of making such areas more attractive to a variety of
wildlife as well as generally improving the aesthetic quality of
such areas. Seidel (1969) recommends the addition of the closely-
related *S. lacustris* to artificial ponds in urban areas. The plants
increase the aesthetic quality of such ponds, and in addition, they
effectively eliminate some components of urban pollution (milk,
starches, and some water-oil mixtures). This aspect of the manage-
ment and use of *S. acutus* and *S. validus* in North America could
prove very worthwhile, but requires considerable research.

The re-vegetation of 'waste areas' such as borrow pits
and the excavations in abandoned gravel pits could also be aided by
bulrushes. Propagation programs, if properly carried out, would
effectively "speed up" succession and prepare the area for coloni-
zation by other species.

There are a number of potential uses for *S. acutus* and
S. validus; which species will be most effective for a particular
purpose will depend upon the type of habitat involved. This study
provides a basic premise for successful management, namely that
S. acutus and *S. validus* are distinct species with distinctly
different environmental requirements. Management success will be
maximum if these distinctions are employed.

CHAPTER V

SUMMARY

1. The growth response of *S. acutus* and *S. validus* to several environmental parameters was measured at 60 sites in southern Manitoba from 1970 to 1972; sites were chosen from five study areas which were selected on the basis of differences in parent material, topography, and climate. The study was initiated to obtain data on the environmental requirements of these two taxa in order to provide a better understanding of the taxonomic relationship of the two.

2. Although sympatric throughout central North America, edaphic factors affect the local distribution of *S. acutus* and *S. validus*. *S. validus* is restricted to non-calcareous soils of lacustrine or deltaic origin, whereas *S. acutus* is found on a wide range of soil types.

3. The growth and reproductive biology of the two taxa was studied in 1971. Culm initiation begins in early May and continues into June and July for both *S. acutus* and *S. validus*. The maximum mean rate of culm elongation of 2.5 cm/day is attained in mid-June for *S. acutus* while the peak for *S. validus* (2.8 cm/day) is reached at the end of June. The length of growing season for *S. acutus* is approximately 65 days, while that of *S. validus* is approximately 86 days. Flowering begins approximately one month after culm initiation. The flowers are protogynous, flowering in individual spikelets being acropetalous. Receptive styles wither 48 hours after exsertion; four to six days later the anthers begin to release pollen. Eighty-five days after culm initiation, ripe achenes are present in the basal florets. After

falling from the inflorescence ripe achenes will float for as long as 22 days before sinking.

Achenes of *S. validus* germinate more readily under field conditions than those of *S. acutus*; germination of *S. validus* achenes is usually in response to drawdown conditions.

The environmental requirements for germination were examined in the laboratory; a period of cold storage in the dark in mud or water produced rates of germination from 74 to 85% in *S. validus*, but germination rates in excess of 2% for *S. acutus* did not occur under any conditions.

The biomass of *S. acutus* and *S. validus* stands were compared; values ranged from 60 g/m^2 to 570 g/m^2, the variability within and between stands making meaningful comparisons impossible. Similar variability was found in a comparison of aerial and subterranean components of the biomass. The subterranean component represented 47 to 79% of the total plant biomass.

4. The relationship between these bulrushes and other plant and animal components of the reed-swamp community is considered. Fifty-one species of rooted vascular plants were found in association with *S. acutus* and *S. validus*. Different species compositions are associated with the two bulrushes.

Twenty species of birds were found nesting in bulrush stands during the study period and eight species of ducks examined had eaten the achenes. The use of both *S. acutus* and *S. validus* by muskrats as

a food source and as material for lodge construction is also described.

5. Stand Performance, a combined measure of vitality and vigor, was calculated from density and fertility data collected for sites 1 to 60. Densities ranged from 27.8 to 258 culms/m^2, with no significant difference between the *S. acutus* and *S. validus* stands. Fertility rates ranged from 16.6 to 88.4%, again with no difference between the taxa.

6. Taxonomic assessment of sites 1 to 60 was accomplished by the use of the hybrid index technique. Characters used in the calculation of the hybrid index were selected in part through a factor analysis of 13 characters. A general inflorescence factor involving inflorescence length, the number of primary rays, the combined number of secondary, tertiary and quaternary rays, and the number of single- or double- spikelet clusters accounted for one-third of the variability. A second factor, interpreted as an achene size factor involving achene length and width accounted for a further 13% of the variance. A further 10% of the variance could be attributed to a factor involving the single character, spikelet width. The remaining nine factors were composed of single characters and each accounted for less than 10% of the variance. From the analysis of the thirteen characters, four showed a bimodal frequency distribution. Three of these characters and three additional ones not employed in the factor analysis were used in calculating the hybrid index values. The

characters used are:

1. inflorescence length

2. number of primary rays

3. presence or absence of tertiary and quaternary rays

4. presence or absence of spikelet clusters composed of five or more spikelets

5. lacunar diameter

6. culm color

Excellent agreement in scoring stands occurred for all six characters. Of the 60 sites examined, 19 were scored as being of the *S. validus* type, three were intermediate (a mixture of the two morphological types), and 38 were of the *S. acutus* form. Complete morphological discontinuity existed between the two morphological types.

Evidence for hybridization was obtained for only one site (site 20), where a few morphologically intermediate specimens were scattered along the zone of overlap between stands of *S. acutus* and *S. validus*. The intermediates were sterile, suggesting a hybrid origin for these specimens.

In addition to the six characters used in the hybrid index, three additional characters showed some agreement with the hybrid index values. These were floral scale color, floral scale length and spikelet length.

7. The response of the bulrushes in the 60 sites to a number of environmental parameters was measured. Mean water depths ranged from 0 to

70 cm, with *S. acutus* occupying the complete range. *S. validus* however was restricted to mean depths less than 30 cm. The habitat types occupied by *S. acutus* and *S. validus* differed, *S. acutus* being most common in stable lakes or marshes, whereas *S. validus* was most common in temporary creeks or ponds.

No difference between the soil textures of *S. acutus* and *S. validus* were found at sites 1 to 60.

S. acutus was found at higher concentrations of calcium, magnesium and sulfate ions than *S. validus*, although the difference was statistically significant only for magnesium and sulfate. An intolerance for high concentrations of these ions may be the factor limiting the distribution of *S. validus* in Manitoba.

Attempts to examine the response of these plants to calcium, magnesium and sulfate ions in nutrient culture were unsuccessful.

8. The habitats occupied by *S. acutus* and *S. validus* are different; the two are occasionally found growing together, but this is attributed to a recent change in the habitat, usually water levels. Even when the two are found in close association, the occurrence of morphologically intermediate specimens is rare; this indicates the existence of a substantial barrier to gene flow. This evidence as well as the complete morphological discontinuity found in the 60 stands examined suggests that the specific level of distinction be retained for *S. acutus* and *S. validus*.

9. Several recommended management practices are suggested by this study:

(a) Propagation of *S. acutus* will be most successful when entire blocks of soil containing rhizomes are transplanted.

(b) Maximum stand performance of established *S. acutus* stands will be obtained under stable water levels and water depths of 15 to 40 cm.

(c) Eradication of *S. acutus* can be accomplished by flooding with 1.5 m of water or by a prolonged drawdown, the results depending upon the nature of the rooting medium.

(d) *S. validus* can be propagated by either seeding after a drawdown or by transplanting rhizomes.

(e) Optimum growth of *S. validus* will be obtained in shallow waters (less than 15cm) with low magnesium and sulfate concentrations.

(f) The rapid growth from seedlings and abundant seed production of *S. validus* can be made accessible to waterfowl and muskrats by fall flooding and spring drawdowns.

(g) Eradication of *S. validus* can be accomplished by prolonged flooding with 50 cm or more of water.

(h) Additional uses of these bulrushes in artificial ponds are suggested as possible avenues of research.

LITERATURE CITED

Anderson, E. 1936.   The species problem in *Iris* Ann. Mo. Bot. Gard. 23: 457-509.

Anderson, S. 1968. A new craniometer and suggestions for craniometry. J. Mammal. 49(2): 221-228.

Arata, A.A. 1959. Ecology of muskrats in strip mine ponds in southern Illinois. J. Wildl. Mgt. 23(2): 177-186.

Arnon, K.I. and D.R. Hoagland 1940. Crop production in artificial solutions and in soils with special reference to factors influencing yields and absorption of inorganic nutrients. Soil Sci. 50: 463.

Bartlett, M.S. 1947. The use of transformations. Biometrics 3(1): 39-52.

Beetle, A,A, 1940. Studies in the genus *Scirpus* L. I. Delimitation of the subgenera Euscirpus and Aphylloides. Am. J. Bot. 27(2): 63-64. 63-64.

_____ 1941. Species studies in the genus *Scirpus* L. III. The American species of the section Lacustris Clarke. Am. J. Bot. 28(8):691-700.

_____ 1944. Studies in the genus *Scirpus* L. VII. Conspectus of sections represented in the Americas. Am. J. Bot. 31(5): 261-265.

_____ 1950. Bulrushes and their multiple uses. Economic Botany 4: 132-138.

Bellrose, F.C. 1950. Relationship of muskrat populations to various marsh and aquatic plants. J. Wildl. Mgt. 14(3): 229-315.

Brairerd, E. 1904. *Scirpus validus* and its allies in the Champlain Valley. Rhodora 6:231-232.

Buckman, H.O. and N.C. Brady 1960. The Nature and Properties of Soils. Macmillan Co., New York. 367 pp.

Burt, W.H. and R.P. Grossenheider 1946. A Field Guide to the Mammals. 2nd. edition. Houghton-Mifflin, Boston. 284 pp.

Catenhusen, J. 1944. Some aquatic and sub-aquatic plants from the region of glacial lake Wisconsin. Trans. Wisc. Acad. of Sci., Arts and Letters 36:163-169.

Cattell, R.B. 1965. Factor analysis: an introduction to essentials. II. The role of factor analysis in research. Biometrics 21: 405-435.

Chamberlain, E. B. 1948. Ecological factors influencing the growth and management of certain waterfowl food plants on Back Bay National Wildlife Refuge. Trans. N. Amer. Wildl. Conf. 13: 347-356.

Chamberlain, J. L. 1959. Gulf coast marsh vegetation as food of wintering waterfowl. J. Wildl. Mgt. 23(1): 97-102.

Chase, Agnes. 1904. The North American allies of *Scirpus lacustris*. Rhodora 6: 65-7.

Clausen, J. and W. M. Hiesey. 1958. Phenotypic expression of genotypes in contrasting environments. Report, 1958, Scottish Pl. Breeding Station 69-75.

Curtis, J. T. 1959. The vegetation of Wisconsin. Univ. Wisc. Press, Madison. 657 pp.

Dabbs, D. L. 1971. A study of *Scirpus acutus* and *Scirpus validus* in the Saskatchewan River delta. Can. J. Bot. 49: 143-153.

Dane, C. W. 1959. Succession of aquatic plants in small artificial marshes in N. Y. state. N.Y. F. and Game Jour. 6(1): 59-76.

Daubenmire, R. 1968. Plant Communities: A Textbook of Plant Synecology. Harper and Row, N.Y. 300 pp.

Davis, P. H. and V. H. Heywood. 1963. Principles of Angiosperm Taxonomy. Van Nostrand Co., Inc.; N.Y. 585 pp.

Dykyjova, D. 1971. Production, vertical structure, and light profiles in littoral stands of reed-bed species. Hydrobiologia 12: 361-376.

Ehrlich, W. A., E. A. Poyser, and L. E. Pratt. 1957. Report of Reconaissance Soil Survey of Carberry Map Sheet Area. Manitoba Soil Survey, Soils Report 7.

Ehrlich, W. A., L. E. Pratt, F. P. Leclaire, and J. A. Barr. 1960. Report of Detailed Soil Survey of Pasquia Map Area in Northern Manitoba. Manitoba Soil Survey Soils Report 11.

Emerson, F. B., Jr. 1961. Some aspects of the ecology and management of wildlife marshes in New York State. N. Y. State Conservation Dept. Job Completion Report, Job III-A. 115 pp. mimeo.

Errington, P. L. 1948. Environmental control for increasing muskrat production. Trans. N. Am. Wildl. Conf. 13: 596-605.

_____. 1963. Muskrat Populations. Iowa State Univ. Pr., Ames. 665 pp.

Fassett, N. C. 1930. The plants of some north-eastern Wisconsin lakes. Trans. Wisc. Acad. Sci., Arts and Letters 25: 156-168.

_____ 1940. Manual of Aquatic Plants. Univ of Wisconsin Pr., Madison. 405 pp.

Fernald, M. L. 1920. *Scirpus acutus* Muhl. Rhodora 22: 55.

_____ 1943. Studies in North American species of *Scirpus*. Rhodora 45: 283-286.

_____ 1950. Gray's Manual of Botany (8th. edition). Amer. Book Co., N.Y. 1632 pp.

Fellows, N. W., Jr. 1951. Results of a waterfowl food planting survival study in Maine. Maine Game Division Bull #1. 23 pp.

Gates, F.C. 1948. Colonization of certain aquatic plants on an open shoal. Ecology 29(2): 205-208.

Gleason, H. A. 1941. *Scirpus validus* for demonstrating procambium. Rep. Mich. Acad. Sci. 20: 153.

_____ 1952. The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. (vol. 1). N. Y. Bot. Gardens. 482 pp.

Godfrey, W. E. 1966. The Birds of Canada. Nat. Mus. of Canada Bull. #23, Biol. Ser. #73. Queen's Printer, Ottawa. 428 pp.

Harris, S. W. and W. H. Marshall 1960. Germination and planting experiments with hardstem and softstem bulrush. J. Wildl. Mgt. 24(2): 158-166.

_____ 1963. Ecology of water-level manipulations on a northern marsh. Ecology 44(2): 331-343.

Heslop-Harrison, J. 1952. Statistical methods in plant taxonomy. Taxon 1: 53-59, 73-78.

Hicks, G. C. 1928. Chromosome studies in the Cyperaceae, with special reference to *Scirpus* . Bot. Gaz. 86: 295-317.

Hoel, P. G. 1960. Elementary Statistics. John Wiley and Sons, N.Y. 351 pp.

Hulten, E. 1940. Flora of Alaska and Yukon. Hakan Ohlssons Boktryckeri, Lund. 978 pp.

Isely, D. 1944. A study of conditions that affect the germination of seeds. Mem. N. Y. (Cornell) Agric. Exp. Sta. #257. 28 pp.

Jacob, A. 1958. Magnesium, the Fifth Major Plant Nutrient. Staples, London. (Translated from German by N. Walker). 159 pp.

Keith, L. B. and R. P. Stanislowski 1960. Stomach contents and weights of some flightless adult pintails. J. Wildl. Mgt. 24(1): 95-96.

Kiel, W. H., Jr. 1955. Nesting studies of the coot in southwestern Manitoba. J. Wildl. Mgt. 19(2): 189-198.

Killmer, V. J. and L. T. Alexander 1949. Methods of making mechanical analysis of soils. Soil Sci. 68: 15-24.

Klugh, H. E. 1970. Statistics, the Essentials for Research. John Wiley and Sons, N.Y. 387 pp.

Koyama, T. 1962. The genus *Scirpus* L.: some North American aphylloid species. Can. J. Bot. 40: 913-937.

_____ 1963. The genus *Scirpus* L.: critical aspects of the section Pterolepis. Can. J. Bot. 41: 1107-1131.

Levitt, J. 1972. Responses of Plants to Environmental Stresses. Academic Pr., N.Y. 697 pp.

Lissey, A. 1962. Surficial Mapping of Groundwater Flow Systems with Application to the Oak River Basin, Manitoba. Univ. of Saskatchewan Ph. D. Thesis, Saskatoon. 244 pp.

Lokomon, J. T. 1966. Breeding ecology of the redhead duck in western Montana. J. Wildl. Mgt. 30(4): 668-681.

Low, J. B. and F. C. Bellrose, Jr. 1944. The seed and vegetative yield of waterfowl food plants in the Illinois River Valley. J. Wildl. Mgt. 8(1): 7-22.

Martin, A. C. and F. M. Uhler 1939. Food of Game Ducks in the United States and Canada. U.S.D.A. Tech. Bull. #634. 527 pp.

Martin, A. C. H., H. S. Zim, and A. L. Nelson 1951. American Wildlife and Plants. Dover, N.Y. 500 pp.

Metcalf, F. P. 1931. Wild Duck Foods of North Dakota Lakes. U.S.D.A. Tech. Bull. #221. 44 pp.

Millar, J. B. 1969. Observations on the ecology of wetland vegetation. Saskatchewan Wetlands Seminar, Saskatoon. C.W.S. Rep. Ser. 6: 49-56.

Misra, R. D. 1938. Edaphic factors in the distribution of aquatic plants in the English Lakes. J. Ecol. 26: 411-451.

Moss, E. H. 1959. Flora of Alberta. Univ. of Toronto Pr. 456 pp.

Moyle, J. B. 1956. Some aspects of the chemistry of Minnesota surface waters as related to game and fish management. J. Wildl. Mgt. 20(3): 303-320.

Muenscher, W. C. 1944. Aquatic Plants of the United States. Comstock Publishing Associates, Itasca N.Y. 374 pp.

Munsell Book of Color (12th. edition, revised and rearranged. Munsell Color Co., Baltimore, Md. 62 pp.

Parlour, J. W., T. S. Major, and A. E. Rattray 1972. The Red River Delta. Univ. of Manitoba, Nat. Res. Inst., Winnipeg. 213 pp.

Proctor, J. 1970. Magnesium as a toxic element. Nature 227: 742-743.

Rickett, H. W. 1921. A quantitative study of the larger aquatic plants of Lake Mendota. Trans. Wisc. Acad. Arts, Sci., and Letts. 20: 501-527.

Riley, H. P. 1938. A character analysis of *Iris fulva*, *I. hexagona* var. *giganticaerulea* and natural hybrids. Am. J. Bot. 25: 727-738.

Rydberg, P. A. 1932. Flora of the Prairies and Plains of Central North America. N.Y. Bot. Garden. N.Y. 969 pp.

Scoggan, H. J. 1957. Flora of Manitoba. Nat. Mus. Canada Bull. #140, Queen's Printer, Ottawa. 619 pp.

Seidel, K. 1969. Higher quatic plants in their environment: a new orientation. Rev. Roum. Biol. Ser. Zool. 14(2): 149-156 (abstr.)

Sigler, W. F. 1948. Aquatic and shore vegetation of Spirit Lake, Iowa. Iowa State Coll. J. of Sci. 23(1): 103-123.

Smith, S. G. 1969. Natural hybridization in the *Scirpus lacustris* complex in the North Central United States. In Current Topics in Plant Science (J. E. Gunekel, ed.) 175-200.

Sneath, P. H. A. 1958. Some aspects of Adansonian classification and of the taxonomic theory of correlated features. Ann. Microbiol. Enzymol. 8: 261-268.

Snedecor, G. W. 1956. Statistical Methods Applied to Experiments in Agriculture and Biology. Iowa State College Pr., Ames, Iowa. 485 pp.

Snow, L. M. 1914. Contribution to the knowledge of the diaphragms of water plants. I. *Scirpus validus*. Bot. Gaz. 58: 495-517.

Sokal, R. R. and P. H. A. Sneath 1963. Principles of Numerical Taxonomy. W. H. Freeman and Co., San Francisco, Cal. 359 pp.

Solbrig, O. T. 1960. Principles and Methods of Plant Biosystematics. Collier-Macmillan, Toronto. 226 pp.

Steenis, J. H. 1939. Marsh management on the Great Plains waterfowl refuges. Trans. N. Am. Wildl. Conf. 4: 400-405/

Stewart, R. E. and H. A. Kantrud 1969. Proposed classification of potholes in the glaciated prairie region. Saskatoon Wetlands Seminar, C. W. S. Rep. Ser. 6: 57-69.

Strogonov, B. P. 1964. Physiological Basis of Salt Tolerance of Plants. Israel Program for Sci. Trans., Jerusalem. 279 pp.

Uhler, F. M. 1956. New habitats for waterfowl. Trans. N. Am. Wildl. Conf. 21:453-469.

Valentine, D. H. and A. Love 1958. Taxonomic and biosystematic categories. Brittonia 10: 153-166.

Walker, J. M. 1959. Vegetation Studies on the Delta Marsh, Delta, Manitoba. Univ. of Manitoba M. Sc. Thesis, Winnipeg. 203 pp.

_____ 1965. Vegetation Changes with Falling Water Levels in the Delta Marsh, Manitoba. Univ. of Manitoba Ph. D. Thesis, Winnipeg. 272 pp.

Ward, R. L. 1973. Cytotaxonomic study of the *Scirpus lacustris* complex in the North Central United States. Paper given at the Seventh Annual Prairie University Biology Students' Conference, Feb. 23-24, Winnipeg, Manitoba.

Weaver, J. E. and W. J. Himmel 1930. Relation of increased water content and decreased aeration to root development in hydrophytes. Pl. Phys. 5: 69-92.

Weir, T. R. 1960. Economic Atlas of Manitoba. Man. Govt., Dept. Industry and Commerce, Winnipeg. 81 pp.

Williams, W. T. and D. A. Barber 1961. The functional significance of aerenchyma in plants. Symp. Soc. Exper. Biol. 15: 132-144.

Williams, C. S. and C. A. Sooter 1941. Canada goose habitat in Utah and Oregon. Trans. N. Am. Wildl. Conf. 6: 384-385

Willis, J. C. 1955. A Dictionary of the Flowering Plants and Ferns. Cambridge Univ. Pr., Cambridge. 752 pp.

Wolf, K. 1955. Some effects of fluctuating and falling water levels on waterfowl production. J. Wildl. Mgt. 19(1): 13-23.

Yeager, L. D. 1945. Capacity of Illinois land types to produce furs. Trans. N. Am. Wildl. Conf. 10: 79-86.

APPENDIXES

APPENDIX I.   DETAILED SITE LOCATIONS

Site	Map Sheet Reference	Grid Reference			Site	Map Sheet Reference	Grid Reference		
1	62J/7W	14U	NL	094833	31	63F/14W	14U	LQ	475654
2	62J/7W	14U	NL	092837	32	62J/1E	14U	NL	543527
3	62J/1W	14U	NL	448566	33	62J/1W	14U	NL	524501
4	62I/7	14U	PL	571787	34	63F/12W	14U	LQ	152527
5	62J/7W	14U	NL	171815	35	63F/12W	14U	LQ	155545
6	62J/4W	14U	ML	387525	36	63F/14E	14U	LQ	580678
7	62I/7	14U	PL	571792	37	62J/1W	14U	NL	452573
8	62I/7	14U	PL	586797	38	62J/7W	14U	NL	144833
9	62J/7W	14U	NL	157816	39	62J/1W	14U	NL	448540
10	62J/7W	14U	NL	118815	40	62I/7	14U	PL	576796
11	62J/4W	14U	ML	395546	41	63F/12W	14U	LQ	152525
12	62I/7	14U	PL	586796	42	63F/12W	14U	LQ	163558
13	62J/7W	14U	NL	105817	43	63F/14E	14U	LQ	559659
14	62J/7W	14U	NL	116816	44	62J/1W	14U	NL	418577
15	62J/7W	14U	NL	179814	45	62J/1W	14U	NL	416582
16	62J/4W	14U	ML	396538	46	62J/1W	14U	NL	428584
17	62I/7	14U	PL	479819	47	63F/14E	14U	LQ	578678
18	62I/7	14U	PL	565778	48	62J/1W	14U	NL	451573
19	62I/7	14U	PL	587795	49	62J/1W	14U	NL	398593
20	62J/1E	14U	NL	542539	50	62J/1W	14U	NL	416577
21	62J/4W	14U	NL	332446	51	62J/1E	14U	NL	691616
22	62J/1E	14U	NL	549487	52	62J/1W	14U	NL	429586
23	62J/1W	14U	NL	429529	53	62J/1W	14U	NL	441553
24	63F/14W	14U	LQ	474654	54	62J/1W	14U	NL	399584
25	62J/4W	14U	ML	373524	55	62J/1W	14U	NL	479548
26	62J/4W	14U	ML	352523	56	62J/1W	14U	NL	407575
27	62J/4W	14U	ML	333508	57	62J/1W	14U	NL	427585
28	62J/1E	14U	NL	544557	58	62J/1W	14U	NL	428583
29	62J/4W	14U	ML	397583	59	62J/1W	14U	NL	407574
30	62J/1E	14U	NL	544503	60	62J/1W	14U	NL	432582
100	62J/1W	14U	NL	437582	102	62J/1W	14U	NL	445567
101	62J/1W	14U	NL	512487	103	62J/1E	14U	NL	544502

The Universal Transverse Mercator Grid (Military Grid) references were obtained from map sheets in the National Topographic System (Scale 1:50,000).   The map sheet descriptions are as follows:

Red River Delta	62I/7	Edition 2 MCE	Series A 743
MacDonald	62J/1W	Edition 2 ASE	Series A 743
MacDonald	62J/1E	Edition 2 ASE	Series A 743
Moore Park	62J/4W	Edition 1 ASE	Series A 743
Langruth	62J/7W	Edition 1 ASE	Series A 743
The Pas	63F/14W	Edition 1 ASE	Series A 743
The Pas	63F/14E	Edition 1 ASE	Series A 743
Culdesac Lake	63F/12W	Edition 1 ASE	Series A 742

APPENDIX II.   MORPHOLOGICAL DATA FROM SITES 1 TO 60.

Site	Inflorescence Length		No. of Primary Rays		No. of Secondary Rays	
	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.
1	38.2	11.6	4.84	1.91	0.2	0.577
2	37.5	11.6	4.88	1.2	0.44	0.87
3	42.8	14.3	4.96	2.99	0.48	1.16
4	100	26.9	16.4	5.38	36.8	19.3
5	38.4	13.6	4.96	1.54	1.76	1.51
6	40	10.2	5.72	1.21	1.72	1.62
7	111	17.8	13.1	2.43	25	5.8
8	87.8	21.6	16.5	5.77	29	11.3
9	30.8	8.6	4.96	0.79	1.44	1.19
10	36	9.35	5.16	1.03	2	1.38
11	46.7	10.7	5.68	1.68	3.04	2.56
12	74	18.6	9.12	4.63	13.7	7.52
13	38.2	13.3	5.48	1.48	1.52	1.56
14	24.9	10.8	3.8	1.91	0.32	0.802
15	31.3	10.3	4.92	1.38	0.36	0.907
16	37.4	11.6	3.8	1.61	1.2	1.5
17	98.2	21.6	14.7	3.05	19.2	9.16
18	74.3	24	14.4	5.2	19.8	10.3
19	73.8	17.5	11.1	4.84	14.4	7.64
20	58.2	22.2	8.64	4.98	5.88	10.3
21	36.1	9.72	4.6	1.8	2.44	1.78
22	107	17.5	19.6	2.69	32.7	9.49
23	77.8	22.6	12.2	5.04	13.7	9.13
24	107	18.1	16.5	3.06	19.6	8.69
25	32.4	15.2	4.68	1.82	1.44	2.08
26	28.8	11.7	4.24	2.4	0.4	0.816
27	38.9	13.8	4.48	1.81	0.72	1.37
28	73.6	20.1	13.4	4.96	15.2	11
29	31.8	12.2	4.16	2.12	1.04	2.19
30	93	20.2	14.8	2.98	24	10.7
31	86.5	17.6	15	5.42	25.4	14.1
32	99.2	19.3	17.6	3.61	22.4	9.28
33	81.7	12.6	14	3.2	19.7	10.6
34	48.3	21.3	7.64	4.05	5.12	9.17
35	38.6	12.9	4.8	2.04	0.12	0.44
36	38.8	12.8	3.28	1.72	0	0
37	80.4	22.1	14	4.64	20.2	9.99
38	22.8	7.82	4.12	2.01	0.28	0.614
39	79.9	10.2	18.3	2.51	33	9.8
40	77.1	11.1	15	4.42	24	12.6
41	28.6	7.77	4.96	1.93	0.32	0.69
42	32.3	6.69	3.96	2.09	0.44	0.87
43	40.4	9.44	4.12	1.3	0	0
44	34.4	9.17	5.4	2.22	0	0
45	45.7	14.1	4.64	2	0	0
46	38.2	9.76	3.72	1.84	0	0
47	29.7	6.67	2.24	1.2	0	0
48	75.6	13.5	14.1	4.15	23.7	14.2
49	36.1	8.72	4.36	1.63	1.32	1.11
50	38.3	8.35	4.6	1.76	0.84	1.11
51	43.4	11	5.12	1.69	0.84	0.8
52	39.3	10.2	5.64	1.11	1.6	1.61
53	50	21.6	7.52	4.39	7.04	8.39
54	40.2	8.19	5.32	1.68	0.84	0.943
55	92.6	15.8	16.6	3.24	35	10.8
56	37.4	7.69	4.28	2.09	0.56	0.712
57	32.6	14.2	2.56	2.27	0.56	0.961
58	42.5	15.3	4	2.29	0	0
59	33.3	7.7	3.6	1.53	1.16	0.688
60	31.6	7.06	4.72	1.95	0.52	0.77

APPENDIX II.   MORPHOLOGICAL DATA (cont.)

Site	Awn Length (mm)		Achene Length (mm)		Achene Width (mm)	
	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.
1	0.421	0.251	2.27	0.206	1.54	0.131
2	0.303	0.219	2.16	0.154	1.59	0.113
3	0.409	0.166	2.36	0.163	1.61	0.141
4	0.248	0.136	2.04	0.119	1.48	0.0748
5	0.417	0.206	2.19	0.164	1.5	0.115
6	0.488	0.166	2.34	0.136	1.63	0.102
7	0.212	0.0506	1.99	0.108	1.49	0.0518
8	0.226	0.111	2.02	0.114	1.45	0.116
9	0.434	0.289	2.02	0.205	1.47	0.159
10	0.391	0.327	2.08	0.473	1.36	0.312
11	0.343	0.171	2.27	0.226	1.61	0.153
12	0.25	0.049	2.03	0.166	1.46	0.0656
13	0.401	0.155	2.15	0.177	1.51	0.155
14	0.479	0.217	2.25	0.144	1.51	0.129
15	0.66	0.235	2.25	0.194	1.62	0.132
16	0.311	0.185	2.31	0.124	1.65	0.12
17	0.28	0.106	2.1	0.172	1.4	0.125
18	0.154	0.122	2.03	0.195	1.46	0.102
19	0.222	0.129	2.03	0.21	1.53	0.0951
20	0.336	0.217	2.14	0.298	1.48	0.15
21	0.468	0.156	2.11	0.164	1.58	0.102
22	0.262	0.0833	2.21	0.151	1.38	0.11
23	0.209	0.0914	2	0.123	1.43	0.105
24	0.254	0.133	1.91	0.172	1.32	0.148
25	0.54	0.173	2.23	0.148	1.59	0.137
26	0.463	0.185	2.23	0.218	1.56	0.152
27	0.477	0.192	2.1	0.184	1.6	0.232
28	0.421	0.19	2.02	0.17	1.41	0.147
29	0.672	0.217	2.16	0.143	1.72	0.136
30	0.283	0.168	2.38	0.143	1.38	0.0779
31	0.301	0.115	2.33	0.228	1.4	0.0952
32	0.277	0.128	2.15	0.423	1.43	0.135
33	0.271	0.188	2.2	0.127	1.31	0.137
34	0.457	0.131	1.96	0.291	1.4	0.169
35	0.538	0.132	1.88	0.164	1.43	0.175
36	0.49	0.0889	2.1	0.205	1.63	0.11
37	0.277	0.176	2.09	0.138	1.52	0.14
38	0.579	0.198	2.1	0.101	1.51	0.088
39	0.338	0.0894	2.28	0.0872	1.27	0.0763
40	0.298	0.125	2.13	0.101	1.31	0.0998
41	0.598	0.133	2.4	0.127	1.46	0.152
42	0.464	0.163	2.47	0.137	1.56	0.142
43	0.47	0.142	1.99	0.106	1.4	0.104
44	0.447	0.153	2.28	0.194	1.52	0.18
45	0.52	0.151	1.96	0.178	1.49	0.16
46	0.538	0.157	2.05	0.215	1.62	0.174
47	0.452	0.142	2.04	0.2	1.48	0.186
48	0.354	0.151	2.28	0.125	1.28	0.0858
49	0.473	0.118	2.29	0.0783	1.56	0.126
50	0.453	0.118	2.42	0.139	1.73	0.171
51	0.442	0.155	2.27	0.112	1.57	0.104
52	0.448	0.123	2.3	0.153	1.56	0.134
53	0.404	0.127	2.13	0.179	1.57	0.146
54	0.493	0.0941	2.22	0.0914	1.49	0.107
55	0.262	0.0807	1.87	0.0693	1.5	0.0776
56	0.514	0.138	2.19	0.16	1.71	0.135
57	0.46	0.155	2.14	0.232	1.58	0.121
58	0.412	0.121	2.3	0.146	2.03	0.148
59	0.459	0.104	2.22	0.102	1.3	0.101
60	0.439	0.149	2.34	0.162	1.66	0.122

APPENDIX II. MORPHOLOGICAL DATA (cont.)

Site	No. of Tertiary Rays		No. of Quaternary Rays		No. of Clusters < 5 Spikelets	
	x̄	s.d.	x̄	s.d.	x̄	s.d.
1	0	0	0	0	4.6	2.29
2	0	0	0	0	5.68	1.84
3	0	0	0	0	5.64	2.84
4	10.7	10.5	0.44	1.26	67	40.3
5	0	0	0	0	5.92	2.34
6	0	0	0	0	6.16	1.99
7	6.68	4.06	0	0	13	1.93
8	6.16	6.09	0.04	0.2	18	10.1
9	0	0	0	0	5.72	1.24
10	0	0	0	0	6.32	1.55
11	0	0	0	0	7.24	4.32
12	5	6.22	0.8	2.02	27.8	13.5
13	0.12	0.6	0	0	6.56	2.36
14	0	0	0	0	3.56	2.02
15	0	0	0	0	4.64	2.75
16	0	0	0	0	3.68	2.04
17	10.4	5.45	1.68	3.01	25.4	6.75
18	3.72	4.88	0	0	19	8.81
19	2.56	2.42	0.04	0.2	16	6.74
20	1.28	4.67	0.04	0.2	15.7	18
21	0.28	0.737	0	0	6.92	1.85
22	10.3	5.33	0	0	21.9	3.93
23	3.44	3.1	0.08	0.4	17.6	6.55
24	7.88	4.46	0.12	0.44	18.2	5.71
25	0	0	0	0	5.58	4.14
26	0	0	0	0	4.48	2.2
27	0.04	0.2	0	0	5.2	2.72
28	3.72	5	0.08	0.4	23.6	13.8
29	0	0	0	0	3.68	2.64
30	9.76	6.97	0.08	0.277	18.4	6.02
31	10.6	10	0.2	1	13.4	3.46
32	9.72	7.28	0	0	19.1	6.5
33	5.44	4.57	0.24	0.597	29.2	13.1
34	1.24	2.73	0	0	8.04	8.5
35	0	0	0	0	2.24	1.36
36	0	0	0	0	2	1.08
37	8.48	5.84	0.36	1.08	17.2	8.39
38	0	0	0	0	2.44	1.73
39	16.3	7.11	0	0	19.4	5.85
40	8.96	7.27	0	0	23	13.3
41	0	0	0	0	3.08	1.58
42	0	0	0	0	2.32	1.68
43	0	0	0	0	1.48	0.586
44	0	0	0	0	3.48	1.64
45	0	0	0	0	2.88	2.13
46	0	0	0	0	3.28	2.05
47	0	0	0	0	0.6	0.577
48	12.1	8.88	0.16	0.8	24.3	6.96
49	0	0	0	0	4.8	2.06
50	0	0	0	0	4.64	1.99
51	0	0	0	0	4.44	1.92
52	0	0	0	0	5.96	1.88
53	3.16	4.57	0	0	16	16.2
54	0.04	0.2	0	0	5.04	1.84
55	18.4	8.84	1.72	3.78	22	6.28
56	0	0	0	0	3.28	1.79
57	0	0	0	0	2.68	2.84
58	0	0	0	0	3.2	1.83
59	0.12	0.332	0	0	3.52	1.39
60	0	0	0	0	4.12	2.11

APPENDIX II. MORPHOLOGICAL DATA (cont.)

Site	No. of Clusters > 5 Spikelets		Spikelet Length (mm)		Spikelet Width (mm)	
	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.
1	1.36	0.569	8.45	1.53	4.04	0.872
2	0.96	0.841	8.12	1.39	4.58	0.849
3	0.68	0.748	9.09	1.06	4.52	0.699
4	0.04	0.2	5.8	0.778	4.07	0.402
5	0.6	0.957	5.91	1.49	3.38	0.841
6	1.76	0.97	7.42	1.13	3.99	0.624
7	0	0	6.92	1.55	4.12	0.762
8	0	0	5.84	0.937	4	0.624
9	0.6	0.645	5.43	1.51	3.01	0.627
10	0.8	0.913	5.18	0.997	2.89	0.662
11	2.4	1.22	7.95	1.75	3.54	0.398
12	0.08	0.277	5.2	0.685	4.09	0.692
13	0.84	0.943	6.3	1.9	3.11	0.695
14	0.88	0.666	7.23	1.32	3.1	0.656
15	0.4	0.5	8.21	1.24	3.78	0.633
16	2	1.76	7.99	1.2	4.05	0.517
17	0.04	0.2	6.06	0.35	4.88	0.599
18	0	0	5.56	0.967	3.82	0.5
19	0	0	5.18	0.725	4.19	0.511
20	2.36	1.78	6.79	1.25	3.84	0.773
21	1.44	1.5	6.07	0.811	3.77	0.489
22	0	0	7.03	1.07	4.17	0.375
23	0	0	5.7	0.489	4.33	0.382
24	0	0	5.97	0.61	4.85	0.478
25	0.88	0.781	7.57	1.65	3.52	0.834
26	1.44	1	6.4	1.33	3.63	0.632
27	0.92	0.812	8.59	1.77	4.15	0.503
28	0.88	1.27	7.94	1.37	3.72	0.45
29	1.72	1.28	8.5	1.64	3.69	0.591
30	0.04	0.2	5.35	0.711	3.36	0.367
31	0.04	0.2	7.06	0.938	4.32	0.517
32	0.04	0.2	6.08	0.867	3.74	0.595
33	0.16	0.374	5.84	0.834	3.19	0.587
34	2.88	1.64	7.35	1.14	3.6	0.573
35	3.64	1.82	8.48	0.606	3.66	0.387
36	2.24	1.16	8.05	0.554	3.78	0.365
37	0.28	0.843	6.71	1.55	3.22	0.433
38	1.8	1.32	8.1	1.41	3.5	0.693
39	0	0	6.01	0.329	2.38	0.385
40	0.28	0.737	5.76	0.769	3.09	0.363
41	3.12	1.3	8.55	0.625	3.68	0.351
42	3.04	1.49	8.36	0.588	3.77	0.429
43	3.48	1.16	8.2	0.623	3.79	0.545
44	2.84	1.49	7.52	0.621	3.31	0.319
45	2.8	1.38	8.89	0.771	4.14	0.474
46	1.28	1.06	8.17	1.12	3.46	0.535
47	2.56	1	8.24	0.821	3.68	0.404
48	0	0	6.25	1.47	3.16	0.636
49	1.64	0.7	7.67	0.848	3.57	0.347
50	2.32	1.25	7.69	0.784	3.8	0.429
51	2.28	0.792	7.81	0.533	3.75	0.434
52	1.44	1.33	7.86	0.912	4	0.451
53	1.48	1.45	6.4	1.48	3.38	0.535
54	1.96	1.17	7.75	0.708	3.51	0.405
55	0.04	0.2	6.21	0.79	3.64	0.522
56	2.36	1.22	7.86	0.655	3.74	0.409
57	1.32	0.69	8.03	1.28	3.46	0.586
58	1.64	0.757	8.17	0.798	3.65	0.48
59	2.28	1.24	7.7	0.545	3.79	0.334
60	2.12	0.927	7.48	0.803	3.52	0.559

APPENDIX II. MORPHOLOGICAL DATA (cont.)

Site	Bract Length (mm)		Lacunar Diameter (mm)		Culm Color Score	
	$\bar{X}$	s.d.	$\bar{X}$	s.d.	$\bar{X}$	s.d.
1	33.6	8.16	0.56	0.16	2.0	0
2	36.2	7.03	0.57	0.16	2	0
3	49	20	0.51	0.15	1.76	0.44
4	40.8	13.4	2	0.58	0	0
5	41.4	12.2	0.56	0.16	2	0
6	44.8	8.35	0.61	0.17	2	0
7	47	3.47	1.8	0.53	0.24	0.44
8	47.9	19	2	0.56	0	0
9	40.2	19.5	0.53	0.15	2	0
10	32.2	9.86	0.48	0.14	2	0
11	51.1	12.5	0.62	0.18	2	0
12	41.6	12.1	1.7	0.49	0	0
13	44.1	11.2	0.57	0.16	2	0
14	29.9	7.83	0.52	0.15	2	0
15	33.8	11	0.52	0.15	2	0
16	51.1	13.8	0.51	0.15	2	0
17	43.2	15.8	1.5	0.43	0	0
18	44.7	14.8	1.9	0.54	0	0
19	46.6	19.5	1.9	0.54	0.16	0.47
20	46	20.4	0.68	0.19	1.43	0.88
21	39.3	9.78	0.57	0.16	2	0
22	39.9	9.29	1	0.29	0.19	0.4
23	36.1	8.96	1.5	0.42	0.32	0.63
24	37.2	10.3	2.1	0.59	0	0
25	58.2	9.08	0.58	0.17	2	0
26	46.3	4.86	0.62	0.18	2	0
27	53	14.2	0.59	0.17	1.92	0.28
28	38.2	10.4	0.9	0.26	0.90	0.83
29	42.2	11.1	0.57	0.16	2	0
30	35	10.5	1.7	0.48	0.12	0.33
31	39.5	12.4	2.1	0.59	0	0
32	45.4	16.7	1.7	0.49	0.28	0.540.
33	46.1	9.52	1.6	0.45	0.17	0.49
34	31.9	10.8	0.98	0.28	0.96	0.76
35	38	7.25	0.65	0.18	2	0
36	45.7	10.4	0.72	0.2	2	0
37	45	14.2	1.8	0.53	1.96	0.2
38	31.9	7.38	0.55	0.16	2	0
39	35.6	13.2	1.2	0.35	0.52	0.51
40	37.4	9.26	1.7	0.48	2	0
41	37.1	9.59	0.64	0.18	2	0
42	37.8	9.17	0.67	0.19	2	0
43	49	6.46	0.52	0.15	2	0
44	49	11.5	0.51	0.14	2	0
45	53.8	10.7	0.56	0.16	1.12	0.33
46	51.4	14.9	0.6	0.17	2	0
47	36.9	8.44	0.82	0.23	0.17	0.48
48	36.1	12.8	1.3	0.38	2	0
49	40.4	8.16	0.62	0.18	2	0
50	44	13	0.53	0.15	2	0
51	45.4	16.5	0.59	0.17	1.56	0.51
52	48.3	9.65	0.61	0.17	0.83	0.65
53	40.4	12.2	0.65	0.19	2	0
54	41.2	9.05	1.3	0.37	0	0
55	40.2	8.07	0.46	0.13	2	0
56	41.6	7.54	0.64	0.18	2	0
57	40.4	8.28	0.6	0.17	2	0
58	56.1	9.99	0.56	0.16	1.52	0.51
59	39.1	7.51	0.53	0.15	1.16	0.37
60	32.8	9.18	0.62	0.13	2	0

APPENDIX II. MORPHOLOGICAL DATA (cont.)

Site	Scale Length (mm)		Scale Width (mm)		Scale Color Score	
	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.
1	1.89	0.21	2.84	0.247	2.4	0.5
2	2.81	0.231	2.03	0.296	2.48	0.51
3	3.05	0.263	2.01	0.273	2.92	0.277
4	2.36	0.352	1.7	0.179	1.64	0.638
5	2.81	0.33	1.87	0.268	2.28	0.542
6	2.77	0.288	2.07	0.256	2.64	0.49
7	2.13	0.132	1.77	0.121	1.	0
8	2.32	0.167	1.62	0.137	1.2	0.5
9	2.63	0.243	1.78	0.268	2.4	0.5
10	2.55	0.209	2.08	2.13	2.52	0.51
11	2.87	0.445	2.03	0.251	2.56	0.651
12	2.39	0.188	1.64	0.15	1.08	0.4
13	2.71	0.243	1.88	0.286	2.8	0.408
14	2.87	0.25	1.74	0.193	2.64	0.49
15	2.97	0.256	1.93	0.253	2.4	0.645
16	2.96	0.367	1.91	0.289	2.6	0.5
17	2.39	0.127	1.52	0.14	1.28	0.458
18	2.33	0.255	1.61	0.19	1.08	0.4
19	2.39	0.202	1.71	0.166	1.2	0.408
20	2.65	0.316	1.77	0.227	2.2	0.707
21	2.63	0.131	2.05	0.176	2.76	0.436
22	2.46	0.108	1.57	0.0984	1.12	0.332
23	2.3	0.139	1.6	0.144	1.24	0.436
24	2.49	0.0806	1.6	0.155	1.04	0.2
25	2.85	0.431	1.98	0.305	2.52	0.586
26	2.71	0.368	1.9	0.217	2.32	0.627
27	2.93	0.442	2.05	0.263	2.56	0.583
28	2.73	0.258	1.81	0.214	1.84	0.473
29	3.04	0.386	2.16	0.273	2.56	0.583
30	2.58	0.152	1.49	0.105	1.16	0.374
31	2.46	0.265	1.52	0.132	1.12	0.332
32	2.39	0.184	1.56	0.131	1	0
33	2.63	0.206	1.54	0.151	1.12	0.332
34	2.32	0.124	1.43	0.127	2.28	0.737
35	2.35	0.0975	1.49	0.147	2.64	0.49
36	2.79	0.178	2.14	0.278	2.64	0.49
37	2.37	0.243	1.69	0.19	1.56	0.768
38	2.86	0.0978	1.73	0.138	2.44	0.507
39	2.55	0.0707	1.46	0.101	1.24	0.436
40	2.31	0.152	1.39	0.103	1.32	0.476
41	2.92	0.202	2.25	0.16	2.56	0.507
42	2.88	0.191	2.26	0.229	2.64	0.49
43	2.22	0.205	1.41	0.117	2.52	0.51
44	2.67	0.298	1.65	0.296	2.56	0.507
45	2.34	0.126	1.91	0.251	2.96	0.2
46	2.28	0.216	1.69	0.174	2.48	0.51
47	2.71	0.173	2.16	0.171	2.56	0.507
48	2.47	0.162	1.38	0.0966	1.12	0.332
49	2.79	0.174	2.26	0.152	2.92	0.277
50	2.57	0.185	2.24	0.217	2.6	0.5
51	2.54	0.122	2.09	0.139	2.56	0.507
52	2.74	0.261	2.15	0.257	2.56	0.507
53	2.39	0.326	1.72	0.217	2.2	0.957
54	2.37	0.152	1.77	0.1	2.8	0.408
55	1.95	0.0944	1.53	0.0822	1	0
56	2.67	0.111	2.04	0.172	2.6	0.5
57	2.67	0.222	2.04	0.26	2.52	0.51
58	2.67	0.243	2.27	0.22	2.28	0.458
59	2.38	0.115	1.4	0.122	2.52	0.51
60	2.74	0.177	2.12	0.16	2.56	0.507

APPENDIX III. SCIENTIFIC NAMES OF BIRDS LISTED IN TABLES
VIII AND IX. THE SEQUENCE AND NOMENCLATURE
FOLLOW THE A.O.U. CHECKLIST (5th EDITION)
AS APPLIED BY GODFREY (1966).

Western grebe	*Aechmorphorus occidentalis* (Lawrence)
Pied-billed grebe	*Podilymbus podiceps* (Linnaeus)
American bittern	*Botaurus lentiginosus* (Rackett)
Mallard	*Anas platyrhynchos* Linnaeus
Gadwall	*Anas strepera* Linnaeus
Pintail	*Anas acuta* Linnaeus
Blue-winged teal	*Anas discors* Linnaeus
American widgeon	*Mareca americana* (Gmelin)
Shoveler	*Spatula clypeata* (Linnaeus)
Redhead	*Aythya americana* (Eyton)
Canvasback	*Aytha valisineria* (Wilson)
Lesser scaup	*Aytha affinis* (Eyton)
Ruddy duck	*Oxyura jamaicensis* (Gmelin)
Sora rail	*Porzana carolina* (Linnaeus)
American coot	*Fulica americana* Gmelin
Killdeer	*Charadrius vociferus* Linnaeus
Forster's tern	*Sterna forsteri* Nuttall
Black tern	*Chlidonias niger* (Linnaeus)
Long-billed marsh wren	*Telmatodytes palustris* (Wilson)
Short-billed marsh wren	*Cistothorus platensis* (Latham)
Yellow-headed blackbird	*Xanthocephalus xanthocephalus* (Bonaparte)
Red-winged blackbird	*Agelaius phoeniceus* (Linnaeus)

APPENDIX IV. CITATION OF HERBARIUM SPECIMENS EXAMINED.

A. Specimens of *S. acutus*

(University of Manitoba)7695, 7696, 7700, 7698, 11145, 7697,
7699, 7685, 7687, 7692, 7693, 7694, 7691, 7686, 7688, 7689, 7690,21626,
1114, 1148, 1149; (National Museum of Canada)261496, 254855, 28948,
28949, 29465, 29465, 29468, 29466, 29469, 29470, 29471, 29472, 29473,
29474, 29476, 29477, 29478, 29479, 29480, 29481, 28950, 124231, 28951,
28947, 29461, 29460, 29458, 29459,29457, 29456, 28945, 32598, 320710,
317152, 310146, 304791, 30047, 286658, 256016, 231242, 231244, 231243,
230474, 221248, 221245, 29455, 29456, 28943, 28942, 28941, 28940, 28939,
305832, 305831, 305829, 116570, 116571, 231245, 221244, 221246, 221247,
221243, 29453, 29454, 29452, 29649, 28935, 28936, 28938, 28937, 28934,
28933, 29643, 29451, 29448, 29450, 29446, 28930, 28931, 239920, 28932,
28929, 29444, 29445

B. Specimens of *S. validus*

(University of Manitoba)6566, 28141, 27881, 26549, 26506,
26039, 25350, 21713, 25138, 21714, 21715, 21709, 21708, 21707, 21706,
21710, 21711, 24239, 21639 1148, 1149, 21640, 21638; (National Museum
of Canada)297031,165418, 165419, 165420, 333703,165421, 214005, 165422,
254849,165423, 165424, 29697, 29698, 29695, 283010, 29694, 29693,
275246, 268026, 29696, 29686, 29687, 263885, 29691, 124224, 29690,
29688, 29689, 29685, 29684,310785, 29464, 29463, 29675, 196303, 225019,
29681, 29682, 29683, 29679, 29680, 29678, 281161, 309884, 309883,
203962, 203961, 29674, 29673, 29671, 29672, 209288, 209287, 155403,
155402, 113510, 113508, 113507, 113506, 113505, 113504, 201587,
201586, 113503, 113502, 206275, 216930, 124215, 29670, 29669, 29668,
203455, 29667, 254030, 231697, 231698, 231699, 116582, 116575, 116576,
116577, 116578, 116579, 116580, 116581, 116583, 325294, 325292,
318993, 317157, 316527, 304798, 300481, 300482, 286673, 286675, 259871,
242146, 227181, 228140, 228139, 225777, 325970, 196922, 124230, 29666,
29665, 29664, 29663, 29662, 29661, 29660, 29659, 29658, 29657, 29656,
29655, 29653, 323390, 323638, 321198, 321222, 321205, 318974, 302385,
302386, 277026, 29650, 29652, 213220, 221241, 264416, 29651, 152553,
29642, 240180, 29648, 29647, 29644, 29645, 29646, 211401, 29447, 29641