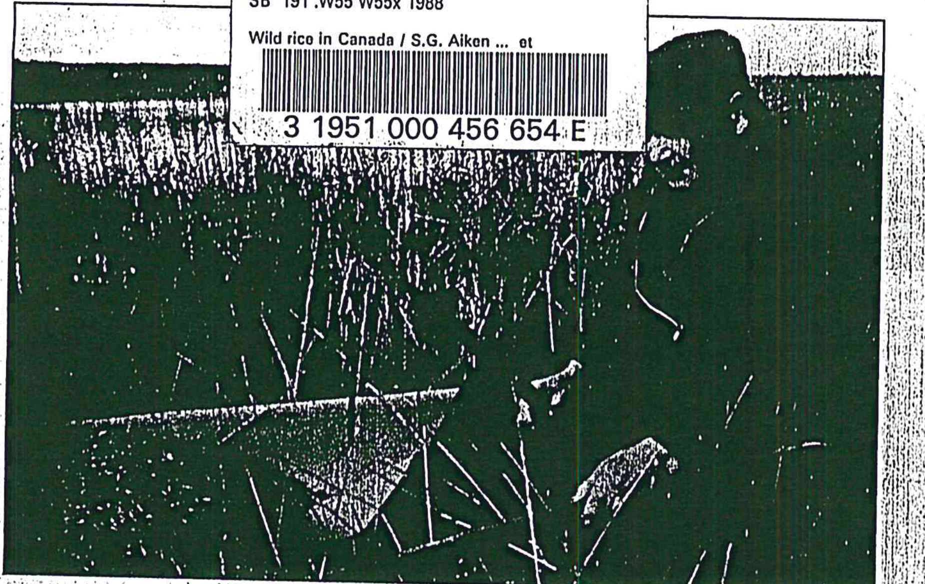

Traditional 2-stick method of harvesting rice.

Wild rice was first described by Gronovius of Holland, in 1743. A member of the grass family, wild rice has been a staple in the diet of North American Native peoples, particularly those of the Great Lakes Basin. Long prized by gourmets for its distinctive flavor and texture, varieties of wild rice are being grown commercially in increasing quantities.

Wild Rice in Canada is a reproduction of and expansion upon the earlier work by William G. Dore, lavishly illustrated with historic photos, botanical drawings, maps, and graphs, including four pages of color plates.

The text includes regional variations, range, habitat, paddy and natural growing and harvesting techniques, diseases, and pests.

A must for those interested in ecology, plant biology and genetics, aquaculture, and native studies.

William G. Dore is a distinguished authority on wild rice with over 25 years of expertise. **S.G. Aiken,** Botany Division, National Museum of Natural Science, Ottawa, Ont. K2P 6P4; **P.F. Lee,** Department of Biology, Lakehead University, Thunder Bay, Ont. P7B 5E1; **D. Punter** and **J.M. Stewart,** Department of Botany, University of Manitoba, Winnipeg, Man. R3T 2N2.

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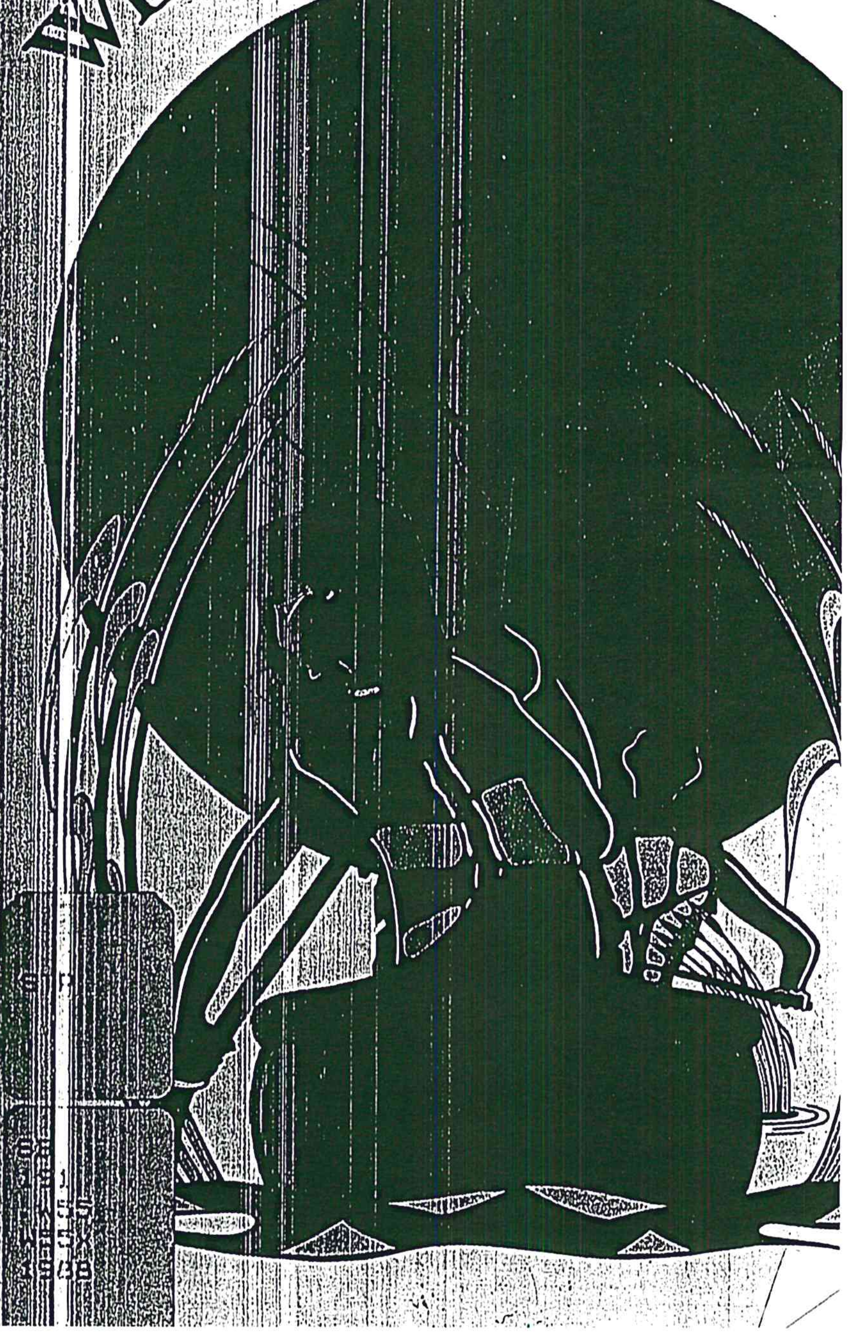

WILD RICE IN CANADA

S. G. Aiken

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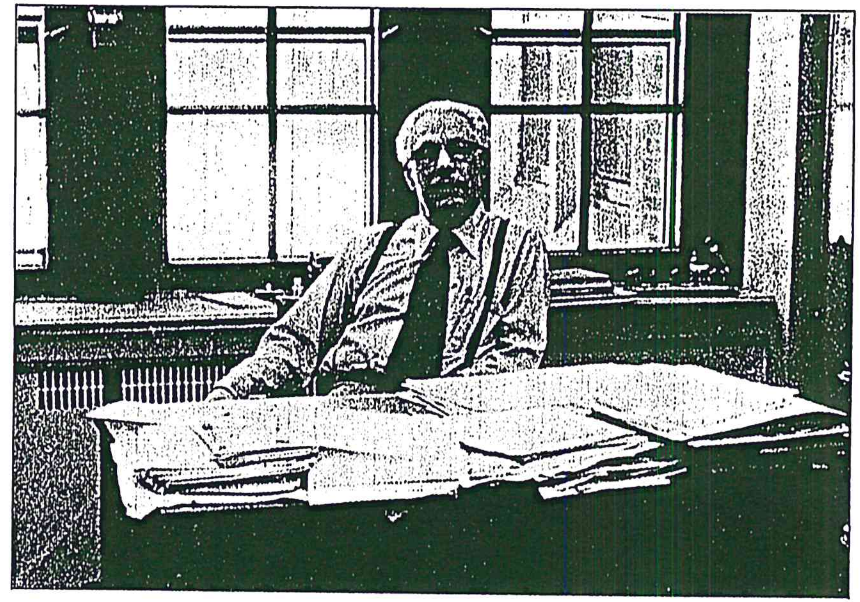
To William (Bill) G. Dore



It is with great pleasure that the authors, under the auspices of the Biosystematics Research Centre, Agriculture Canada, dedicate this publication to Dr. W. G. Dore, the Canadian authority on wild rice during the past 25 years. The original intent was to publish a second edition of Dore's publication on wild rice (Agric. Can. Publ. 1393) with minor alterations. Some portions of the original publication are unchanged, particularly much of the introduction, the description of the wild rice plant, and the section on early methods of harvesting and processing. Information in the taxonomic section has been reorganized, most of the observations having been made by Bill Dore. Since the issue of the first edition, however, much new information has become available. Advances have been made in our understanding of wild rice: environmental interactions; habitat requirements; competition; population dynamics; diseases; and the domestication and cultivation of this cereal as a crop. The present authors accept responsibility for the new sections.

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Introduction

Wild rice (*Zizania* L.) is an annual aquatic grass that grows in shallow lakes and rivers throughout eastern and north central North America. It is best known as a culinary delicacy and as an export product, in addition to being a visible component of Indian culture. Of the wild grasses in Canada, it is the only one that grows from seed each year and produces a grain of sufficient size to be used extensively as food by people. The other cereals, wheat, oats, barley, rye, and corn, are "tame" grasses in the sense that they are completely dependent on the farmer's care and attention for survival in Canada's climate. These crop plants had their origin in foreign lands, and for many centuries they have been so modified by selection and cultivation that they are now quite unlike their wild progenitors. In contrast, wild rice is essentially the same today as it was when the first explorers found certain Indian tribes of the interior of North America using it as a main food.

The natural "wild rice bowl" where the grain has been used for centuries as a food, extends over an area west of Lake Superior to southern Manitoba and into the adjacent states of Wisconsin and Minnesota (Jenks 1901). Several rivers and lakes in the north central states and in Canada have received their names from the presence of stands of wild rice. Rice Lake near Peterborough, Ont., is perhaps the largest and best known of these lakes in Canada. Another lake, at 50°31'N, 93°31'W, northeast of Kenora, is called Zizania Lake.

Wild rice is found mainly in shallow water along the shores of rivers and streams, where stands are dense and continuous. In lakes, where it is usually less abundant, stands are generally concentrated near the inlet and outlet, where the current is more or less constant. Its lighter green color usually distinguishes wild rice from bordering stands of cattails and other shallow-water plants. Natural wild rice stands are economically valuable and ecologically, as well as aesthetically, desirable.

Historically, wild rice was an important food item in the diet of Indians west of Lake Superior (Jenks 1901). The tribes of the Algonquin and Sioux linguistic groups were the traditional wild rice gatherers of the "wild rice bowl." On the basis of preserved wild rice grains found during archaeological excavation of burial mounds, Johnson (1969) believes that wild rice was an important Indian food for at least 1000 years. The dependence of the Indian culture on the wild rice crop was such that when it failed, famine resulted. Although the reasons for failures were many and varied in the historical records, high water levels drowning out the wild rice were invariably linked to poor yields.

The many names for wild rice reflect the influence of Indians, explorers, fur traders, and early settlers on the use of this food: Indian rice, Canadian rice, water oats, water rice, and *manomin* (Densmore 1974). The last one was derived from an Indian name. The early French explorers called the plant *folle avoine.* Today direct translations, for example, *riz sauvage* and *zizanie,* are used in writings in French. However, *folle avoine* is also the common name for wild oats *(Avena fatua),* and this dual use is confusing. Many producers of wild rice, as well as discerning naturalists and sportsmen who wish to be precise about the plant, use the name zizania. This is written without a capital letter and in ordinary print, but otherwise the word is identical with the Latin name of the genus to which our species of wild rice belong. Because such usage conforms with botanical principles of priority, zizania is clearly understood internationally.

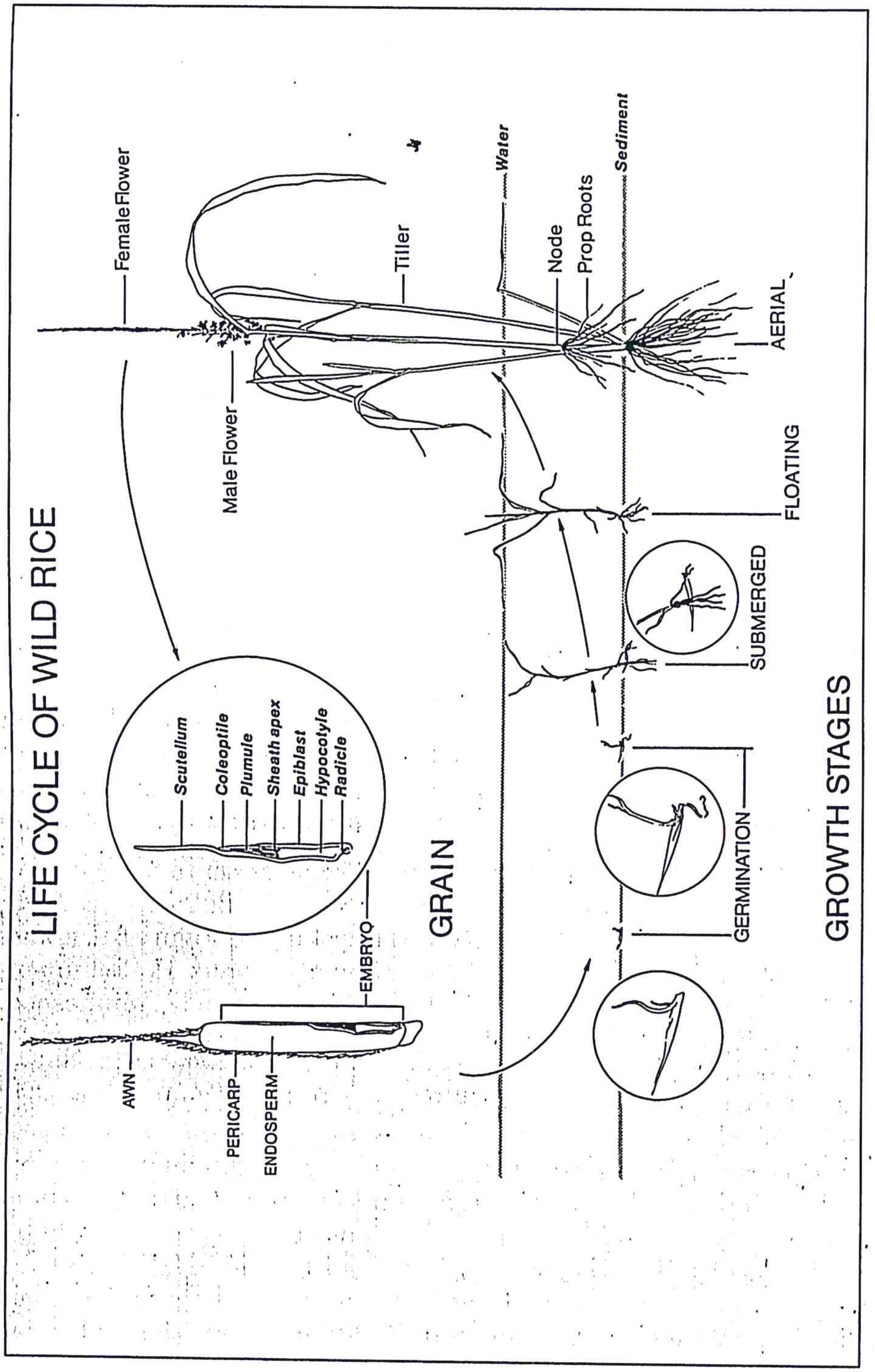
In Agric. Can. Publ. 1393, *Wild-rice,* Dore explained that the hyphen in the name was used to reduce confusion in parts of the world where rice *(Oryza sativa)* is the chief cereal crop. All the native species of *Oryza* L. in Asia, as well as weedy strains of *O. sativa* that infest the fields in southern United States, are appropriately called wild rice, that is, rice that grows wild. The single word, wildrice, has been used to distinguish North American *Zizania* from Asian *Oryza* wild rice. Although this is useful if the subtlety is understood, the single-word form has not been widely accepted. Many recent publications, especially those from Minnesota, have used the two-word form, unhyphenated. This is consistent with the guidelines suggested in *Hortus Third* and by Alex et al. (1980).

Research has been initiated in Northwestern Ontario, Saskatchewan, and Alberta to provide the necessary background information before large-scale "farming" (aquaculture) of selected wild rice lakes can occur (Lee 1984). Stands of wild rice tolerate wide ranges in environmental conditions, for example, water depths (0.05–2.50 m), sediments (clay to peat), and latitudes (30° to 56°N). Because wild rice grows in a changing physical, chemical, and biological environment, the production of biomass is rarely predictable; consequently, good or bad years of wild rice production are considered normal. A key to stabilizing production would be to control the environmental factors causing fluctuations. This is one of the strategies used in modern agriculture, but its use is predicated upon our scientific understanding of those environmental factors whose interactions determine the success or failure of the yearly wild rice crop.

In order to stabilize environmental variables and control growing conditions, wild rice has been grown in paddies, particularly in the United States (Brooks 1981). Wild rice grown in such fields now accounts for about 90% of all rice marketed, but paddy production is relatively expensive and is still at the experimental stage in Canada. Here, many lakes suitable for growing wild rice are still being discovered and developed. In the process, interest in and the production of lake-grown wild rice crops is expanding. It is hoped that this publication will further this interest.

Acknowledgments

The authors thank J. A. Percich for allowing them to use some of the colored photographs illustrating diseases of wild rice; C. E. Beddoe for taking Figures 2 and 6; S. J. Darbyshire for Figure 5 *d, e;* and M. Jomphe for detailed drawings. They also thank H. Schumer, North Central Experimental Station, Grand Rapids, Minnesota, and Dr. E. A. Oelke, M. McClellan, and the team at the University of Minnesota, St. Paul, for sharing enthusiastically information about work being done in Minnesota; and P. Sain, Manitoba Department of Natural Resources, Winnipeg, for information on wild rice in Ontario. They express their sincere thanks to many people involved in the production of this publication: M. A. Martin for typing the manuscript; B. M. Hilliker for extensive word processing help; P. M. Catling, S. J. Darbyshire, T. A. Steeves, and S. I. Warwick for reading the manuscript and suggesting improvements; and Sheilah Balchin, Dodie Archibald, and Sharon Rudnitski for their editorial assistance.



I

Wild Rice Plant

Figure 1 illustrates the life cycle of wild rice. Wild rice, like most other vascular plants, is composed of roots, stems, leaves, flowers, and fruits. To supplement the following description of these structures, morphological details are illustrated and described (Figs.1–6).

Roots

The primary root is the first root to emerge from a germinating seed (Aiken 1986) (Fig. 2). It pushes through the seed covering close to the point where the seed was attached to the parent plant and persists for about a month. Soon after the primary root appears, a permanent adventitious root system develops from the first stem node and later from higher nodes. These roots are similar to the prop roots of corn; they grow into the mud diagonally and anchor the plant firmly against the lift force of waves and currents. The adventitious roots are straight, spongy, and light-colored or often rust-tinged from iron deposited on their surface. They have short, horizontal rootlets and no true root hairs, which makes wild rice unusual among grasses. The root system of a mature plant is shallow (up to 35 cm deep) with a lateral spread approximating the circumference of the aerial leaf coverage.

Fig. 1 *(opposite)* Life cycle of wild rice illustrating a longitudinal section of a wild rice grain and the germination, submerged, floating, and aerial stages of growth relative to water levels.

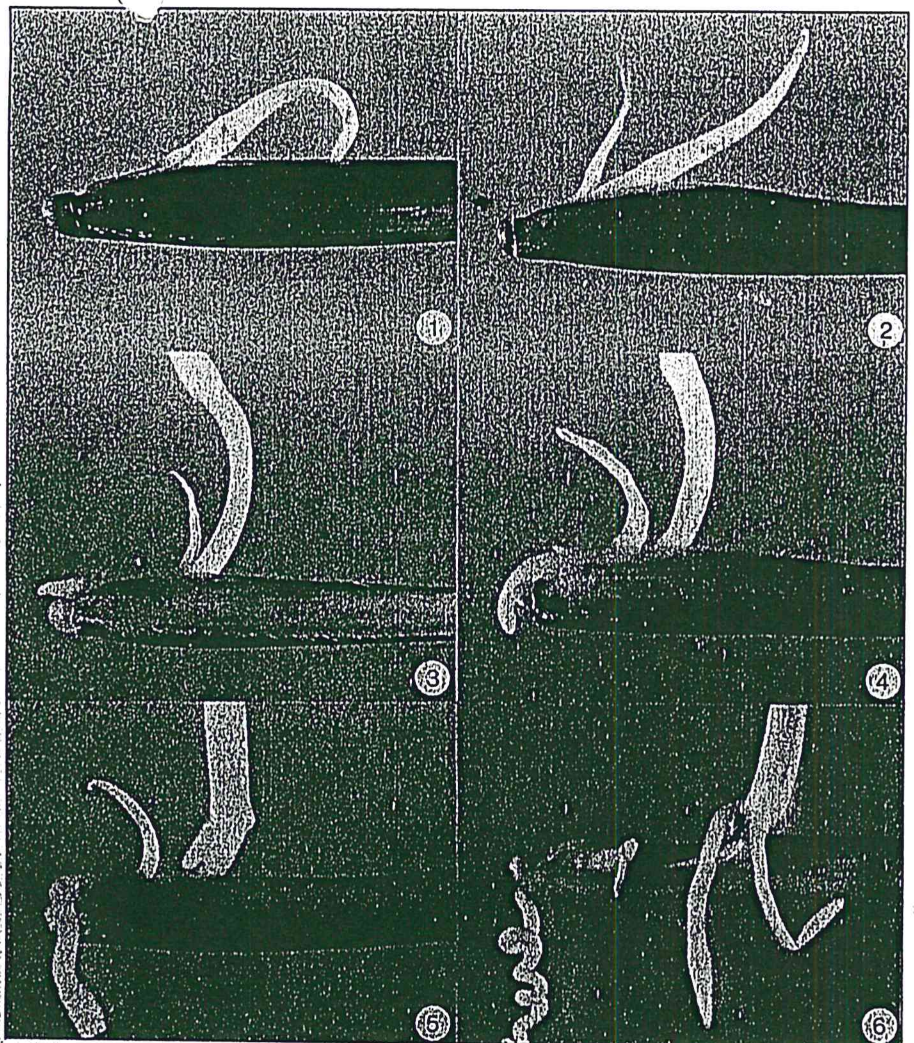


Fig. 2. Stages in the germination of a wild rice grain: *(1)* The epiblast has been pushed out through the lemma surrounding the grain by the seedling mesocotyl and coleoptile; the two structures are still closely associated. *(2)* The epiblast *(left)* has separated from the elongating mesocotyl *(center)*. *(3)* The root tip *(left)* is emerging through the seed covering close to where the seed was attached; the epiblast *(center)*; the elongated mesocotyl *(right)*, which in wild rice may be 1–6 cm long. The bulge toward the top of the photograph is the transition between the mesocotyl and the base of the coleoptile. *(4)* The elongating root *(left)* is curving toward the substrate. The intact lemma can be seen between the root and the epiblast. *(5)* A well-developed primary root *(left)*; secondary roots *(center)* beginning to develop from the base of the stem. *(6)* A curled primary root *(left)* showing curling that appeared to result from growing the seedling in a glass container of water (not known to occur in a mud substrate); the two secondary roots are developing rapidly to become the permanent rooting system *(center)*. Photographs

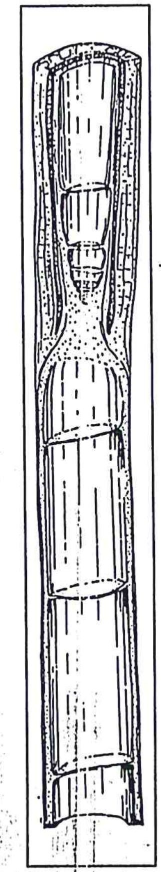


Fig. 3. Lengthwise section of stem through one node, showing parchment-like cross-partitions. Approximately 4.2×.

Stems

The first shoot structure to appear is a sheath (coleoptile), that covers the first leaf (Fig. 2). The structure most commonly referred to as a stem, or culm, develops from near the base of the first leaf and elongates to become the supporting axis that bears the leaves and flowers. In wild rice, the embryo stem (mesocotyl) may elongate up to 6 cm to allow the seedling to emerge through overlying sediments; however if the seeds germinate on the sediment surface, very little basal elongation occurs.

The stems of grasses are surrounded by closely enveloping sheaths. Ordinarily the stems of wild rice are visible in the emergent stage and vary in height from 0.6 to 3.0 m (rarely 5.0 m) depending on the variety, plant density, competition, nutrient status, water depth, and other associated environmental factors. Stems in the middle of a wild rice stand are usually uniform in height, whereas the height of those near the margins of the stands is influenced by the depth of water. Branch stems (tillers) arise from the basal nodes and are usually shorter than the main stem. A typical wild rice stand in water 1 m deep with four plants per 900 cm^2 would have from three to five tillers per plant, but as many as 50 tillers per plant have been reported from stands in shallow water.

At the emergent stage, the culm is cylindrical with band-like joints and fine, felt-like hairs at the nodes. In cross section these nodes are a mass of continuous tissue. The stem section between the nodes is called the internode, and there are from three to five internodes in mature plants. The lower internodes are about 30 cm long and the upper ones can be as long as 90 cm. The internodes are smooth and are usually constant in number for each ecotype. Internally, the internodes are hollow, air-filled cavities that act as air locks and assist the buoyancy of the whole plant; hence, plants that are uprooted float to the surface and never regain a roothold. Within the cavities are thin, delicate, cross-partitions of remnant pith tissue that is porous and allows the diffusion of gases up and down the stem (Fig. 3). In aquatic plants, good aeration must extend to the roots, which grow in sediments that may be anaerobic (Sculthorpe 1967).

Leaves

Following the emergence of the coleoptile, the next two or three leaves to appear are thin, pale green, and ribbon-like. They grow rapidly and are characterized by the absence of epicuticular wax.

Each succeeding leaf is larger than the preceding one. When later leaves reach the water's surface, the submerged leaves senesce and slough off, leaving the lower culms smooth.

As the leaves reach the water's surface, wax forms on the upper epidermis (Hawthorn and Stewart 1970). At this stage, internal tis-

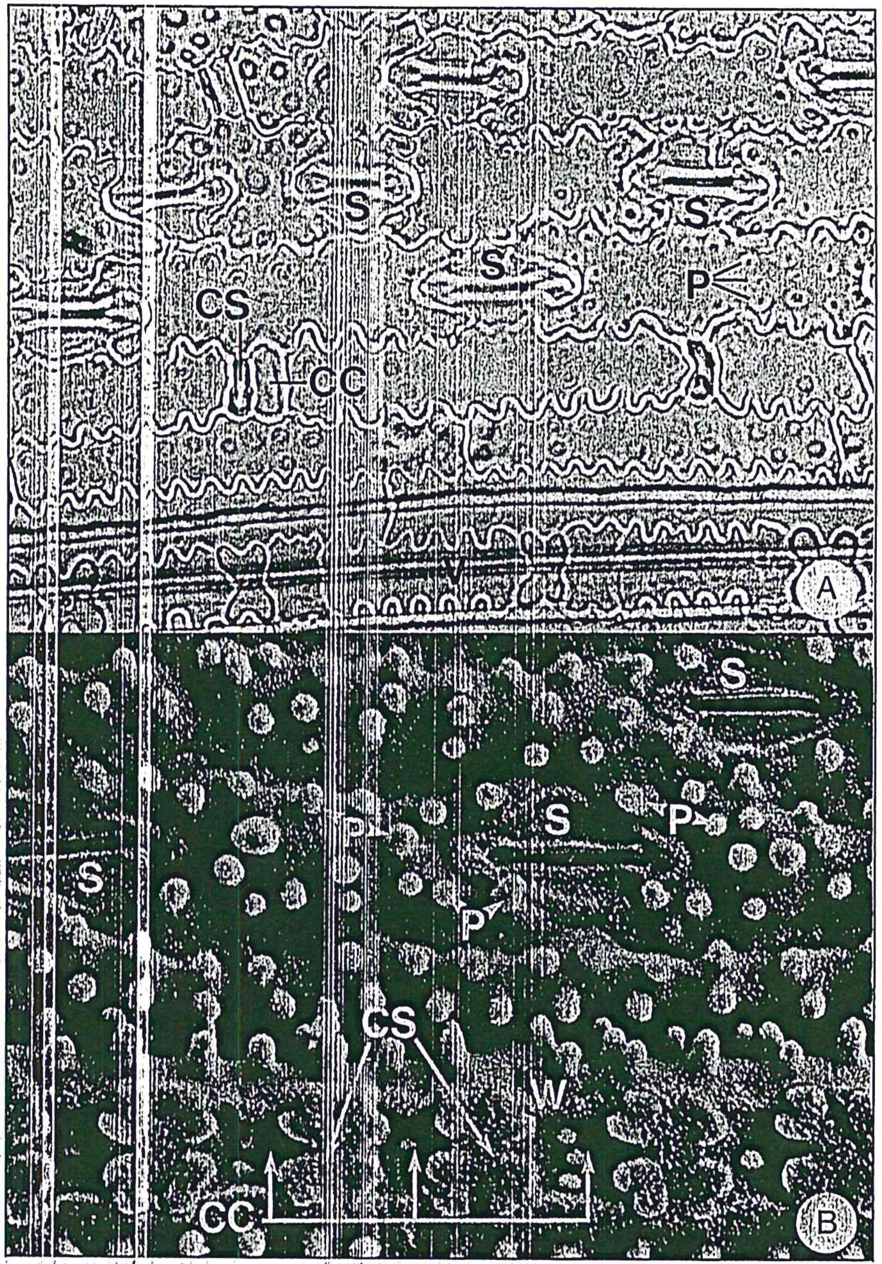


Fig. 4. *(right top)* Microscopic view of a leaf of *Z. aquatica* var. *brevis* from which the lower (abaxial) epidermis has been removed and specially treated to show the diagnostic dumbbell-shaped costal silica bodies *(CS)* over a vein *(V)*. Long cells with wavy cell outlines alternate with papillae *(P)*, stomata *(S)*, and cork cells *(CC)*. Approximately 150×.
(Right bottom) A scanning electron microscope photograph of the abaxial surface of *Z. palustris* with stomata *(S)*, overarching papillae *(P)*, and extruded (W). Exposed costal silica bodies *(CS)* are paired with cork cells *(CC)*. Approximately 400×.

sue differentiation allows air to reach all parts of the plant. The long and ribbon-like floating leaves lie on the water's surface and are moved about by the waves and prevailing wind. There are usually two or three floating leaves per plant and they persist until the aerial leaves are well established.

When the aerial leaves emerge above the water's surface, their sheaths surround the culm. The blades are larger and more robust than those of the submerged or floating leaves. The upper and lower leaf blade surfaces are covered with epicuticular wax (Fig. 4). The leaf blades are commonly 30–70 cm long and 1–4 cm wide, depending on variety. The midrib is off center in the blade and more prominent on the lower surface. At the junction between the sheath and the blade is a scale-like appendage, or ligule, a membrane 3–11 mm long that is firm at the base but thinner and often frayed at the tip. The uppermost leaf on the stem is called the flag. It is shorter than the other aerial leaves and during its unfolding surrounds the developing inflorescence.

Flowers

Separate male and female spikelets are borne on a terminal flowering panicle that is 40–55 cm long. Male spikelets (containing male flowers) are borne on lower flexible branches (Fig. 5). Above the male spikelets are stiff branches that bear the female spikelets (containing female flowers). This arrangement is the opposite positioning of the spikelets on corn where the terminal tassels are composed of many male spikelets. The segregation of the sexes promotes cross-fertilization because in the same panicle the female spikelets emerge and are mature 3 or 4 days before the male spikelets shed pollen. However, sometimes transition spikelets between the male and female ones have both stigmas and anthers and these could self-pollinate. Wind-pollination starts in late July and continues until the last of the tillers have flowered. Pollen viability is very sensitive to weather conditions. Recently, Terrell and Batra (1984) reported that bumble bees collect pollen from male spikelets but observed no visits by pollen-laden bees to female spikelets, and they concluded that these bees are not pollinators of wild rice.

The male spikelets vary in color from yellow to greenish pink or dark red. They hang down on thread-like stalks from the spreading panicle branches. The two outer scales (glumes) found in other grasses [illegible] reduced to a rudimentary ring of tissue in *Zizania*. [illegible] round the six stamens and separate widely to expose the anthers. The stamens consist of long filaments that allow the anthers (pollen-bearing sacs) at the ends to hang outside the spikelets. Pollen is released about 2 hours after sunrise and by evening many male spikelets with empty anthers are shed. In the cultivated varieties the male spikelets remain on the plant, indicative of the non-shattering grain characteristic.

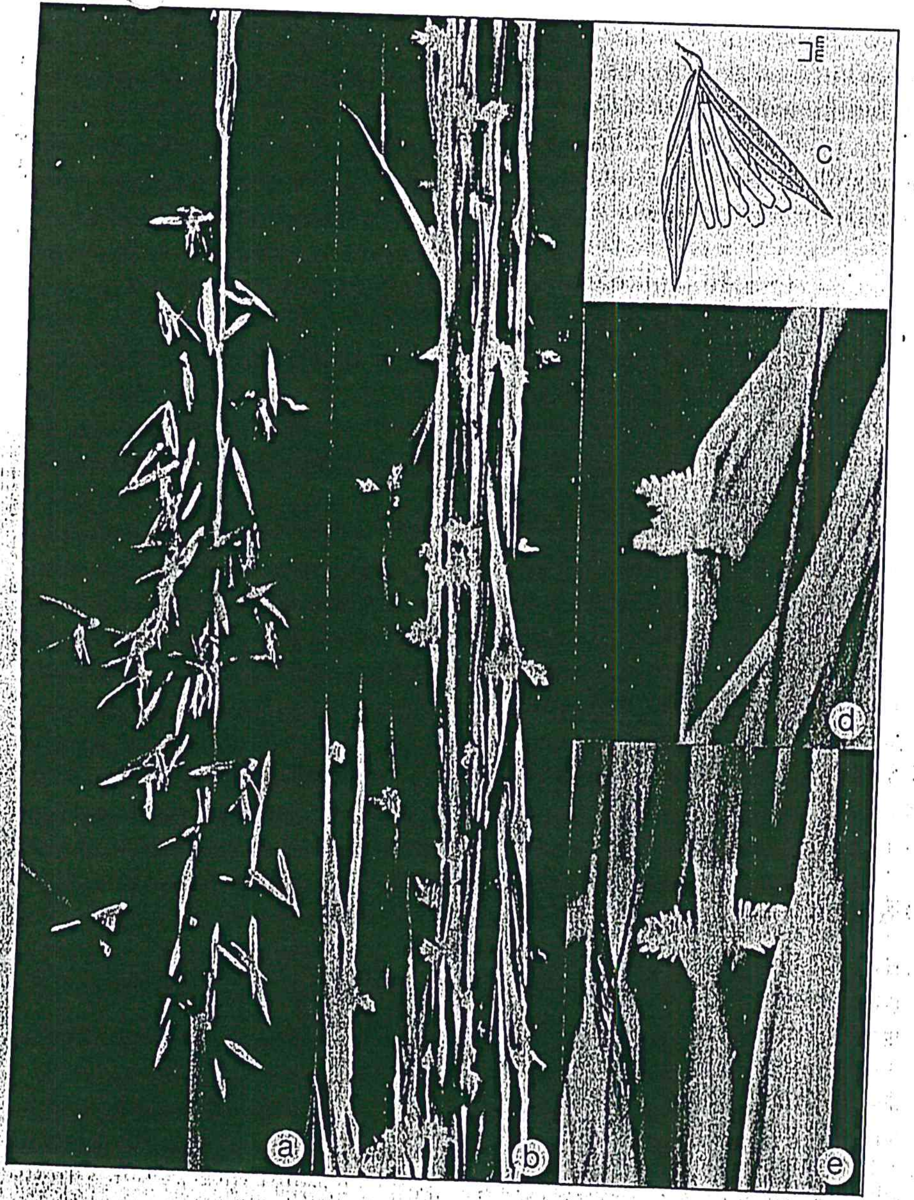
The female spikelets are borne erect from the panicle branches on short, firm stalks (Fig. 5). Each female spikelet has two conspicuous, interlocking scales, a lemma with a long, rough bristle (awn) at the tip and an unawned palea. As the spikelets push up above the leaf sheath, the palea kinks near the base of the spikelet, allowing the two white feathery stigmas to be exposed, one on either side. The number of female spikelets is variable depending on the variety and on environmental stresses to which the plant is exposed. In cultivated wild rice the female inflorescence produces up to 400 grains per panicle.

Wild rice harvesters report that not all female spikelets in a panicle produce mature grains. The amount of sterility varies and may be as high as 80% in southern wild rice. The causes of such sterility have not been studied, but they may be associated with both pollination and fertilization. Factors in the environment, such as wet, cold, or calm weather conditions, may interfere with the shedding of pollen or its transference to the stigmas.

Grains

About 24 hours after the stigmas are pollinated, they wither and the ovary begins to enlarge with subsequent grain development. The grains, often called seeds, of wild rice are composed of an inner cary-

Fig. 5. (*next page*) Like corn, but unlike most other grasses, wild rice has separate male and female spikelets. (*a*) The male spikelets at the lower part of the panicle are just emerging from the leaf sheath and are not yet open, whereas those in the middle are in bloom and shedding their pollen. Toward the top, the withered spikelets have fallen off. Approximately 0.6×. (*b*) Female flowers at the top of the panicle in full bloom. Approximately 0.6×. (*c*) A male spikelet in full bloom, with six anthers exposed. Scale bar = 1 mm. (*d* and *e*) Two views of female spikelets in full bloom, with feathery stigmas exposed toward the base of the spikelet, through a gap where the palea has kinked outward. The stigmas shrivel soon after the pollen tubes penetrate them and fertilize the ovary, but they remain receptive for [illegible]ral days if



opsis that contains the embryo plant and food reserves, tightly surrounded by the lemma and the palea. The grains are shed about 4 weeks after fertilization (Elliott 1980). The grains change from light green with a firm-dough texture to olive brown and finally to dark brown/black with a hard kernel. Grain shedding occurs from 7 to 12 days after the firm-dough stage. Although many grains mature and shatter from the top of the panicle downward, there are plants in which maturation apparently takes place randomly throughout the panicle.

After leaving the parent plant, the grain falls through the water and plummets into the sediment, directed on its course by its rudder-like awn and the greater weight at the opposite end. Consequently it lodges close to the parent plant even in fast-flowing water.

A grain consists of an embryonic plant, or germ, that extends the whole length of the grain along the grooved side, and a reservoir of starchy endosperm. These structures are surrounded by a thin but tough and impermeable pericarp that contributes to seed dormancy. The grains of wild rice are longer than those of any other native grass and longer than most cereals in Canada. Each grain is tightly enclosed by the hull, which is made of the interlocking lemma and palea. The hull is not attached to the grain; hence the grain can be threshed clean following parching. However, it is difficult to remove the hull until it has been heated. The narrowness and relative brittleness of the dry grain make it susceptible to breakage when it is mechanically processed.

Grain germination and viability

The percentage of wild rice germination can be high when grains are allowed to lie in their natural position at the bottom of a river over winter, or when stored in water at low temperatures. Grains incompletely matured on the stalk do not possess the same degree of germination. Grains fully ripened on the stalk have a definite dormancy and will not germinate for at least 3 months after ripening (Simpson 1966), even if temperature, moisture, and substrate are satisfactory for growth. They must pass through an afterripening period under freezing or near-freezing temperatures before the embryo breaks dormancy and develops into a new seedling plant.

There are conflicting opinions about the number of years wild rice grains remain dormant in the bottom of a body of water. Some observers maintain that plants can suddenly reappear in a pond after two, three, or several years of absence. Oelke et al. (1982) have recovered viable seeds from continuously flooded and summer-flooded soils 6 years after burial. Breeders have routinely fumigated their wild rice nurseries with methyl bromide as a means of eliminating this source of contamination (Elliott 1980).

When grain is stored dry, it rapidly loses its ability to germinate. In one of the earliest reported tests, Fyles (1920) observed that the rate of germination declined by 45% after 4 weeks and by a further 14% after 6 weeks. These observations, supported by the subsequent experiences of wild rice harvesters and farmers, indicate that wild rice grains intended for planting should not be allowed to dry out.

The development of wild rice cultivars for paddy fields in the United States and in Canada has required more than one generation of wild rice per year. A procedure to force germination was used by Elliott (1974). It involves removing the lemma and palea from dormant grains by forceps and breaking the impermeability of the pericarp by scraping. Germination proceeds when the scraped grains are submerged in water (Cardwell et al. 1978, Woods and Gutek 1974). Elliott (1974) reports that in a test of 43 lines using this scraping procedure, the success in plant establishment differed among the genetic lines. An average success rate of 30% suggested that factors other than pericarp presence are involved.

II

A Taxonomic Review of the Genus, Species, and Varieties

Genus *Zizania*

The genus *Zizania* was named from a plant collected in Virginia by John Clayton in 1739. This specimen (Clayton No. 574) was sent to J. F. Gronovius in Leyden, Holland, for him to describe, which he did in 1743. The name chosen was from the Greek word *zizanion,* a weed of Mediterranean grain fields, thought to be the tares of the Scripture parable. In 1753, Linnaeus, the father of modern botanical and zoological nomenclature, provided the binomial *Zizania aquatica* for the Clayton specimen. Thus, it became the nomenclatural type for the genus. It is preserved in the Gronovian Herbarium at the British Museum of Natural History in London, England. The following are the main characters of this genus.

Plants annual, Asian *Z. latifolia* and North American *Z. texana* perennial, usually 0.25–3.5 m high but sometimes 4–5.5 m high; with a single stem (culm) or with tillers at the base, or rhizomes *(Z. latifolia),* the lower part of the culm sometimes decumbent and lying along the mud. Culm nodes are usually hairy, the internodes hollow and with stellate pith diaphragms present in the cavities (Fig. 3). The presence of these diaphragms allows rice straw to be distinguished from straw of other grasses or cattails. Aerial leaves 0.5–7.5 cm wide, with a ligule 3–25 mm long at base of blade and an open sheath surrounding the culm; aerial leaves have epidermal cells studded with low papillae and a thin, waxy cuticle. Silica deposits (Fig. 4), dumbbell-shaped in rows within epidermal cells, over vascular tissue, and scattered elsewhere in abaxial epidermis (Terrell and Wergin 1979, 1981).

The flowering stalk (inflorescence) is a terminal panicle 5–35 cm long, the lower branches are spreading with male spikelets that hang down, whereas the upper branches are usually upright with female spikelets stiffly erect. Widely spreading female branches, a condition known as "crowsfoot" inflorescence by plant breeders, are sometimes observed. Both male and female spikelets are borne on short, persistent stalks (pedicels). Shattering, or breaking, of these pedicels occurs just below a collar-like ridge of tissue that is thought to represent remnants of the vestigial glumes. Male spikelets usually drop as soon as pollen is shed; however, in cultivated varieties, and rarely, in native populations, male spikelets remain attached and are still conspicuous when the grain is ripe. They are (0.3–) 0.7–1.5 mm, have an outer, membranous bract (lemma) that is folded, with five veins, two of them at the margin, and a pointed tip or a short, straight awn. Inside the lemma are six anthers and a long bract (palea) that has three veins. Female spikelets are 2–20 mm long (without the awn). The lemmas have a straight awn usually about as long as the body of the lemma but often much longer, and 3–5 veins. Their margins curl inward, interlocking around the curled margins of the underlying palea and forming a zip-lock-like closure. At fertilization the palea is held at the apex by the enclosing margins of the lemma and kinks outwards opposite the top of the ovary, allowing the two fluffy white stigmas to be exposed (Fig. 4). After fertilization, the palea returns to its original position and remains tightly closed around the developing grain but is not attached to it. This interlocking lemma and palea structure is unusual in grasses and makes dehulling (removing the lemma and palea) more difficult in wild rice than in other cereal grasses. The parching process that dries and presumably shrinks the hulls releases the tight grip of the zip-lock.

The ovary, which is smooth and has two styles that are free to their bases, matures to form a cylindrical caryopsis 1–2 cm long. Inside, an embryo extends the full length of the grain. The base chromosome number for the genus is $x = 15$. All the North American taxa have the same chromosome number $2n = 30$ (Brown 1950, Dore 1969). The chromosome number of the Asiatic *Z. latifolia* is $2n = 34$ and this species produces sterile hybrids when crossed with *Z. palustris,* one of the annual North American species (Bondar 1958).

Taxonomic categories within the genus *Zizania*

Two species of wild rice are perennial. One is native to Asia, occurring from Manchuria to northeastern India; the other is native and very localized along the San Marcos river in Texas. The annual varieties of wild rice, which are native to North America, can conveniently be divided into four categories, but there have been differences of opinion as to whether these categories should be treated as one or two species. The categories recognized by Dore (1969) and used here, as well as the names suggested for them by other workers, are summarized in Table 1.

Table 1. Categories within the genus *Zizania*

Categories used by Dore (1969)	Categories used by Fassett (1924), Fernald (1950), and Gleason and Cronquist (1963)
Annuals Found in Canada	
1*a*. *Z. aquatica* var. *aquatica* L. **southern wild rice**	*Z. aquatica* L. *Z. palustris* L.
1*b*. *Z. aquatica* var. *brevis* Fassett **estuarine wild rice**	*Z. aquatica* var. *brevis* Fassett
2*a*. *Z. palustris* var. *palustris* L. **northern wild rice**	*Z. aquatica* var. *angustifolia* A. S. Hitchc.
2*b*. *Z. palustris* var. *interior* (Fassett) Dore **interior wild rice**	*Z. aquatica* var. *interior* Fassett
Perennials Found Elsewhere	
3. *Z. texana* A. S. Hitchc. **Texas wild rice**	
4. *Z. latifolia* Turcz. **Manchurian water-rice**	

Dore (1969) based his recognition of two species of annual wild rice (*Z. aquatica* and *Z. palustris*) on his experience and his interpretation of the original concepts of Linnaeus who proposed the two species names at different times but without cross reference. Unfortunately some later European and American authorities have not agreed on the application of these names or even on their separate validity. In North America, when A. S. Hitchcock reviewed the genus in the seventh edition of *Gray's Manual of Botany* (1908), he accepted Linnaeus's names as representing two distinct species but deliberately applied the names in reverse order, recognizing *Z. palustris* L. (= *Z. aquatica* of auth., not L.). This mistake, appearing in such an important manual, accounts for the confusion that continues to arise whenever reference is made to records or specimens accumulated between 1908 and 1924. Chambliss's work, published by the U.S. Department of Agriculture in 1922, followed Hitchcock's treatment, but the eighth edition of *Gray's Manual of Botany* (Fernald 1950) reversed the use of the names, recognizing *Z. aquatica* (Typical) (= *Z. palustris* of 7th ed., not L.).

Wiegand and Eames (1925) used the two names correctly, but their treatment was eclipsed by the critical monograph of Fassett (1924) in which he recognized one species, *Z. aquatica,* and four varieties. Fassett (1927) considered it necessary to reiterate his concept and to explain that, in his opinion, the variety *interior* in its morphology completely bridged the gap between the two proposed species. Fassett's treatment was followed by the major works of Fernald (1950) and Gleason and Cronquist (1963).

The question of the taxonomic level appropriate for the categories of annual wild rice has persisted. Initial results from isoenzyme studies among the taxa found in Canada strongly favor the recognition of two species (Warwick and Aiken 1986). Dore (1969) suggested that distinct species status may be appropriate for the variety *brevis,* because its short awn, small grain, and short height are characteristic and perpetuated under cultivation. The unique tidal habitat of var. *brevis* imposes distinct and intense selection pressures not affecting other varieties. However, a scanning electron microscope study of epidermal features of this taxon showed only minor ways in which it differs from *Z. aquatica* (Darbyshire and Aiken 1986) and no isoenzyme distinctions were found (Warwick and Aiken 1986).

Geographic separation is the chief factor that keeps varieties within the two species distinct. When they occur at the same place, intermediate individuals are usually found. Plants that look intermediate between varieties *palustris* and *interior* occur often, but at least some of these result because northern wild rice grown in nutrient-rich conditions produces large plants that look like interior wild rice plants grown in nutrient-poor conditions. Isoenzyme distinctions were found between varieties *interior* and *palustris* (Warwick and Aiken 1986).

There are some unusual plants localized in Bear Brook, near Ottawa, with many of the general features of the southern variety but with short awns. They were first pointed out by Fassett (1924) and named variety *subbrevis* by Boivin (1967). However, *Zizania aquatica* in the southern United States has spikelets with very variable awn lengths, not uncommonly only 0.2–0.6 cm long (E. E. Terrell, pers. commun., 1984). Dore and McNeill (1980) speculated that Bear Brook on the South Nation drainage system was influenced by estuarine waters of the retreating Champlain Sea; the variety *subbrevis* may represent the descendants of plants adapted to tidal conditions. They also observed that the type specimen of var. *subbrevis* happens to be considerably dwarfed in stature because it represents a plant browsed on during its early growth, and they refer to several other collections from the South Nation drainage system that reveal an almost complete gradation from varieties *aquatica* through *subbrevis* to *brevis*. Isoenzyme tests on collections from Bear Brook gave results identical with those obtained for *Z. aquatica* from other sites (Warwick and Aiken 1986). Thus, var. *subbrevis* appears to represent a portion of an ecocline within *Z. aquatica,* another portion of which was recorded for a population of particularly large plants from the Wading River, New Jersey (Ferren and Good 1977).

Within varieties, individual plants have inherent morphological variations of a minor nature. Their variations include differences in color of the plant, height and number of culms, length of the spikelet awns, size and shape of the grain, number of grains to a branch, time of ripening, and how readily mature panicles shatter. Selection by man for agronomically desirable qualities in wild rice has resulted in cultivars that are sometimes called varieties commercially but should not be confused with taxonomic varieties.

Key to the annual varieties of wild rice

1. Female inflorescence branches usually spreading at maturity; lemmas of female spikelets delicate, thin, papery, dull-opaque, scabrous over the whole surface and slender vein ribs; paleas scabrous; aborted spikelets[1] appearing thread-like (Fig. 6), less than 1 mm thick. Male spikelets usually less than 1.5 mm wide before anthesis.
   2. Plants usually (0.8–)1–3(–5.0) m high; leaves 10–80 mm wide; ligules (6–)10–20(–25) mm long; body of mature female lemma 10–20 mm long, usually minutely roughened; awn usually 10–75 mm long (Fig. 7).
   ...... 1*a*. *Z. aquatica* var. *aquatica*
   2. Plants usually 0.25–1 m high; leaves 3–12 mm wide; ligules about 3 mm long; body of mature female lemma 5–10 mm long, smooth or roughened; awn 1–8 mm long; freshwater tidal flats of the lower St. Lawrence River.
   .... 1*b*. *Z. aquatica* var. *brevis*.

1. Female inflorescence branches usually remaining erect and adpressed at maturity; lemmas of female spikelets firm, tough, straw-like, lustrous, scabrous on the margins at the apex, along the awn, and sometimes along the prominent corrugated vein ribs, elsewhere glabrous; paleas glabrous; aborted spikelets[1] not thread-like (Fig. 6), 1.5–2 mm thick. Male spikelets usually 1.5–2 mm wide before anthesis.
   3. Plants 0.7–1.5 m high; leaves 4–12(–15) mm wide; ligules 3–5(–10) mm long; lower female branches with 2–6 spikelets; lower or middle male branches with 1–15 spikelets (Fig. 8).
   ...... 2*a*. *Z. palustris* var. *palustris*
   3. Plants 0.9–3 m high; leaves 10–30(–40) mm wide; ligules 10–15 mm long; lower female branches with 10–30 spikelets; lower or middle male branches with (20–)30–60 spikelets.
   .... 2*b*. *Z. palustris* var. *interior*

[1] There is an unfortunate mistake in the keys presented in Dore and McNeill (1980) with the word "male" appearing where the word "sterile" was intended (W. G. Dore, pers. commun. 1985).

Fig. 6. A comparison of sterile and fertile spikelets of *Z. aquatica* (*a, b, e, f*) and *Z. palustris* (*c, d, g, h*). (*a* and *c*) Fertile spikelets. Approximately 3.5×. (*b*) The sterile spikelet of *Z. aquatica* is rounded and thread-like. (*d*) The sterile spikelet of *Z. palustris* is flattened and 1–2 mm wide. (*e*) Dorsal view of *Z. aquatica* spikelet showing scabrous prickles along the veins from the apex to the base and scattered prickles on the lemma surface. Approximately 8×. (*f*) Ventral view of spikelet of *Z. aquatica* showing scabrous prickles on the margins of the lemma and on the palea surface. Approximately 3.5×. (*g*) Dorsal view of a spikelet of *Z. palustris* showing scabrous prickles extending along the veins near the lemma apex, but elsewhere the lemma is glabrous. Approximately 3.5×. (*h*) Ventral view of spikelet of *Z. palustris* showing scabrous prickles along the veins at the margins of the lemma and a glabrous palea surface.

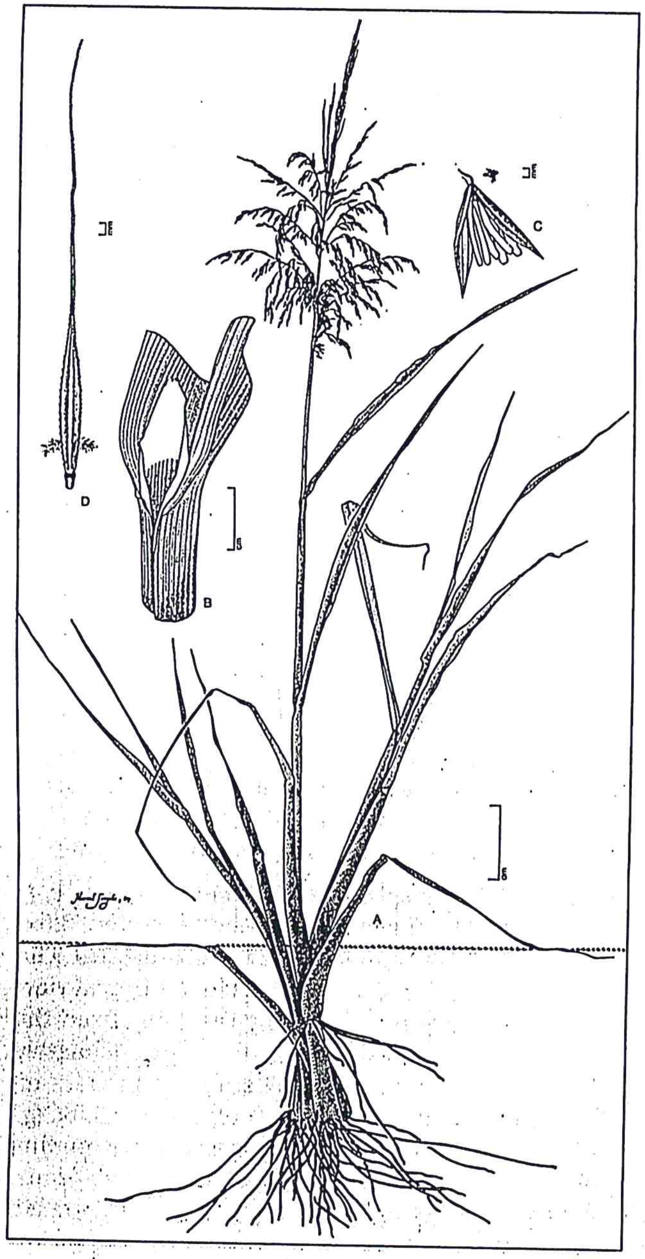


Fig. 7. *Zizania aquatica*. *(A)* Flowering plant, approximately 2 m high. *(B)* Junction between leaf sheath and blade showing ligule. Scale bar = 1 cm. *(C)* Pendulous male spikelet at anthesis showing six anthers. *(D)* Erect female spikelet with long awn. Scale bar = 1mm.

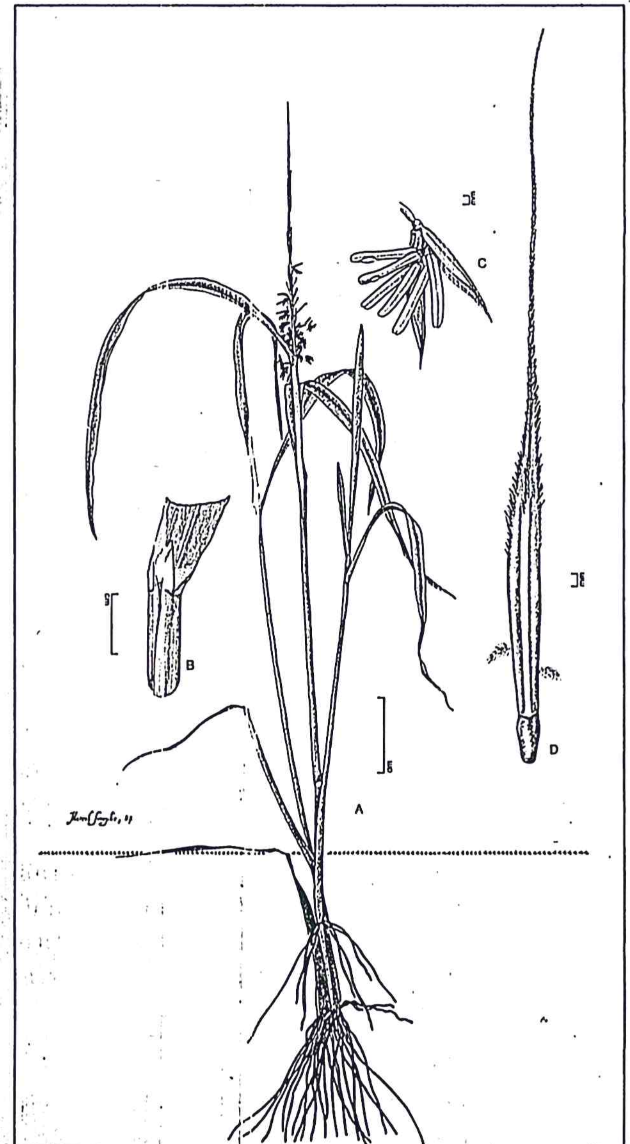


Fig. 8. *Zizania palustris*. *(A)* A flowering plant approximately 1.5 m high. *(B)* The junction between leaf sheath and blade showing ligule. Scale bar = 1 cm. *(C)* Pendulous male spikelet at anthesis, showing six anthers. Scale bar = 1 mm. *(D)* Erect female spikelet with long awn. Scale bar = 1 mm.

Zizania aquatica

1. *Zizania aquatica* L. Sp. Pl. ii. 991. 1753.

Type: United States, Virginia. J. Clayton 574 before 1739. (Gronovian Herbarium, at British Museum.)

Annual, 0.25–3.0 (rarely to 5.5) m high; hull of grain thin, papery, dull, and minutely roughened on the surface; aborted spikelets shrinking and becoming thread-like, less than 1 mm thick. Two varieties are recognized.

1*a*. *Zizania aquatica* var. *aquatica* L. SOUTHERN WILD RICE, SOUTHERN ZIZANIA. This is the typical variety of the species (Fig. 7).

Plants usually (0.8–)1–3(–5.0) m high; culms often 2–3 cm thick at base; leaf blades 1–8 cm wide, pale green, usually drooping outward at the top; panicles large, usually 25–80 cm long, many-branched, with numerous spikelets; female spikelets often sterile; awn usually 1–7.5 cm long.

Southern wild rice is present in Canada along the shores of the Great Lakes and along muddy shores of streams and ditches in southern Ontario and Quebec. It occurs throughout Florida, Louisiana, and the eastern seaboard states. Because the grain is short and thin there is little commercial interest in it, and the places where it is now found in Canada are mostly sites of natural distribution.

Dore (1969) documented the limited and disjunct distribution of this southern variety in Canada and concluded that because of its lack of aggressiveness, it is unlikely to extend northward under present climatic conditions. The map (Fig. 9) is essentially the same as that published by Dore.

1*b*. *Zizania aquatica* var. *brevis* Fassett. Rhodora 26:157. 1924.

Type: Canada, Quebec, St. Lawrence River, rocky tidal flats, Levis. 9 Aug. 1923, H. K. Svenson and N. C. Fassett, no. 853 (Gray Herbarium). ESTUARINE WILD RICE, ESTUARINE ZIZANIA.

Plants 0.25–1 m high; culms slender, flexible; leaf blades 3–8 (–12) mm wide, dull green; panicles 10–25 cm long, sparsely branched, few spikelets; female spikelets with an awn usually less than 1 cm long.

Estuarine wild rice grows in the extensive tidal flats of the St. Lawrence River estuary where, although tides occur twice a day, the water is fresh rather than salty. During progressive inundation by the tide, the plants offer little resistance. Their stems lean forward

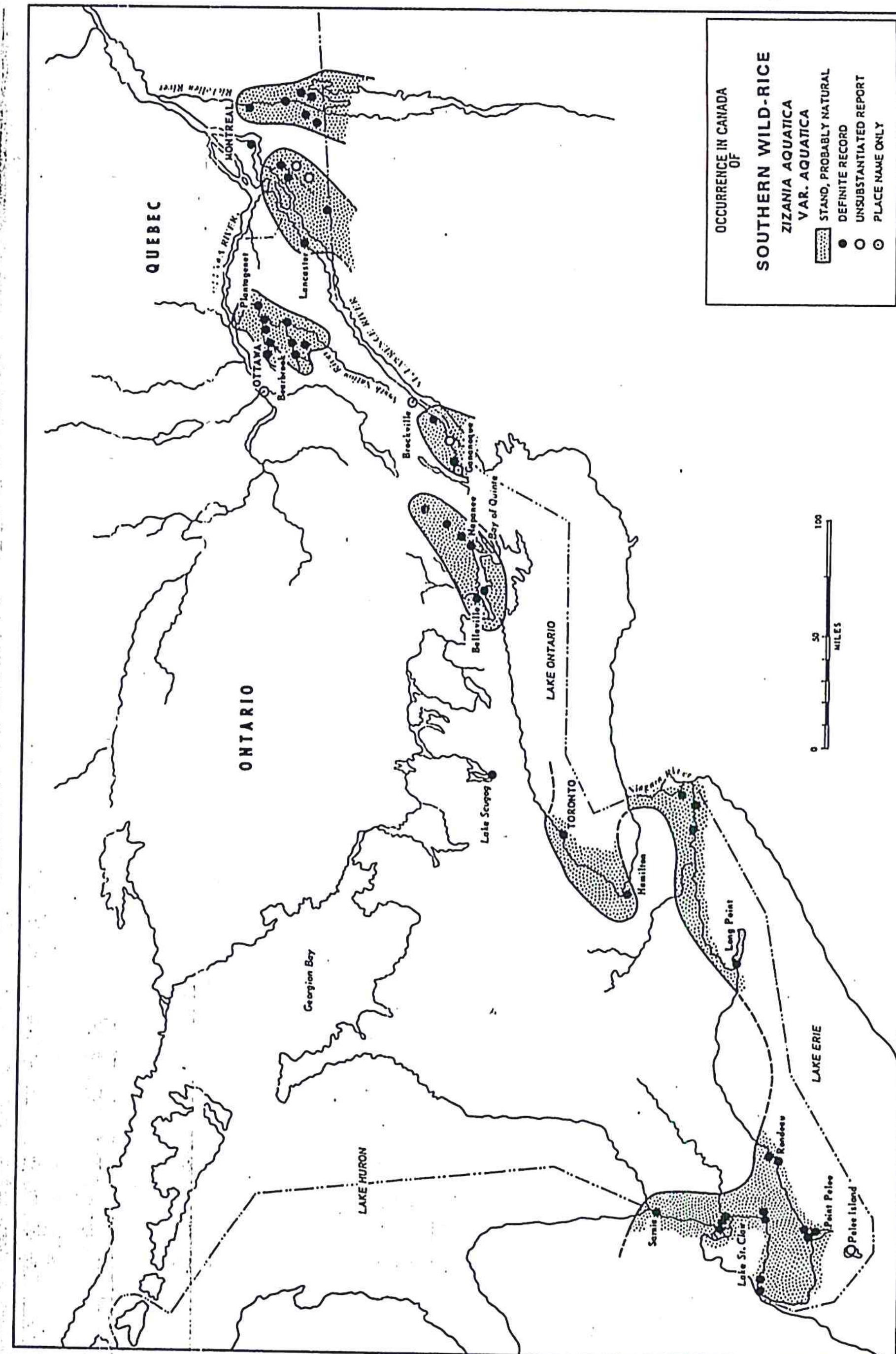


Fig. 9. Map of the distribution of *Z. aquatica*.

with the water currents and eventually the plants become completely submerged. The performance is repeated as the tide flows out. Often drifting debris and freshwater algae are caught in the panicle and a veneer of mud is left on the whole plant. The plants cannot tolerate very salty water and this intolerance defines the lower limit of their range: about 80 km downstream from Quebec City on the south shore, at Trois-Saumons, and about 30 km downstream on the north shore, at Sainte-Anne-de-Beaupré and at the northeastern tip of the Île d'Orléans. The variety occurs almost continuously upstream for about 80 km from Quebec City to Grondines (Fig. 10).

There are morphological differences in the plants, apparently in response to the saline gradient along the estuary; thus, where the salt concentrations are higher, the green stems and leaves have a somewhat succulent or rubbery texture not found in plants upstream. These plants also grow remarkably tall for the variety, and develop long, stiff, and spreading panicle branches. The anatomical basis for these intravarietal differences has not been investigated, but the differences are presumed to be largely environmental rather than inherent.

Plants reach their optimal development and bloom earlier on the shoreward portion of the flats, where, when the tide is in, they are submerged for a shorter time. A few are inundated only at times of high spring tides. Probably the water temperature and the varying interval of submergence affect development time. Consequently, ripening of grain takes place over an extended period. This, and the small size of the grain, are the reasons estuarine wild rice has never been harvested commercially. Nevertheless, the plant provides a valuable crop of food for migratory birds and other wild fowl that flock to the tidal flats each year. Several commercially desirable morphological features are expressed in this variety and it may well prove to be a useful source of genes in future crop development.

Estuarine wild rice is the only variety of *Z. aquatica* that grows in the tidal flats of the St. Lawrence River estuary, and it is not known from other tidal estuaries along the Atlantic coast. A logical conclusion is that it has evolved in the present or former estuary of the St. Lawrence and is endemic to that region.

Zizania palustris

2. *Zizania palustris* L. Mant. 295. 1771.

Type: The type specimen of *Zizania palustris* L. is preserved in the

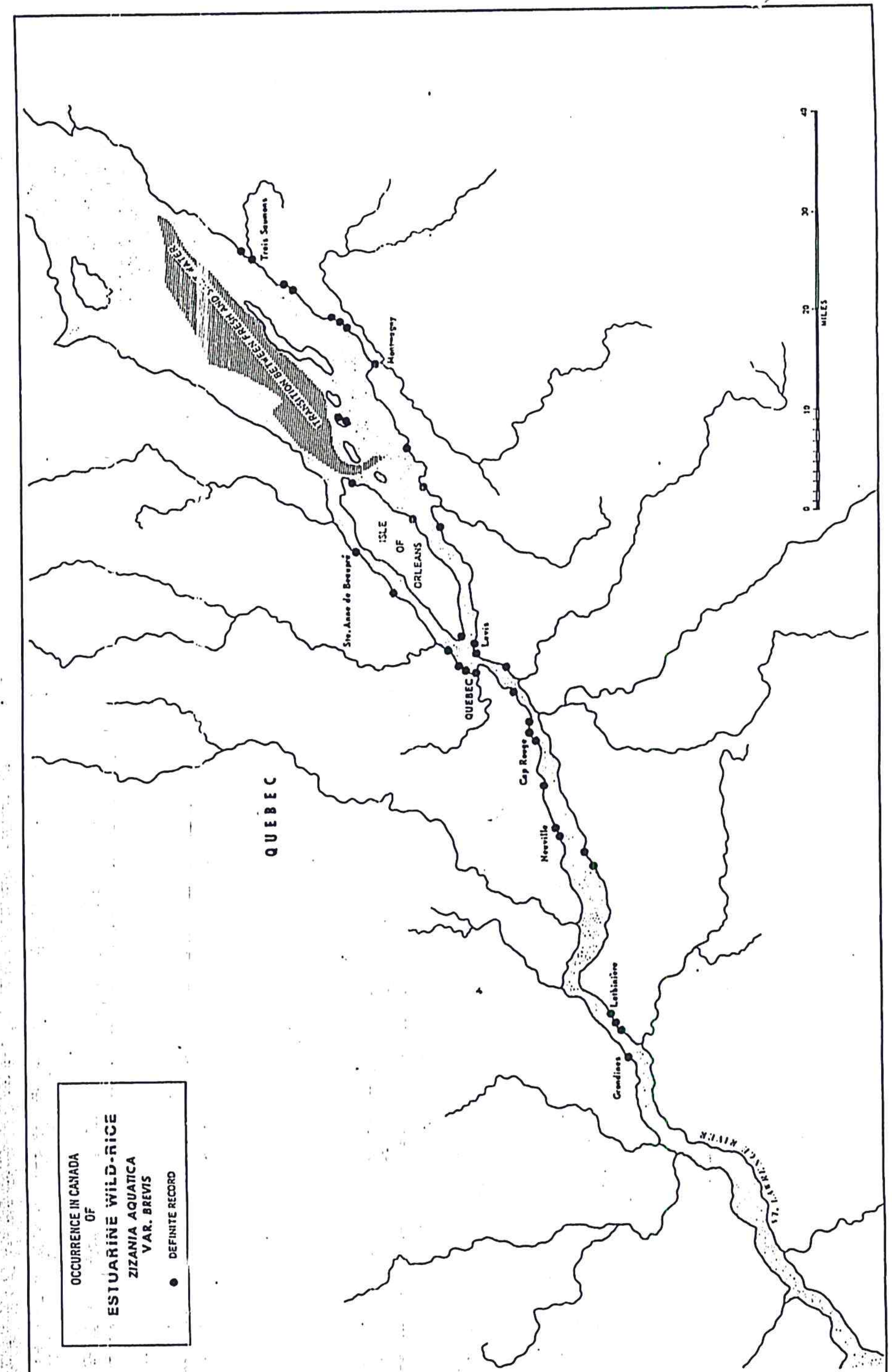


Fig. 10. Map of the distribution of *Z. aquatica* var. *brevis*.

British Museum of Natural History. On the herbarium sheet Linnaeus wrote only "*Zizania*" at the left of the base of the stalk and "H U" at the right, which meant the plant was grown in his garden, *Hortus Upsalensis,* at Uppsala, Sweden. From other sources we know that the grain was collected near Montreal by his student, Pehr Kalm, in 1749. The other annotation faintly showing on the sheet was made later by the authority J. E. Smith: "*palustris vix ob aquatica diversa*" (*palustris,* scarcely different from *aquatica),* an opinion that led later students to doubt the specific distinctness Linnaeus wished to designate.

Annual, 0.5–3 m high; hull of grain firm and leathery, shiny and smooth on the surface but with scabrous prickles along the veins. Two varieties are recognized.

2*a*. *Zizania palustris* var. *palustris* L. (*Z. aquatica* var. *angustifolia* A. S. Hitchc.) Rhodora 8:210. 1906.

Type: United States, Maine, Belgrade. Aug. 1895, F. L. Scribner. (Gray Herbarium.) NORTHERN WILD RICE, NORTHERN ZIZANIA (Fig. 8).

Stems slender, 0.5–1.5 m high; leaf blades 4–12(–15) mm; panicles slender and few-flowered; male spikelets usually less than 15 on a branch, female spikelets 2–6 on a branch.

Northern wild rice grows extensively along many rivers or their lakelike expansions from the southern edge of the Precambrian area in Alberta and Saskatchewan (range extended by planting) through Manitoba and northwestern Ontario. It is widespread in southern Canada where considerable stands are found in waters of the Trent Canal System and rivers flowing into the Ottawa from the north and west. It occurs as far east as Nova Scotia and extends southward into the northern United States (Fig. 11).

Northern wild rice is the most common and commercially important variety in Canada. This variety is popular among private and governmental sectors for plantings in rivers and lakes. As a consequence of this planting the range of this variety has been extended and there is an admixture of tall broad-leaved types that intergrade with the next variety.

2*b*. *Z. palustris* var. *interior* (Fassett) Dore. Can. Dep. Agric. Publ. 1393. 1969.

Type: United States, Iowa, Armstrong. 27 Aug. 1897, L. H. Pammel and R. J. Cratty, no. 764 (Gray Herbarium). INTERIOR WILD RICE, INTERIOR ZIZANIA.

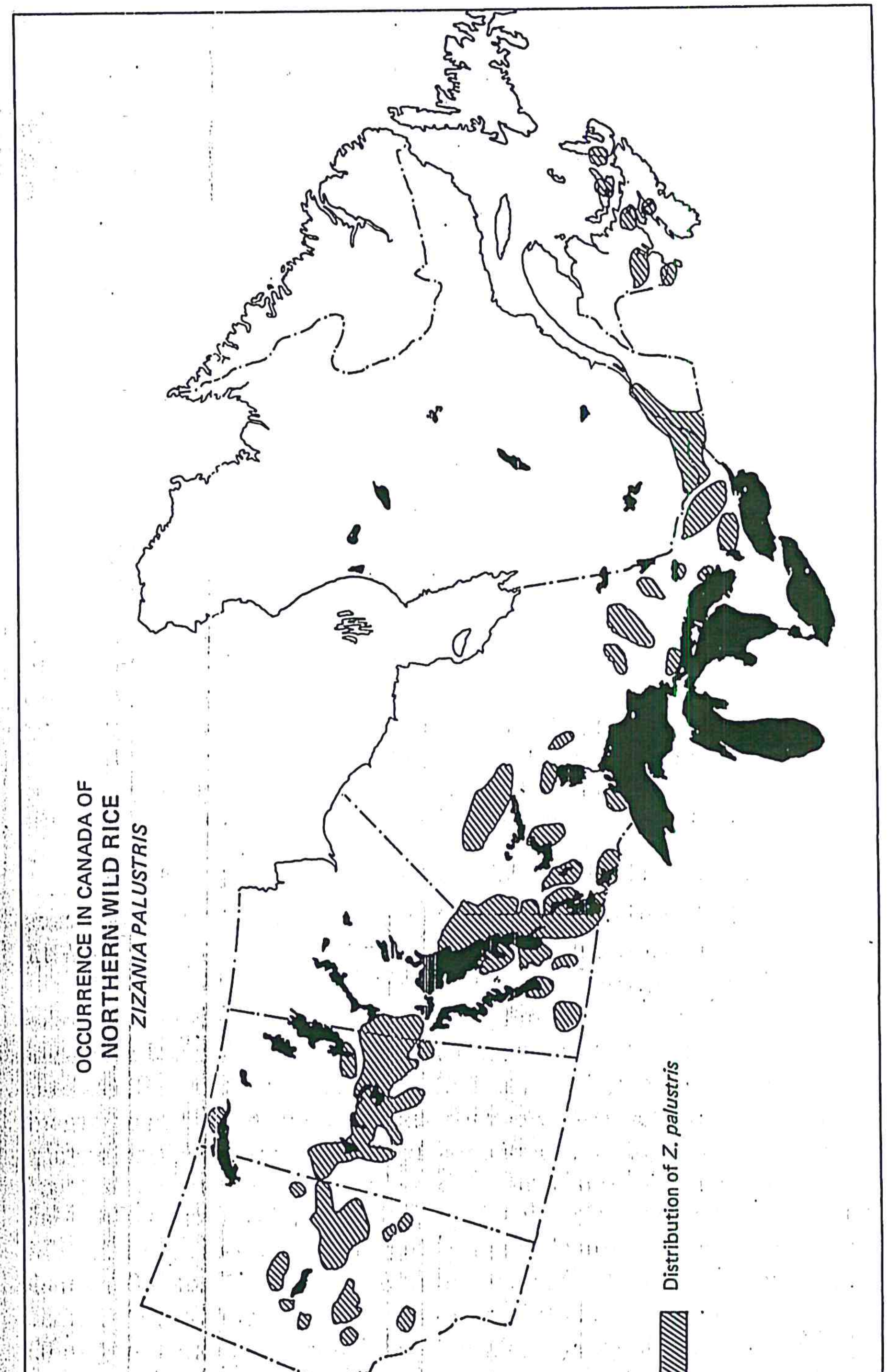


Fig. 11. Map of the distribution of *Z. palustris*

Stems usually 0.9–3 m high; leaf blades 10–40 mm wide; panicles spreading, branches generally divergent and many-flowered; male spikelets (20–)30–60 on a branch, female spikelets 10–30 on a branch. Interior wild rice grows on muddy shores and in water up to 30 cm deep mainly in the North Central United States. In Canada, natural stands occur only in the southernmost portion of Manitoba. Scattered stands occur at various points where it has been planted, from Manitoba and adjoining Ontario, to New Brunswick where it is abundant in the lower St. John River. In natural habitats it grows where the water retreats in the summer leaving flats of muddy alluvium. It forms spikelets and ripens earlier than the northern variety. The grains are somewhat shorter than those of the northern variety, but they are produced in greater abundance.

The two varieties are closely related and often difficult to distinguish morphologically, especially when plants are not fully developed. Variety *interior* grain is harvested throughout Alberta, Saskatchewan, Manitoba, and northern Ontario and often sold for new plantings. Thus, the northern and interior varieties come to grow together and many apparently intermediate forms are found making it difficult to separate the two varieties. However, isoenzyme research indicated ways in which the two varieties can be distinguished (Warwick and Aiken 1986).

Zizania texana

3. *Z. texana* A. S. Hitchc. J. Wash. Acad. Sci. 23:454. 1933.

Type: United States, Texas, San Marcos. April 1932, W. A. Silveus, no. 518. (U.S. National Herbarium, no. 1, 174, 537). TEXAS WILD RICE, TEXAS ZIZANIA.

Culms many, decumbent, geniculate, rooting at the lower nodes, forming stolons 1–3 m long (sometimes to 5 m), immersed culms and leaves long-streaming in river currents with only the inflorescence emergent, or in slow currents with upper culms and leaves emergent. Basal sheaths yellowish; ligules usually dark basally, whitish distally, 4–12 mm long, 2–5 mm wide. Submersed leaves to about 1 m long, 7–13(–25 mm) wide. Panicles 16–31 cm long, 1–10 cm wide. Male branches erect or somewhat spreading, to 10 cm long, pedicels 1–9 mm long, expanding to about 0.3 mm in diameter at base of the male spikelets, these 6.5–11.0 mm long, 1.2–2.0 mm wide. Female branches to 7 cm long, pedicels 1–7(–13) mm long, expanding to 0.5–0.9 mm in diameter at base of female spikelets, these 9.0–12.5 mm long, and 1.2–1.8 mm wide, leathery, light brown, greenish, or with the basal half greenish and the distal half whitish, the surface with scattered prickle hairs and the apex tapering to a terminal awn 9–35 mm long. Aborted spikelets 7.5–12.0 mm long, 0.7–1.2(–1.5) mm wide. (Description based on Terrell et al. 1978.).

Known only from Texas, Hays County, in the vicinity of the San Marcos River, near its source, where it grows in the cool, fast-flowing spring-fed water and is considered to be endemic. The stands are reported to be decreasing in size because of increasing pollution in the area (Emery 1977).

There is reason to believe that its perennial nature is due to the constant year-round temperature of the artesian waters. The status of *Z. texana* as a species distinct from *Z. aquatica* was questioned by Dore (1969), but the epidermal features studied by Terrell and Wergin (1981) suggest that it is a distinct species.

Fig. 12. Manchurian wild rice, *Zizania latifolia*, grown by Dr. W. G. Dore in a muddy paddy at Ottawa. This broad-leaved Asiatic species is a perennial, but when grown outside or indoors in the greenhouse it never produced flowers. The clumps were grown from small rhizome pieces set out the previous fall and they produced stems over 1.5 m high.

Zizania latifolia

4. *Z. latifolia* (Griseb.) Stapf. Kew Bull. 385. 1909. Turczaninow. Bull. Soc. Nat. Moscow. 11(1):105, nom. nud. MANCHURIAN WATER-RICE, MANCHURIAN ZIZANIA (Fig. 12).

Plants perennial, spreading by coarse subterranean runners; male and female spikelets borne on stems having a row of microscopic hairs at the tip and a corresponding crown of hairs present at the base of the hull of the floret; hull of grain thin, papery, dull, and rough, as in *Z. aquatica*. In contrast with other species, there are microhairs scattered over the body of the female lemmas (Terrell and Wergin 1981).

It is a native grass of Manchuria, Korea, Japan, Burma, and northeastern India. In parts of the Orient, some stands of *Z. latifolia* are sterile because of infection by a systemic fungus (*Ustilago esculenta* Hennings; Terrell and Batra 1982). The swollen shoots of such plants are highly prized as a vegetable. This species also has potential as a forage grass, and it has been planted for grazing purposes in other countries of Asia and Europe. Flowering plants grown at the Royal Botanic Gardens at Kew provided the material from which Dr. Stapf prepared the first detailed description and compared it with the North American *Z. aquatica*. However, plants of this species grown for several years in a botanical garden and greenhouse in Ottawa, and plants established in a greenhouse at the University of Minnesota, never flowered. At the Patuxent Reserve, near Washington, where the species was first introduced for testing in the 1920s, the plants always flowered, but in some seasons too late to ripen grain (Chambliss 1922).

III
Wild Rice Habitat

Wild rice grows best in shallow, clear lakes or rivers with a soft, organic bottom into which a paddle can easily penetrate, where there is an absence of plant competitors. However, wild rice does grow in a wider range of aquatic environments. Studies on the habitat requirements of wild rice have been few and the following information is based primarily on research done in Minnesota and northwestern Ontario.

Water depth

Water depth is the most important factor influencing a wild rice crop. The ideal depth during the plant's life cycle is about 0.3–0.6 m. If the water is either too deep or too shallow, or if sudden fluctuations in depth greater than 25 cm occur, production is severely affected. Moyle (1944) determined that an increase in depth of 0.3 m from preceding years could almost eliminate the wild rice crop on certain lakes in Minnesota. Similarly, on Lake of the Woods in northwestern Ontario, an increase of mean summer depths of 0.6 m from 1973 to 1974 decreased the harvest by over 400 000 kg (Lee 1975*a*). The problem with deep water is that it does not allow sufficient light penetration for normal photosynthesis to occur. Under such conditions seedlings may die or may have limited growth at their emergence stage. This is particularly apparent in darkly stained lakes, where wild rice grows only at the littoral zone (Fig. 13). Tillering, the production of many stems from one plant, seems

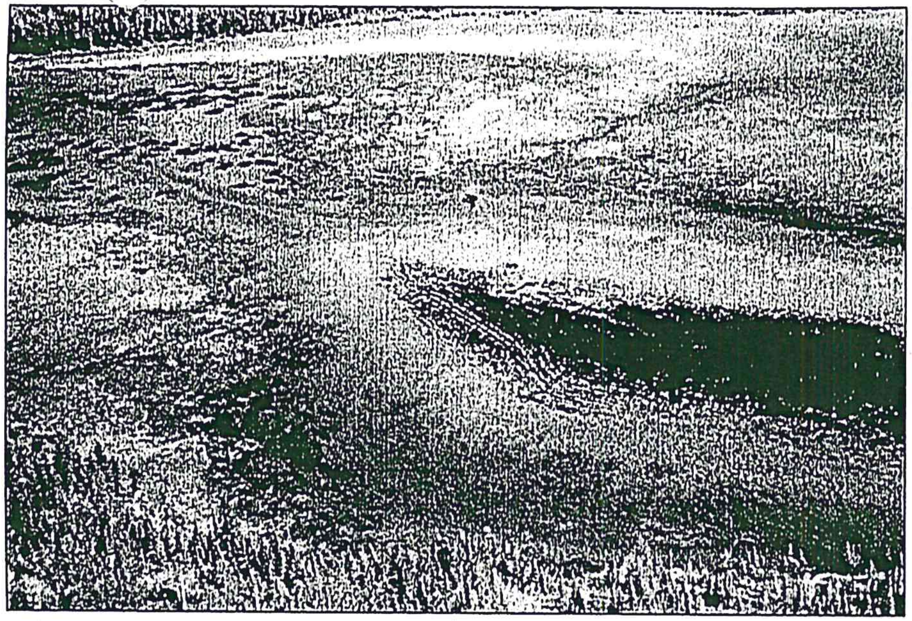


Fig. 13. A lake with darkly stained water in which wild rice grows only in the littoral regions.

to be light induced and is reduced in deeper waters (Lee 1979).

Although water that is too deep is more critical, very shallow waters can affect wild rice production. Weber and Simpson (1967) found that if the depth fell below 10.4 cm during the submersed or floating-leaf stage, the grain yield and amount of dry matter produced were reduced. Thomas and Stewart (1969) reported that a water depth of at least 8 cm was required for normal development.

Sudden fluctuations in water depth are also detrimental to rice production. If the water depth is increased during the floating-leaf stage while the roots are still small, the wild rice plants may be uprooted as the buoyancy in the leaves lifts the roots out of the soft sediments (Chambliss 1940). At the floating-leaf stage, a cuticle forms on the leaves, and the plant is no longer able to obtain dissolved gases from the water over the entire unwaxed leaf surface as it did during the submersed-leaf stage. Now it obtains the gases through small pores (stomates) that develop in the upper waxy surface of the floating leaves (Hawthorn and Stewart 1970). If the leaves are flooded, the stomates close and the plant is unable to take up sufficient amounts of gases through these leaves. During the aerial-leaf stage, if water depth is increased too rapidly, the lower branches of the inflorescence with the male spikelets may be under water and wind pollination cannot occur.

Water chemistry

Wild rice grows in a wide range of water types. In a survey in northwestern Ontario and northeastern Minnesota, the water quality of lakes with wild rice was found to be of two types (Lee 1979). The first had an alkalinity of about 40 mg/L and pH values of about 6.9. This corresponds to Moyle's (1944) description of soft-water flora in Minnesota, which he described as those species living in waters with a total alkalinity less than 40 mg/L, a pH between 6.8 and 7.5, and a sulfate concentration less than 5 mg/L. Moyle included wild rice in this group. The second type of wild rice lake found in Lee's study had an alkalinity of about 80 mg/L and pH values of 7.4. These values were somewhat lower than Moyle's hard-water flora, which he described as occurring in lakes with alkalinities of 90–150 mg/L, a pH of 8.0–8.8, and a sulfate concentration of 5–40 mg/L. Moyle (1945) suggested that sulfate was particularly important in influencing wild rice distribution, with few stands in Minnesota occurring in waters having a sulfate concentration greater than 40 mg/L and no large stands occurring in surface water having sulfate concentrations greater than 10 mg/L.

Evidence exists that wild rice absorbs most of its required nutrients from the soil, which suggests that water chemistry is only indirectly important. Tissue analyses showed that the seasonal trends of inorganic nutrients in wild rice roots were similar to those in the stems and leaves (Lee and Stewart 1983). In controlled greenhouse studies, sulfate concentrations in the water overlying a silica sand substrate, described by Moyle as adversely affecting wild rice, were shown to have no effect on wild rice growth (Lee and Stewart, Unpubl. Rep. 1978). This indicates that the water chemical values suggested by Moyle are important only to the extent that they correlate to the nutrients levels in the underlying soil. In some cases, as in the above study, they clearly do not. In another study (Davis 1979) an average sulfate concentration of 170 was found in the waters of very productive wild rice paddies along the Clearwater River in Minnesota. Another problem from correlating water chemistry to soil chemistry is the tendency for the nutrients in the water to fluctuate greatly in wild rice stands throughout the summer (Lee and Stewart 1981). Such fluctuations in the chemistry of the water, caused simply by time, negate the possibility of relating the concentrations of nutrients in the water to those in the soil.

The need for an adequate oxygen supply may explain the importance of a good flow of water through a wild rice stand, often noted by early researchers (Dore 1969). The gases dissolved in water are important to the submerged stages of wild rice. In highly eutrophic conditions, reduced carbon dioxide has been shown to limit production of wild rice (Lee and Stewart 1981).

Type of soil

Wild rice is known to grow on a wide range of soil types, but it usually grows best on soft alluvial organic soil (Brown and Scofield 1903, Fyles 1920, Lloyd 1939, Chambliss 1940, Moyle 1944). The roots of the rice plants easily penetrate this substrate (Chambliss 1940), and because this type of soil erodes easily, competing perennial species must often be eliminated (Dore 1969). One perennial species, however, actually enhances the growth of wild rice. Northwestern Ontario lakes over mineral soils only become optimal for wild rice after the lakes have been colonized by the underwater plant *Potamogeton robbinsii* (Fig. 14), which adds organic matter to the sediment (Lee 1983*a*).

The submersed condition of soils in which wild rice grows results in characteristics that are different from terrestrial soils. Oxygen is usually limiting, and this causes many of the nutrients required for wild rice growth to occur in their reduced state. Nitrogen is present as ammonium; sulfur as sulfide; and the metals, iron (Fe), manganese (Mn), zinc (Zn), and copper (Cu), in their lower valence states. Changes in the chemical nature of these elements, in turn, affect the availability of other required nutrients. In flooded organic soils, the reduced form of iron does not bind phosphorus and causes phosphorus to be released and become available to the roots of aquatic plants.

The nutrient levels of the soils in which wild rice grows vary considerably and little information exists for specific requirements. A survey of wild rice stands in northwestern Ontario and northeastern Minnesota revealed that the soils were primarily acidic, with pH values of 5.1–7.1. The metals Fe, Mn, Zn, and Cu were present in high concentrations, at times reaching levels toxic for most terrestrial plants (Lee 1979). The concentrations of the cations calcium (Ca), magnesium (Mg), and potassium (K) were present in the order Ca greater than Mg greater than K. The nutrients with the lowest relative concentrations were nitrogen (N) and phosphorus (P). Other studies have consistently shown that P, Ca, and the metals are important factors affecting wild rice productivity (Lee 1982, Lee 1983*b*, Lee and Stewart 1984). Elements that are not nutrients, such as lead, may also be accumulated in wild rice tissues (Behan et

Fig. 14. Enhanced growth of wild rice within the dark, round clumps of *Potamogeton robbinsii*.

al. 1979). Lead in the soil is taken up and translocated to the shoot system, but relatively little lead enters the grains. Concentrations of lead accumulating in tissues of wild rice and other rooted aquatics do not appear to be sufficient to harm herbivorous water fowl or wildlife.

More research is required to determine the optimum levels of nutrients required in the soil for wild rice growth. Conventional soil tests, using dried soil, are inappropriate because drying the soil changes the chemical behavior of the elements. The proper method is to analyze the soils while they are still wet and to express the nutrients by volume rather than by weight. Another problem is that the levels of nutrients fluctuate by as much as a factor of 10 during the season (Lee 1983*b*). Based on the few studies that have been done (Lee 1982, Lee 1983*b*), the most productive rice areas have the following values for extractable nutrients in the fall: N greater than 2.0 g/m^2, P greater than 1.5 g/m^2, and K greater than 3.0 g/m^2.

Competition with other plants

According to Moyle (1944), plants that compete with wild rice are

Fig. 15. *Eleocharis palustris*, spike rush, a perennial emergent species that commonly competes with wild rice. Most of the picture shows spike rush stems sticking up stiffly out of the water. There is a wild rice plant in the foreground with relatively wide and curving leaves.

usually perennials, including emergent, floating-leaf, and submerged species.

Emergent species that have been reported as adversely affecting wild rice are spike-rush (*Eleocharis* spp.), bulrush (*Scirpus* spp.), horsetail (*Equisetum* spp.) (Lee 1982), rigid arrowhead (*Sagittaria rigida*) (Lee and Stewart 1981), and pickerelweed (*Pontederia cordata*) (Coltas 1983). These emergent species start their growth cycle in the spring before wild rice. By the time the rice plants reach the surface of the water, the emergent plants are already well above the water surface. The underground stems rapidly spread out and send up new shoots at frequent intervals (Fig. 15). The result is that these species deplete the nutrient reservoirs of the lake bottoms. Rice plants in these infested areas are small with no tillers. In one lake near Ignace, Ont., rice plants in an *Eleocharis* stand were less than 1 g in dry weight at maturity, whereas in the same lake outside the *Eleocharis* stand, rice plants weighed up to 52 g.

Floating-leaf species, mostly water lilies (*Nymphaea* spp. and *Nuphar* spp.), watershield (*Brasenia* spp.), and bur reed (*Sparganium* spp.), can also have severe effects on wild rice. Like the emer-

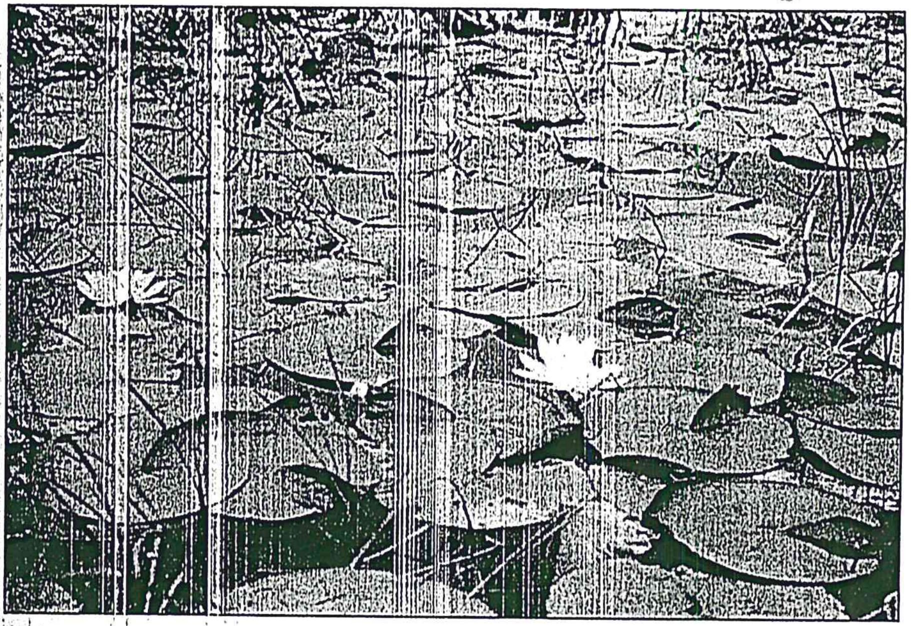


Fig. 16. A dense bed of water lilies with large leaves that have spread across the water surface in the early spring and are shading out the later developing wild rice plants.

gent species, the floating-leaf species start to grow in the spring before wild rice does. If conditions are suitable, large colonies can be formed that eventually converge on one another and impede the growth of any wild rice by stopping light from penetrating the water column. Invasion of *Brasenia* into wild rice stands has recently become a serious problem in Manitoba (Stewart, unpublished observations 1985). Usually water lilies are not a problem, because they do better than wild rice in deeper water. However, in lakes such as Lake of the Woods, where the depth of the water varies by up to 0.6 m per year, the deeper water encourages the growth of these plants over wild rice. When the lake level is lowered, the lilies have become so well established that they prevent wild rice from growing in otherwise ideal areas (Fig. 16).

Submerged species that affect wild rice growth include those with finely dissected leaves, such as *Ceratophyllum* spp. and *Myriophyllum* spp. These species invade more eutrophic wild rice stands and form dense clumps that impede light from reaching the developing wild rice plants or tangle with the submerged leaves and hold the plants under water.

Blooms of free-floating algae sometimes form during the sub-

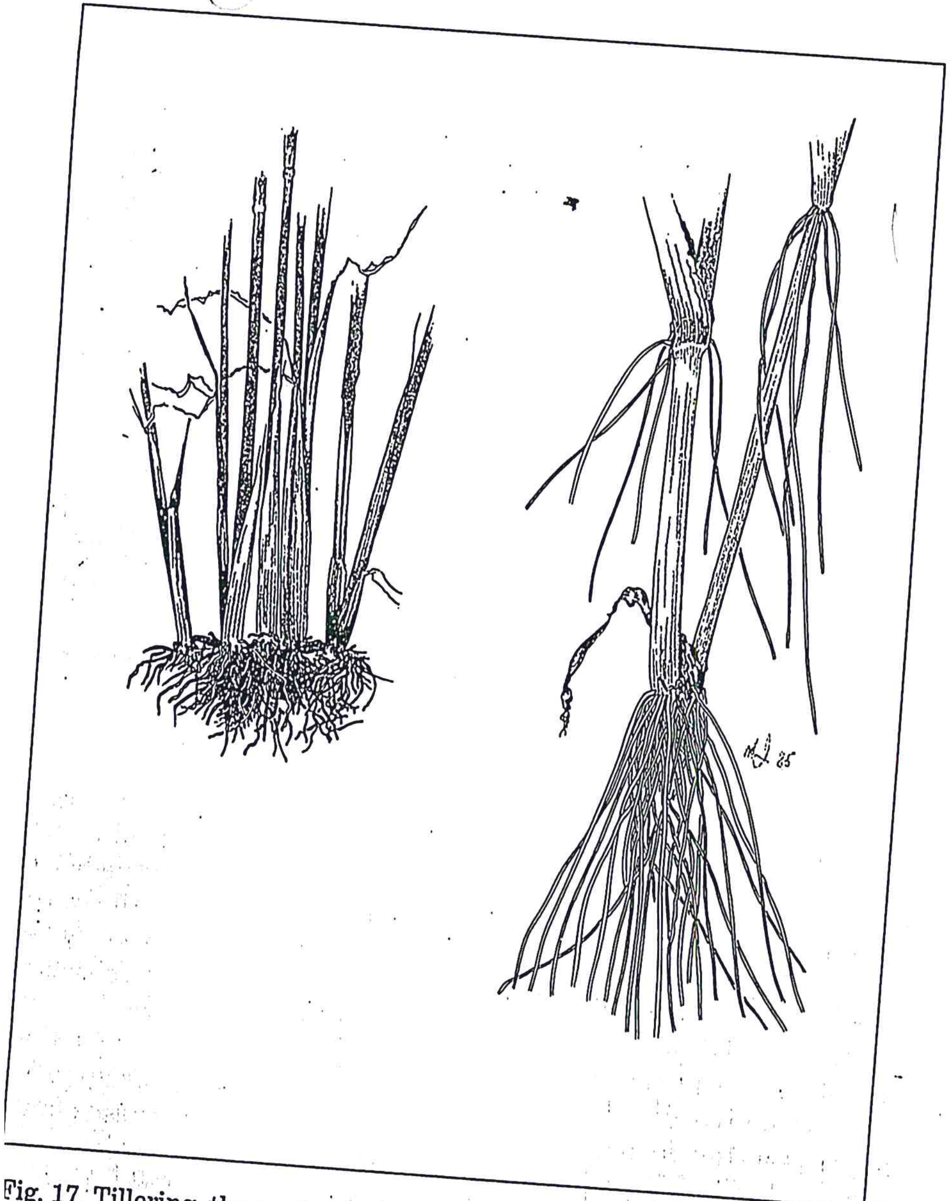


Fig. 17. Tillering, the production of many culms from one base. *(A)* Tillering n a plant that has grown in water 10–20 cm deep. *(B)* Tillering in a plant rown in water more than 50 cm deep.

mersed and floating-leaf stages of wild rice development. The algae cling to the young leaves and thus interfere with their ability to photosynthesize, eventually causing the death of the plants.

Competition within wild rice populations

Wild rice stands are most productive with about 10 plants per square metre. In good growing conditions, tillering (Fig. 17) will occur, producing up to 50 stems per plant. Under usual, natural conditions, the densities are much greater than this, reaching over 300 plants per square metre (Lee 1982) and resulting in lower yields.