FACTORS INFLUENCING PATTERNS OF VARIATION IN SOME MORPHOMETRIC CHARACTERISTICS OF WILD RICE POPULATIONS IN NORTHERN ONTARIO

by

REBECCA L. COUNTS H.B.Sc.

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BY

REBECCA L. COUNTS

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

DOCTOR OF PHILOSOPHY

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This stuff is perty *fraught*! It got some lines in here you could *hang clothes on*!

-Albert Alligator in Walt Kelly's *Pogo.*
Emphasis in the original.

ABSTRACT

Morphometric variation within and among wild rice populations was examined through field studies and a series of progeny tests 1) in the greenhouse, 2) in an experimental lake, and 3) on cultivation rafts. A total of 19 indigenous populations and 7 introduced populations were examined over all studies, the majority from northern Ontario.

Greenhouse experiments revealed that levels of intra-population variability were high for all characteristics examined, but there were also significant differences among populations. Variation among populations in maturation time, shoot and root weight per tiller, height, leaf width, pistillate floret production per tiller, and tiller number appeared to be associated with climatic conditions prevailing at the source. Clinal variation was observed for all of the above parameters except tiller number, which showed a discontinuous pattern of variation. Seed variables (weight and length) did not appear to be directly related to climatic factors. When the relative performance of progeny from 4 populations was considered in 2 greenhouses and an experimental lake, variation in the degree of plasticity in response to varying cultivation conditions was apparent, and appeared to be associated with climatic factors at the source as well. Increased climatic severity was associated with rapid maturation, small size, and reduced leaf width, vegetative vigour, pistillate floret production, and plasticity with varying cultivation conditions. Maximum tiller number was associated with intermediate climates.

Analyses of covariance were performed on field data from 17 indigenous wild rice populations. Variation in morphometric parameters was attributed to effects of local environmental factors (water depth, edaphic variables, and emergent macrophyte competition), variation among individual populations or groups of climatically-similar populations, and interactions between populations and local environmental factors. Differences among populations after correction for variability in the local environment made the largest contribution to explained variation for all plant characters except height. Climatic regime accounted for more variation than local environmental variability for pistillate floret production, leaf width, and seed characters (the last exhibited substantial differences among populations within climatic regions); general trends were similar to those observed in progeny tests in the greenhouse. The ratio of mineral to organic components in the sediment, sediment nitrogen concentrations, and water depth were the most important local environmental parameters. Interaction effects were small, indicating that most populations respond similarly to the range of environmental variation observed.

Divergence between source and introduced wild rice population pairs was examined in 2 studies. Progeny of 2 populations 5 and 50 years after establishment were compared with progeny of the common source population over 8 depth/fertilizer treatment combinations. In a field study 5 introduced populations and their 3 sources were compared 5 or 10 years after establishment of the new stands. There was little evidence of genetic differentiation of source and introduced population pairs in the environments considered, even after 50 years of reproductive isolation. It is suggested that phenotypic plasticity buffers wild rice populations from directional selection pressures of climate, and that the degree of plasticity itself may be a target of natural selection.

Implications of the results of these studies for breeding wild rice for lake cultivation are discussed.

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INTRODUCTION

Review of Species Characteristics

General Habitat

Zizania aquatica L. is an annual emergent aquatic grass. General descriptions of the plant and its characteristic habitat have been published by Fyles (1920), Chambliss (1940), Moyle (1944; 1967), Steeves (1952), and Dore (1969). Most recently, a comprehensive review of the ecology, taxonomy, and anatomy of North American wild rice has been prepared by Aiken et al (1987). Wild rice plants are characteristically found in shallow lakes and at the margins of slow-moving rivers and streams. They may grow successfully in water depths ranging from a few cm to 2 m or more, but occur most commonly at depths of 15 cm to 1 m. A mucky organic sediment is the preferred substrate, but wild rice is also found growing in mineral clay soils and in peat.

Many other plant species, especially those with a submerged or floating habit, may be found in association with wild rice; lists of associated species are given by Moyle (1944), Lee (1979), and Atkins (1986). Other emergent aquatic species, particularly those with a perennial habit and a capacity for vegetative reproduction such as *Phragmites* spp. and *Typha* spp., tend to displace wild rice from the shallowest margins of lakes, placing this species in an early to middle successional role in the hydrosere (Van der Valk 1981; Aiken et al 1987).

Human Utilization

Archaeological evidence for the prehistoric use of wild rice by Indians in Minnesota has been presented by Johnson (1969). Its historical importance to the native peoples and European settlers of the Great Lakes region of the U.S. and Canada both as a foodstuff and in an ethnological context has been described by

Jenks (1900) and Steeves (1952); its use by more northern tribes in Manitoba was reported by Hallowell (1935).

More recently, wild rice has been harvested for commercial purposes. Initially, grain was harvested from natural, unmanaged lake stands, and this remains the prevalent approach to wild rice exploitation in Canada (Lee 1986b). Paddy cultivation of wild rice was initiated in Minnesota in the 1960's, and efforts to domesticate the crop in the U.S. began soon thereafter (Anderson 1978). In recent years the area under wild rice cultivation has increased markedly both in Canada and the U.S. This has resulted in rapid expansion of the wild rice industry, particularly since the advent of production in California in the late 1970's (Nelson and Dahl 1986).

Distribution and Taxonomy

Two perennial species of the genus *Zizania* are known. One of these, *Z. latifolia* Turcz. (Stapf 1909), is native to East Asia and has a haploid chromosome number of n=17 (Hirayoshi 1956; Huang 1978). Attempts at hybridization between *Z. latifolia* and annual *Zizania* species have failed (Bondar 1958; Huang 1978), perhaps due to a postulated heterozygous pericentric inversion in the former (Huang 1978). The other perennial species, *Z. texana* Hitchcock, is endemic to south Texas (Terrell et al 1978). It and all annual members of the genus have n=15.

All of the annual members of genus *Zizania* occur naturally only in North America. Paleobotanical evidence suggests that wild rice occurred in Minnesota approximately 2500 years ago, well before human settlement of the region (McAndrews 1969). As mentioned above, the North American range of wild rice is continually being expanded by human activity. However, the historical range extended north to the St. Lawrence R. in the east, to approximately 52° at the western limits, east to New Brunswick, south along the eastern seaboard to Florida, and west to central Manitoba and the gulf of Mexico (Jenks 1900). Its Canadian range was extended in the Maritime provinces prior to the 1920's (Fyles 1920), west to Saskatchewan in the 1930's (Nielson 1964) and most recently to Alberta in the 1980's (Aiken et al 1987).

The taxonomy of the annual forms of *Zizania* is controversial. At least 4, and possibly 5, varieties exist that are relatively morphologically distinct and occupy (at least historically) different geographic ranges. These varieties, as enumerated by Warwick and Aiken (1986), are:

1. var. *angustifolia* A. Hitchc. (=var. *palustris*). This group has the northernmost distribution, found in southern and central Canada from Manitoba to New Brunswick. It also occurs in the northern U.S.
2. var. *interior* Fassett. This group has been most widely cultivated and harvested for commercial purposes, and is characteristic of the north-central United States. It is also found in southeastern Manitoba and adjoining Ontario.
3. var. *aquatica*. This variety is found throughout the eastern seaboard of the U.S., as well as in parts of southern Ontario and Quebec.
4. var. *brevis* Fassett. This group is endemic to the tidal estuaries of the St. Lawrence R. in Quebec.
5. var. *subbrevis*. This group has been most recently described in localized stands in Ontario and Quebec (Boivin 1967, cited by Warwick and Aiken 1986).

Fassett (1924) recognized one annual species with 4 varieties (1-4 above), citing intermediate morphs in the regions of sympatry. This treatment was subsequently adopted by Gleason and Cronquist (1963) and Fernald (1970), except that the latter do not mention var. *brevis*. However Dore (1969), conforming to what was probably the original intent of Linnaeus, recognized 2 species: *Z. palustris*, which includes vars. *palustris* (=var. *angustifolia*) and *interior*, and *Z. aquatica* with vars. *aquatica* and *brevis*. The division of the genus was justified on the basis of pistillate lemma texture and pubescence and on the appearance of aborted pistillate spikelets. The validity of this treatment has been reiterated by Aiken (1986), and further supported by results of isozyme analysis (Warwick and Aiken 1986). Some very limited and almost entirely ignored cytological evidence presented by Huang (1978) also indicates that the division of the genus into 2 species may be appropriate.

There has not yet been a formal, unanimous acknowledgement of 2 annual species of *Zizania* within the scientific community, although persuasive evidence supporting division of the genus has been accumulating in recent years. Critical experimental work regarding the cytology, capacity for hybridization, and phenotypic plasticity of the 2 putative species is lacking, and should, in my opinion, precede any formal recognition of their specific status. This is particularly true in light of the fact that human activity is a continuing force altering the geographic ranges of various members of the group. For these reasons, this thesis will follow the taxonomic treatment given in the major botanical manuals of Fassett (1957), Gleason and Cronquist (1963), and Fernald (1970), and refer to all annual taxa as varieties of the species *Z. aquatica.*

Life History

Wild rice "seeds" (technically fruits, or caryopses) remain dormant throughout the winter months. The mechanism by which dormancy is maintained is not clearly understood, in spite of considerable research on the subject. The normally obligatory period of after-ripening can be circumvented by disruption of the pericarp by pricking (Simpson 1966), scraping (Woods and Gutek 1974), mechanical scarification (Oelke and Albrecht 1978), or ultrasonic vibration (Halstead and Vicario 1969). This suggests that impermeability of the pericarp may inhibit germination by preventing water and/or gas uptake and/or exchange (Simpson 1966, Gutek 1975) or by mechanical impedance (Cardwell et al 1978). Reduction in the levels of the growth regulator abscisic acid (ABA) may also be involved in breaking dormancy (Albrecht et al 1978).

Early germination events have been documented by Aiken (1986). Successful germination from naturally after-ripened seed and early seedling growth is influenced by the temperature regime (Simpson 1966; Atkins 1986), dissolved oxygen concentration (Svare 1960; Atkins 1986), and growth substances such as giberellic acid (Oelke and Albrecht 1980).

Following germination the wild rice plant passes through 3 distinct phases ("phenophases") of vegetative growth: the submerged phase, during which 2 to 4 submerged leaves are produced, the floating phase, with production of 2 to 3 floating leaves and the aerial phase. Heterophylly is observed, as is commonly the case with aquatic plants that grow at or through the water:air interface (Sculthorpe 1967). Leaf and stem anatomy characteristic of each phenophase in the development of the wild rice plant has been described by Weir and Dale (1960), and developmental changes in superficial leaf anatomy have also been chronicled by Hawthorn and Stewart (1970). Upright stature and the production of basal tillers is usual in annual forms of *Zizania*, although decumbent plants producing axillary branches have been described (Ferren and Good 1977).

The pattern of nutrient accumulation and resource allocation changes in the course of development of the wild rice plant. During early seedling establishment and growth, a greater proportion of biomass is partitioned to root material than to the shoot (Whigham and Simpson 1977). The majority of the root mass is adventitious and lacks root hairs (Stover 1927). After establishment, the primary allocation of resources is shifted to production of shoot biomass (Whigham and Simpson 1977). Nutrient and dry matter accumulation are maximal during this stage of rapid vegetative growth prior to flowering (Grava and Raisanen 1978). Once the flowering panicle emerges net dry matter production declines, although nitrogen accumulation by the plant continues through flowering and grain formation.

Flowering generally commences in mid- to late July and continues through early August. Wild rice is monoecious, protogynous, and anemophilous (Weir and Dale 1960), a combination of features favouring outcrossing. Some self-pollination probably occurs naturally, since self-compatibility has been confirmed through artificial crosses and seed has been obtained from crosses effected up to 4 days after stigma excertion (Elliott 1980).

The caryopsis develops during the 10 to 14 days following fertilization in a manner that is generally typical of cereals (LaRue and Avery 1938). Weir and Dale (1960) have described the structure of the wild rice caryopsis in detail. Mature grains shatter readily in undomesticated strains; the shattering habit has been a target of selection for Minnesota plant breeders, and is believed to be controlled by 2 complementary genes with a dominant allele required at both loci to give the shattering phenotype (Elliott and Perlinger 1977). The species has low vagility as a consequence of the awn borne by the lemma, which tends to direct the caryopsis directly down into the sediment close to the parent plant.

The Study of Intraspecific Variation

The species may be considered the fundamental unit of biological inquiry; experimental or descriptive studies focus on one or more species that are recognized as distinct, and separated by a discontinuity in form or function from other closely related groups (Ross 1974). While the objective, independent reality of the "species" has been a subject of debate among evolutionary biologists (Ehrlich and Holm 1962; Sokal and Crovello 1970; Levin 1979; Merrell 1981), there is no doubt that the concept is necessary and valid at the very least as a convenient construct to facilitate communication between scientists (Merrell 1981). The controversy over the biological species concept has arisen as a consequence of the recognition of the fact that species are not static, but rather are dynamic entities, varying in both the temporal and spatial dimensions.

Charles Darwin's observations of variation within and among species led to the development of his theory of evolution by natural selection. Since his ideas gained general acceptance, the study of variation and the evolutionary process has been of continuing interest to biologists. The concepts of adaptation, natural selection, and evolution provide an interpretive framework for all biological disciplines: natural history, physiology, anatomy, genetics, embryology, ecology, taxonomy, and so forth....it has been said that "nothing in biology has meaning except in the light of evolution" (Dobzhansky 1973).

Many of the early studies on intraspecific variability were conducted using plants. Since plants are sedentary, spatial patterns in variation are more apparent and critical environmental factors are more easily elucidated than is the case for animals (Merrell 1981). Turesson (1922a; 1922b; 1925; 1930) developed the concept of the ecotype, and was one of the first natural historians to interpret patterns of geographic variation in terms of adaptation to environmental conditions. Clinal variation along environmental gradients was first discussed by Huxley (1939). The reknowned monographs of Clausen, Keck and Hiesey (1940; 1948) and Clausen and Hiesey (1958) introduced the reciprocal transplant and common garden approaches to studies of variation within plant species. This and other work pertaining to variability, phylogenetic relationships, and evolutionary trends in plants was summarized and discussed by G.L. Stebbins in his classic (1957) text.

These early studies were almost exclusively concerned with variability in morphological characters (or physiological characters; see Hiesey and Milner 1965), often quantitative traits for which the genetic basis was (and is) poorly understood. More recently modern electrophoretic techniques have been applied to the study of enzyme variants within and among populations. Since proteins (and therefore enzymes) are direct gene products, isozyme data are more readily applied to the classical mathematical population genetics theories developed by R.A. Fisher, J.B.S. Haldane, and S. Wright in the 1930's. These data present difficulties in interpretation, however, since the adaptive significance of environmentally-correlated variation in isozyme complements is usually unknown (Merrell 1981).

The analysis and interpretation of intraspecific morphological and biochemical variability is a subject of continuing interest in the botanical literature. Recent studies have considered differentiation within and among populations in response to micro-environmental differences (e.g. Jain and Bradshaw 1966; Antonovics 1971; Linhart 1974; Brown 1983; Schwaegerle et al 1986; Schwaegerle and Bazzaz 1987). Others have been concerned with the evolution of adaptive strategies, as reflected by levels and partitioning of genetic and plastic variation in relation to the ecology and life-history of species (e.g. Baker 1953; Hickman 1975; Law et al 1977; Stearns 1977; Zangerl et al 1977; Loveless and Hamrick 1984; Hamrick et al 1979; Hamrick and Holden 1979; Hamrick 1982; Carey 1983; Gilmartin et al 1986; Mitchell-Olds and Rutledge 1986).

This thesis presents the results from a series of studies of morphometric variation within and among a number of wild rice populations, primarily from northern Ontario. The primary objective of the research was first to determine if there are genetically-based differences among populations, and if so, to ascertain the relative importance of genetic differentiation and plastic responses to localized environmental differences in creating the patterns observed. I have interpreted the data in an ecological and historical context, and drawn inferences about the forces shaping the ongoing evolution of this species. The influence of climatic factors in particular is considered. The investigation was almost entirely limited to northern Ontario populations of the commercially valuable varieties: *Z. aquatica* vars. *angustifolia* and *interior* . This restriction of scope was adopted because a further goal was to develop a database to assist Canadian growers of lake wild rice to make informed choices regarding appropriate seed sources to upgrade existing stands or develop new ones, and to lay the groundwork for a Canadian wild rice breeding programme.

The thesis is presented as 4 separate but interrelated papers, each addressing rather specific questions relating to the general objectives outlined above. Chapter 1 describes a series of 3 experiments in which progeny of seed from a total of 11 wild rice populations were raised together in greenhouses to study the partitioning of genetic variation in morphometric characteristics within and among them. Results of field surveys of 17 wild rice populations are analyzed in chapter 2 using a statistical treatment to estimate the relative importance of local and regional environmental factors in predicting morphometric characteristics. Chapter 3 addresses the subject of differential plasticity of populations through a comparison of relative performance of progeny from 4 wild rice populations grown in 3 environments. Finally, morphometric divergence of several introduced wild rice populations of known origin from their sources is studied in chapter 4 through analysis of field surveys and a common-garden experiment. A synthesis of the results presented in these chapters is provided in the final concluding remarks. The thesis itself may be briefly summarized in three statements:

1. There has been genetic differentiation among Northern Ontario wild rice populations for a variety of morphometric traits.

2. Both genetic differences and plastic effects contribute to observed variation; their relative importance depends on the character under consideration.

3. Climate has acted as an important selective force influencing the evolution of these populations, particularly with regard to phenological schedules, seed production, and the magnitude of phenotypic plasticity in tiller number and tiller size.

Chapter 1

THE INFLUENCE OF SOME CLIMATIC FACTORS ON THE DIFFERENTIATION OF POPULATIONS

1.1 INTRODUCTION

Wild rice (*Zizania aquatica* L.) is the only cereal indigenous to North America, and occurs naturally only on that continent. Two of the four or five varieties that have been recognized are commercially harvested: var. *angustifolia* and var. *interior*. The grains were traditionally harvested by the Ojibwa and Sioux tribes of Native Americans in the Great Lakes area. More recently, this species has been commercially exploited in the United States and Canada. Paddy cultivation for commercial production is common in the U.S., but in Canada most commercial harvesting is carried out on largely unmanaged wild rice stands in lakes and rivers. Until recently there has been little information regarding appropriate management techniques for lake production of wild rice.

The selection of a suitable seed source is a crucial aspect of the development of new wild rice stands or the improvement of existing stands for commercial harvesting. High yield is the obvious desirable characteristic of a population, and is the product of several components: seed production per tiller, number of tillers per plant, and individual seed size. Yield stability is also important, and may be enhanced by such traits as early maturation. Although variation in such characteristics has been observed among and within wild rice stands across Canada (Moyle 1944; Lee 1979; Archibold and Weichel 1986; Garrod 1984; Aiken et al., 1987), no studies have been reported concerning the extent to which the observed variation can be attributed to environmental effects or genetic differentiation. Developmental plasticity coupled with local and/or regional differences in climate, water depth, plant competition, or sediment nutrition could create phenotypic variability among and within wild rice stands (Rogosin 1958; Weir and Dale 1960; Thomas and Stewart 1969; Oelke et al. 1982). However, the aquatic habit and poor seed dispersal mechanism of wild rice restricts gene flow and results in a patchy distribution of populations that are reproductively isolated. This increases the potential for genetic divergence of populations. Such locally adapted populations may have heritable characteristics that could be important in increasing the production of wild rice.

This paper presents the results of a series of experiments in which plants from several wild rice populations were grown together in the greenhouse. The objective of the study was to determine whether significant genetic differentiation for several economically important characters has occurred among the populations. If genetically-based differences do exist among stands, it should be possible to identify and select suitable source populations for cultivation and for the establishment of a breeding program to develop improved varieties of wild rice.

1.2. METHODS

1.2.1. Seed Sources

Information regarding the populations used as seed sources in each of the three experiments conducted is presented in Table 1.1. Figure 1.1 shows the locations of the Northwestern Ontario populations grouped by climatic similarity (see below). All of the source populations except those from Charnock Lake and Saskatchewan are indigenous; i.e., they are not known to have been deliberately introduced from another location in the recent past. The wild rice in Charnock and Beaveroo Lakes was introduced in 1979 from Lac du Bois, Manitoba (50° 16' N x 95° 42' W). The rice in Saskatchewan also originated in southeastern Manitoba (probably Lac du Bois), and was introduced about 1935 (Neilson 1964). All of the source

FIG. 1.1. Map showing locations of Northwestern Ontario wild rice populations sampled in three experiments. Climatically similar groups of populations were defined by cluster analysis. Note that Beaveroo Lake is in the same location as Charnock Lake. Two additional populations represented in the experiments are not shown: Mercer River, Saskatchewan, and Big Creek in Southern Ontario (see Table 1.1).

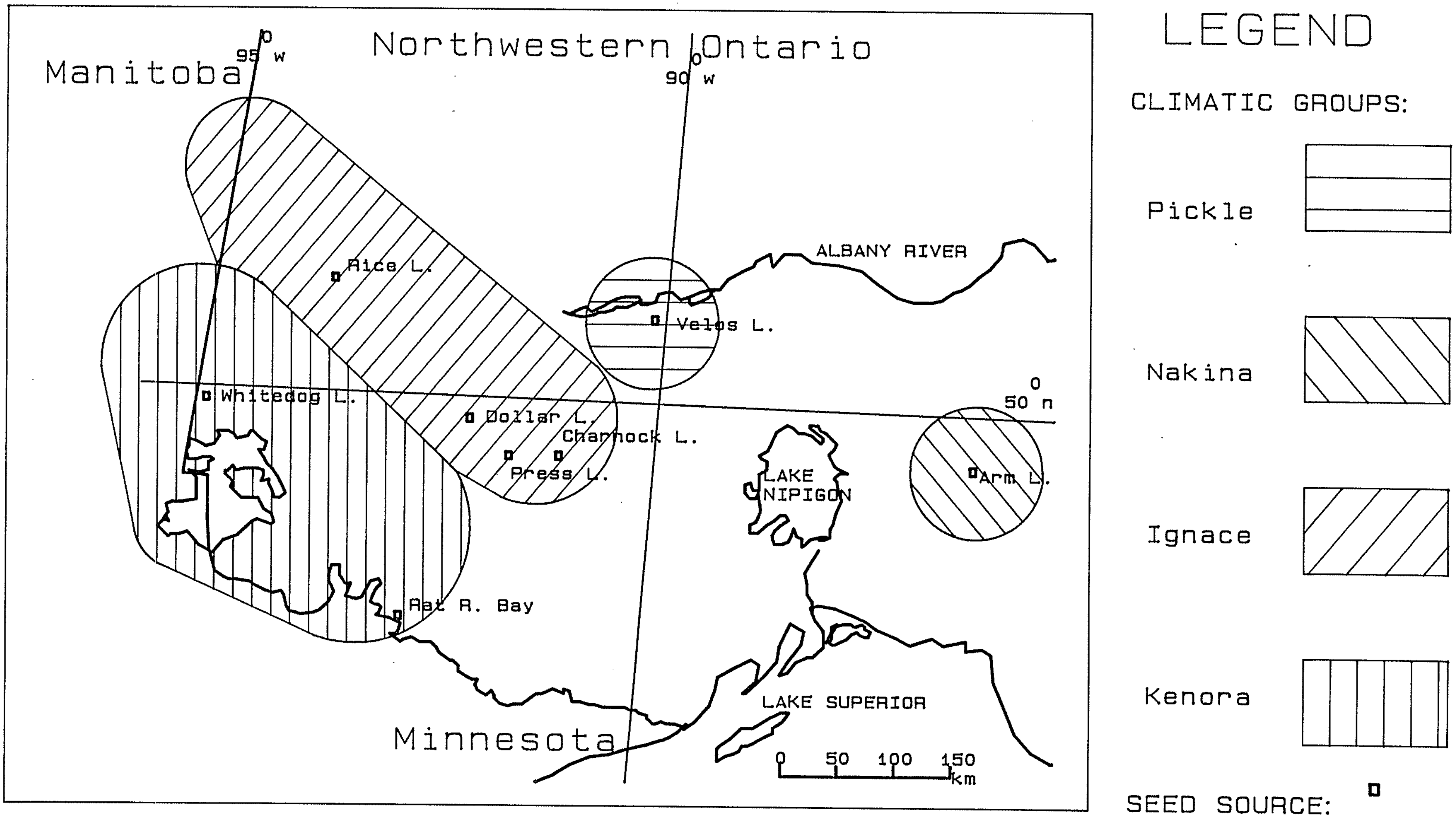

Manitoba
95° w
Northwestern Ontario
90° w
ALBANY RIVER
Rice L.
Velos L.
Whitedog L.
50° n
Dollar L.
Charnock L.
Press L.
LAKE NIPIGON
Arm L.
Rat R. Bay
LAKE SUPERIOR
Minnesota
0 50 100 150 km
LEGEND
CLIMATIC GROUPS:
Pickle
Nakina
Ignace
Kenora
SEED SOURCE:

TABLE 1.1. Locations and climates of wild rice populations represented in three experiments

Population	North Latitude	West Longitude	Annual Growing-Degree-Days (5°C)	Average Date of First Fall Frost (Year-Day)	Probability of Frost Before Sept. 1 (%)	Maximum Daylength (minutes)	Experiment 1	Experiment 2	Experiment 3
Velos Lake	50° 50'	90° 08'	1276.4	250	25	980	X	X	X
Arm Lake	50° 01'	86° 45'	1166.0	241	50	980			X
Saskatchewan	55° 05'	105° 30'	1262.4	253	25	1040			X
Red Lake	51° 13'	93° 03'	1519.9	263	0	990			X
Dollar Lake	49° 40'	91° 53'	1497.4	262	5	970		X	X
Press Lake	49° 46'	91° 26'	1497.4	262	5	970			X
Charnock Lake	49° 41'	91° 19'	1497.4	262	5	970	X	X	
Beaveroo Lake	49° 41'	91° 19'	1497.4	262	5	970			X
Whitedog Lake	50° 08'	94° 53'	1670.4	270	0	980	X	X	X
Rat River Bay	48° 35'	92° 40'	1628.4	252	25	960			X
Big Creek	42° 36'	80° 29'	2093.8	274	0	915	X		

populations considered would be classified by those who recognize two species as *Z. palustris* except for the Big Creek population from Southern Ontario, which is *Z. aquatica* var. *aquatica*.

1.2.2. Growth Conditions

Experiment 1 was conducted from the end of December, 1982 to April 1983. In the second experiment, plants were grown from June to the beginning of October 1983, and the third experiment took place in the period from June to October 1984. Experiments 1 and 2 were conducted entirely in one greenhouse located on the Lakehead University campus in Thunder Bay, Ontario. Experiment 3 was replicated in a second greenhouse 3.3 km north of the campus. Sixteen-hour days at 21° C and eight-hour nights at 16° C (minimum temperatures) were maintained throughout all experiments at both locations, but there were not identical conditions prevailing in both greenhouses. Greenhouse 2 was not shaded by adjacent buildings and received more direct sunlight than greenhouse 1. At the same time it was better ventilated, so maximum daytime temperatures were lower in the second greenhouse. Seeds were surface-sterilized by soaking for 30 minutes in a 5% sodium hypochlorite solution and germinated in tap water at room temperature. After two weeks, 5 seedlings were planted in each 12.7 cm pot and thinned to 1 plant per pot after establishment. Each pot contained 3 g of 'Sierra Blend' (18-7-10) slow-release fertilizer (Sierra Chemical Company, Milpitas, California) mixed with organic muck from Oval Lake (49° 33' N x 92° 02' W) or heavy clay from Pass Lake (49° 41' N x 91° 22' W) in the first two experiments, or greenhouse loam in the third experiment. Different soils were used in the first two experiments to determine if seed sources had variable responses to sediment texture. The pots were submerged in tanks containing 30 cm of intermittently circulating water. Each wild rice seed source was represented by twenty plants in each experiment: ten in each soil type in experiments 1 and 2, and ten at each location in experiment 3.

1.2.3. Laboratory Procedures

The wild rice plants were grown until seed was set. The time from planting to receptivity of pistillate florets (cereal growth stage 55 to 57 in most cases; see Tottman and Makepeace 1979) was noted for each plant. At harvest, the following data were obtained: tiller number, height from the base of the stem to the tip of the main inflorescence, mean maximum aerial leaf width, and the number of pistillate florets per tiller and per plant. Roots and shoots were separated and oven-dried at 80° C to an unchanging weight. Stem and root weights per tiller were calculated by dividing the total weights per plant by the number of tillers. Hundred-seed weight and mean seed length for each plant were estimated from measurement of ten (first two experiments) or twenty (third experiment) hulled, air-dried seeds (hundred-seed weights were obtained by multiplication). The raw data obtained in these three experiments is presented in Appendix 9.

1.2.4. Data Analyses

The main assumptions underlying the parametric statistical procedures used in the analyses are that variables are normally distributed and that among-group variance is homogeneous (Green 1979; Sokal and Rohlf 1981). The data were tested for normality using normal-probability plots and skewness and kurtosis statistics. A natural logarithm transformation was used to normalize stem weights, root weights, and number of pistillate florets. Heteroscedasticity of the data sets was tested using Cochran's C statistic, and was found to be nonsignificant ($p \geq 0.01$) for all variables except for leaf width and stem and seed weight per plant in the first experiment, and shoot weight and number of pistillate florets per plant in the third experiment. Computer programmes from the SAS and SPSS statistical packages were used in the data analysis (Nie et al. 1975; SAS Institute Inc. 1982a, 1982b).

For the first two experiments, stepwise discriminant analysis was used to examine differences among populations and to identify the variables that best distinguished the groups. Heteroscedastic variables were omitted from the analysis. The criterion for variable selection at each step was minimal Wilks' lambda, with the probability-of-inclusion level set at 0.05 (Nie et al. 1975). Two-way analyses of variance (ANOVAs) were also performed on all plant variables; seed source and soil type were the main factors. Factors and interaction terms were tested against the within-cells error term in all cases. A modified least-significant-difference (LSD) test (Nie et al. 1975) at the 0.01 significance level was used to compare pairs of experimental population means for variables found significant in the ANOVA.

In the third experiment, the analysis was concerned with groups of seed sources that were subject to similar climatic conditions. In order to define a "climate group" variable, climatic data (presented in Table 1.1) were used in an average-linkage, hierarchical agglomerative Q-type clustering procedure (SAS Institute Inc. 1982b) which formed groups of populations on the basis of minimum squared Euclidean distance. Annual (5°C) growing-degree-days (GDD), the average date of the first fall frost, and probability of fall frost before September 1 were recorded for the weather stations nearest each population (Environment Canada 1982a, 1982b). Maximum daylength was also estimated from figures in Strahler (1969). Climatically similar population clusters ("climate groups") were defined on the basis of these data. These variables were chosen because they were deemed most likely to influence wild rice growth and development. GDD is a joint function of daily temperature during the growing season and the length of the growing season, both factors that are expected to limit wild rice production as they do other crop species. The average date of first fall frost and the risk of early frost are also expected to be limiting factors, since they signal curtailment of the growing season.

Maximum daylength was included because wild rice growth has been shown to be sensitive to photoperiod (Oelke et al 1982), as are many plant species (Salisbury and Ross 1985). Other climatic factors are important in determining growth patterns for terrestrial species but were not deemed relevant for this emergent aquatic organism. Since wild rice passes the winter months as dormant seed buried in the mud, winter temperatures and precipitation do not affect its survival. Likewise, spring temperatures and risks of spring frost do not directly affect the plants, which are submerged in water and thus protected from fluctuations in air temperature during the early part of the growing season. Average spring and summer precipitation is also not nearly as critical for wild rice as for terrestrial plants, except as it is very indirectly related to risk of rapid increases in water levels. These variables are integral to the delineation of regional boundaries by climatologists. Consequently, regions such as those defined in Chapman and Thomas (1968) were inappropriate for the purposes of this research.

Although the introduced populations (Charnock Lake, Beaveroo Lake, and Saskatchewan) were included in the clustering procedure, they were not grouped with the indigenous populations in subsequent analyses, but were kept separate so that they would not obscure any evolutionary effects of climate on wild rice characteristics. Discriminant analyses of seed sources, climate groups, and locations (greenhouses) were carried out as described above. Nested, two-way analyses of variance were performed for each variable, with climate groups, seed sources within groups, and locations as the factors. Pairs of means were again compared using modified LSD tests.

1.3. RESULTS

1.3.1. Experiments 1 and 2

Although there were quantitative differences in plant morphology and phenology between the first two experiments, the results were quite similar qualitatively. Both the discriminant analyses and the ANOVAs indicated that the experimental wild rice populations were distinct from one another. In the first experiment two discriminant functions explained 98.9% of the total variation in the data set, and successfully classified 79.2% of cases. Characteristics of the discriminant functions are presented in Table 1.2, and the 90% probability ellipses of the discriminant scores for each population are shown in Figure 1.2. The first function, explaining 84.1% of the variance, primarily reflected the number of pistillate florets (potential seed number) per plant; flowering time, stem weight and seed weight were minor contributing variables. This function separated Big Creek plants, which were late to mature and high-yielding with small tillers and light seeds, from all others. Stem and seed weight contributed most strongly to the second function, which accounted for 14.7% of the variance and separated Velos Lake, Charnock Lake, and Whitedog Lake plants. Velos Lake plants were earliest to flower and had small stems, light seeds, and the lowest potential seed number per plant. Whitedog Lake plants were at the opposite extreme for all characters. Charnock Lake plants were intermediate between the two.

Two discriminant functions explained 92.3% of the variance in the data from the second experiment, and correctly classified 78.0% of cases. The first function separated Velos Lake plants at one extreme and Whitedog Lake plants at the other extreme from intermediate Dollar Lake and Charnock Lake plants (Figure 1.3), and accounted for 53.8% of the total variance. This function primarily reflected potential seed weight per plant, stem weight per tiller, and pistillate florets per tiller (Table

TABLE 1.2. Discriminant analyses of wild rice populations

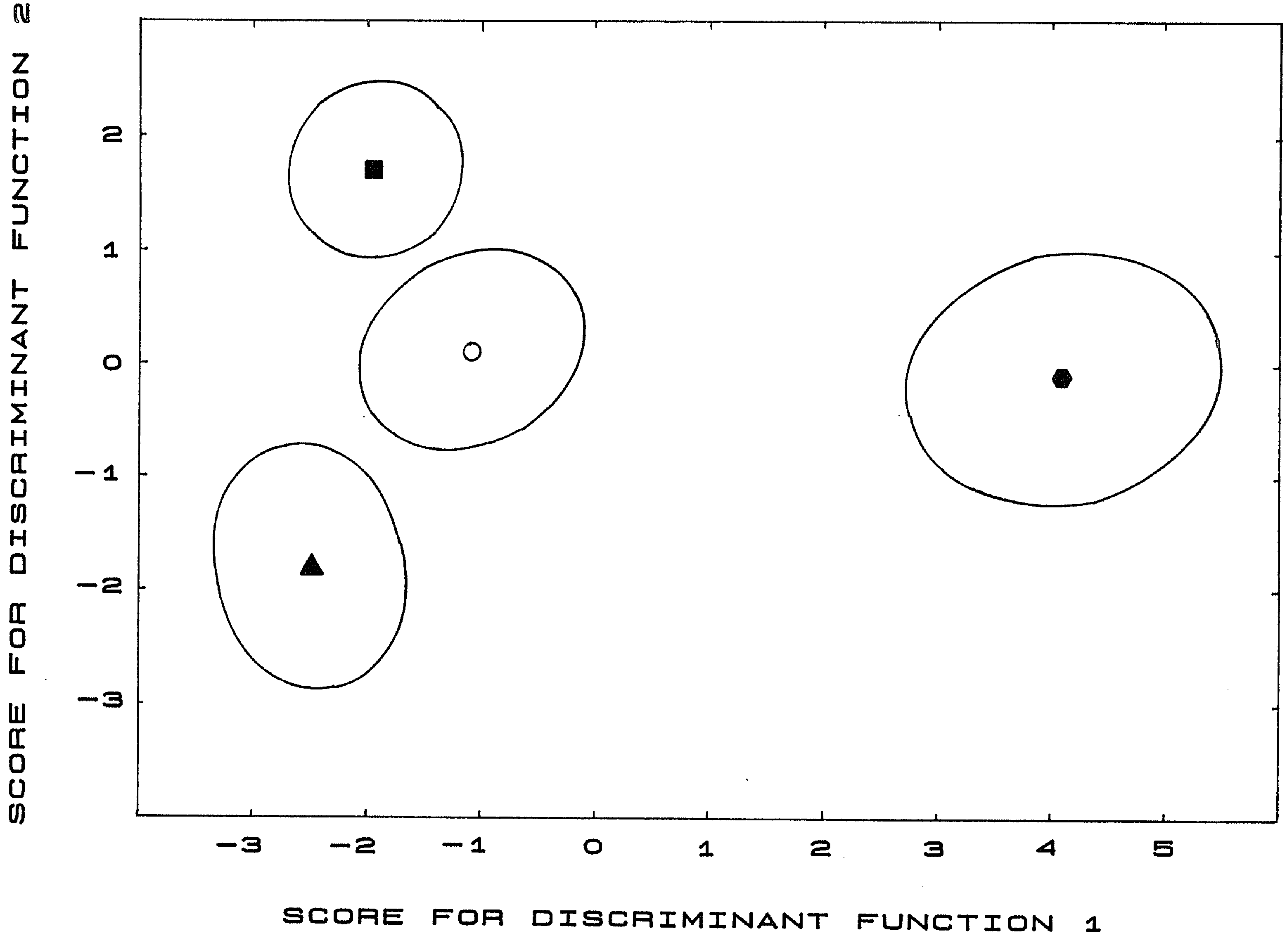
Experiment 1

Discriminant Function	% Variation Explained	STANDARDIZED COEFFICIENTS Pistillate Florets per Plant	Stem Weight per Tiller	Seed Weight	Days to Pistillate Floret Opening
1	84.1	0.964	-0.464	-0.417	0.411
2	14.7	0.230	0.872	0.753	0.447

Experiment 2

Discriminant Function	% Variation Explained	STANDARDIZED COEFFICIENTS Seed Yield	Pistillate Florets per Tiller	Stem Weight per Tiller	Tillers	Days to Pistillate Floret Opening
1	53.8	-1.224	0.881	0.845	0.691	0.403
2	38.6	-0.493	-0.318	0.101	1.136	0.486

FIG. 1.2. 90% probability ellipses of discriminant scores of wild rice populations grown in experiment 1. Symbols mark population centroids: ▲ , Velos Lake; ● , Charnock Lake; ■ , Whitedog Lake; ⬢ , Big Creek.


SCORE FOR DISCRIMINANT FUNCTION 2
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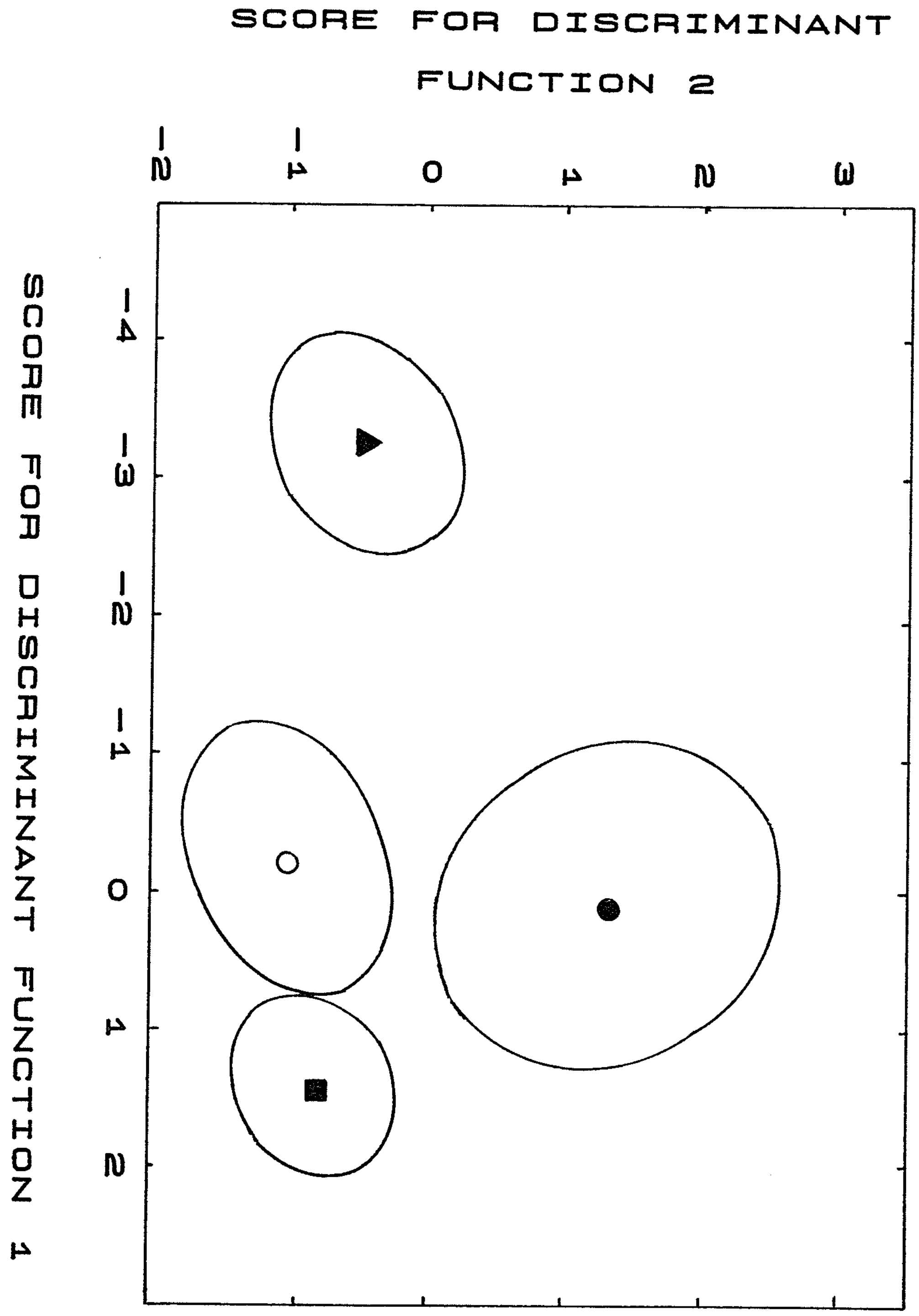
5
SCORE FOR DISCRIMINANT FUNCTION 1

FIG. 1.3. 90% probability ellipses of discriminant scores of wild rice populations grown in experiment 2. Symbols mark population centroids: ▲ , Velos Lake; ● , Dollar Lake; ○ , Charnock Lake; ■ , Whitedog Lake.


SCORE FOR DISCRIMINANT FUNCTION 2
-2
-1
0
1
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3
SCORE FOR DISCRIMINANT FUNCTION 1
-4
-3
-2
-1
0
1
2

1.2). Dollar Lake plants were distinguished from others by the second discriminant function, which accounted for 38.6% of the variance. Tiller number was by far the most important variable; flowering time and potential seed weight per plant made minor contributions.

Figure 1.4 graphically presents the relative mean values for all variables in each seed source examined; actual means and standard deviations are given in Table 1.3. The ANOVAs indicated significant ($p \leq 0.01$) differences among populations for all variables except seed length (both experiments), tiller number (experiment 1), and flowering time and seed weight (experiment 2). Seed source accounted for a minimum of 27% (root weight per tiller in (experiment 2) and a maximum of 82.8% (pistillate florets per plant in experiment 1) of the total variation of characters that differed among seed sources (Fig. 1.4). Seed source explained a larger fraction of the variance of most variables in experiment 1 than in experiment 2, primarily because of the sharp discontinuity between Big Creek plants and those from other populations. These individuals were very tall and late to flower, had large stems and wide leaves, and produced large numbers of small seeds. The distinctiveness of this Southern Ontario seed source was also apparent in the discriminant analysis (Fig. 1.2).

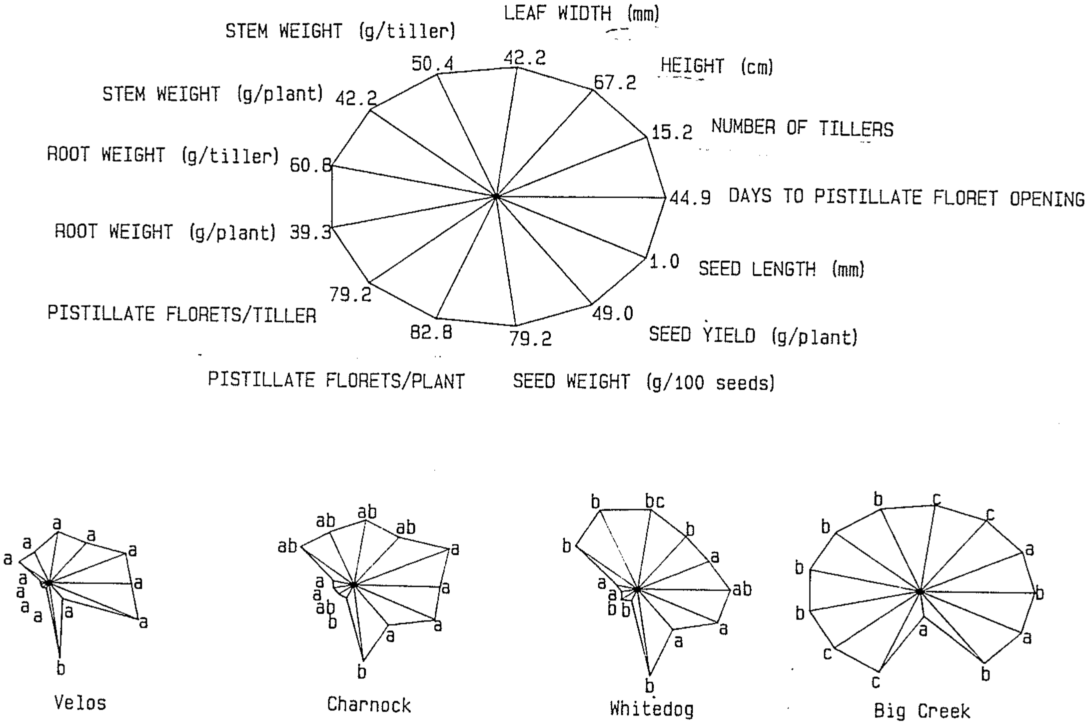
There were no significant population x soil interaction terms in any of the ANOVAs for either experiment, and the discriminant analyses and ANOVAs did not indicate any consistent effect of soil type on plant growth. For most traits textural differences between the soils tested explained less than 3% of the total variation. Consequently, this factor was omitted in the design of experiment 3.

TABLE 1.3. Mean values (± SD) for characteristics of wild rice plants from five populations in two experiments, and % variance explained by population in a two-way ANOVA. Populations followed by the same letter are not significantly different ($p \geq 0.01$) as determined by a modified LSD test

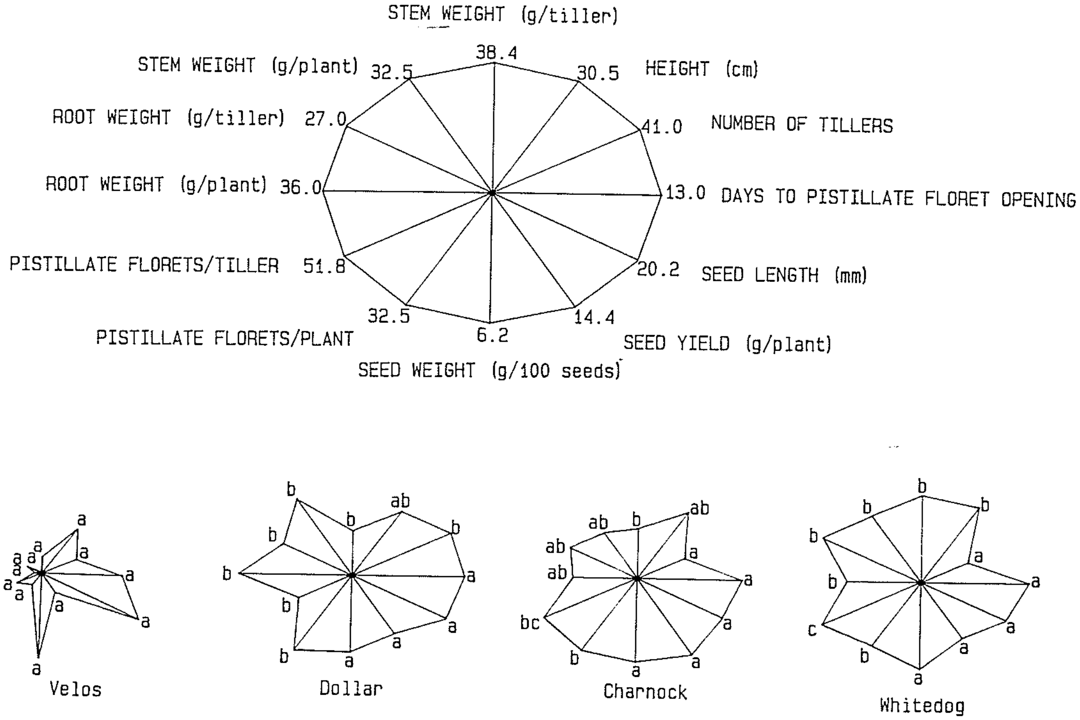
Characteristic	Experiment	Population					% Variance Explained By Population
		Velos	Dollar	Charnock	Whitedog	Big Creek	
Days to Pistillate Floret Opening	1	72.6 ± 14.5a	---	76.9 ± 12.4a	83.0 ± 10.5ab	100.7 ± 13.6b	44.9
	2	39.0 ± 5.5a	55.3 + 14.8a	51.6 ± 10.7a	52.3 ± 12.2a	---	13.0
Tillers	1	7.1 ± 3.0a	---	8.9 ± 2.6a	6.7 ± 1.8a	9.4 ± 3.3a	15.2
	2	16.2 ± 15.8a	47.0 + 19.9b	22.6 ± 14.6a	22.1 ± 5.9a	---	41.0
Height (cm)	1	106.7 ± 21.2a	---	128.3 ± 21.4ab	140.5 ± 19.5b	188.0 ± 26.8c	67.2
	2	80.4 ± 13.4a	114.2 + 22.9ab	118.6 ± 28.3ab	133.3 ± 16.5b	---	30.5
Leaf Width (mm)	1	6.4 ± 0.8a	---	8.1 ± 0.6ab	9.9 ± 1.3bc	10.7 ± 3.2c	42.2
Stem Weight							
(g/Tiller)	1	1.07 ± 0.48a	---	1.81 ± 0.65ab	2.73 ± 0.95b	2.83 ± 0.94b	50.4
	2	0.38 ± 0.14a	1.00 ± 0.38b	1.12 ± 0.61b	1.96 ± 0.95b	---	38.4
(g/Plant)	1	8.67 ± 5.52a	---	15.52 ± 5.55ab	17.96 ± 7.32b	24.34 ± 6.44b	42.2
	2	4.68 ± 3.75a	49.88 ± 29.95b	29.81 ± 27.78ab	43.57 ± 24.59b	---	32.5
Root Weight							
(g/Tiller)	1	0.28 ± 0.16a	---	0.66 ± 0.42a	0.68 ± 0.48a	3.44 ± 1.90b	60.8
	2	0.10 ± 0.06a	0.44 ± 0.29b	0.43 ± 0.41ab	0.62 ± 0.36b	---	27.0
(g/Plant)	1	2.30 ± 1.70a	---	5.55 ± 3.31a	4.52 ± 3.39a	30.66 ± 17.16b	39.3
	2	1.30 ± 1.70a	19.99 ± 15.63b	11.37 ± 11.91ab	12.97 ± 7.42b	---	36.0
Pistillate Florets							
per Tiller	1	14.1 ± 3.2a	---	30.3 ± 14.3ab	33.9 ± 12.5b	176.6 ± 82.8c	79.2
	2	49.4 ± 2.8a	20.5 ± 6.3b	36.1 ± 21.7bc	38.2 ± 14.2c	---	51.8
per Plant	1	98.3 ± 57.7a	---	253.6 ± 109.0b	217.1 ± 84.3b	1497.7 ± 592.6c	82.8
	2	142.2 ± 133.7a	951.3 ± 440.9b	918.7 ± 765.9b	806.8 ± 275.7b	---	32.5
Seed Weight (g/100 seeds)	1	4.80 ± 0.91b	---	4.90 ± 1.10b	5.55 ± 0.78b	1.59 ± 0.75a	79.2
	2	2.60 ± 0.55a	2.36 ± 0.53a	2.57 ± 0.57a	2.67 ± 0.59a	---	6.2
Seed Yield (g/Plant)	1	4.64 ± 2.85a	---	11.92 ± 4.49a	12.06 ± 5.24a	21.62 ± 9.81b	49.0
	2	7.69 ± 3.20a	23.76 ± 8.77a	31.06 ± 16.97a	22.77 ± 8.00a	---	14.4
Seed Length (mm)	1	16.1 ± 1.0a	---	14.8 ± 2.0a	14.6 ± 1.9a	18.1 ± 5.8	1.0
	2	13.2 ± 1.5a	12.8 ± 1.2	11.6 ± 1.7a	11.4 ± 1.5a	---	20.2
N	1	10	---	12	11	15	
	2	5	19	14	12	---	

FIG. 1.4. Characteristics of wild rice plants grown from seed from five populations in two experiments, and % variance in each characteristic explained by population in a two-way ANOVA. Ray length is proportional to the relative magnitude of the population mean for a given variable. Populations with the same letter on corresponding rays were not significantly different ($p \geq 0.01$) in that experiment for that variable in a modified LSD test. The sample diagram presents ray designations and % variance explained by population in experiment 1 (above) or 2 (below)

EXPERIMENT 1



EXPERIMENT 2



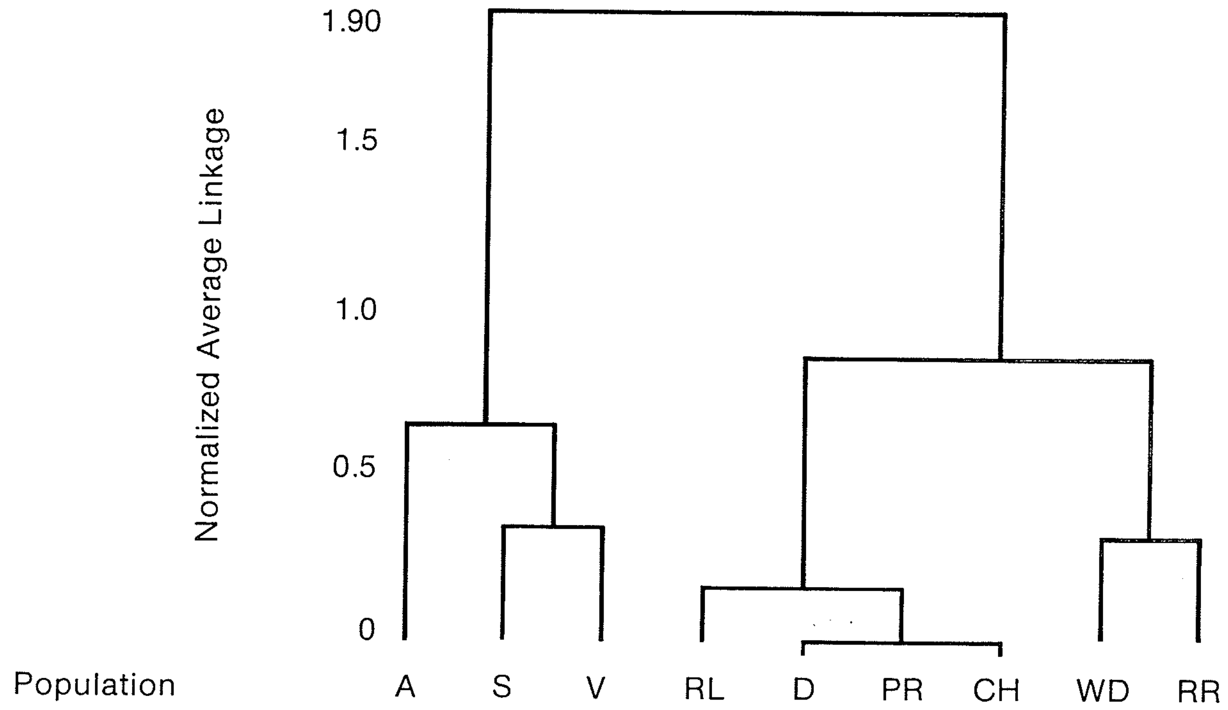
1.3.2. Experiment 3

The results of the first two experiments suggested that climate may be a major factor influencing differentiation in morphology and phenology of wild rice populations. For the four indigenous seed sources represented, increasing severity of climate from Big Creek through Whitedog and Dollar Lakes to Velos Lake appears to be associated with a reduction in development time and in vegetative and reproductive vigour (Tables 1.1 and 1.3; Fig. 1.4). To test the generality of this apparent relationship, analyses of data from the third experiment were carried out using individual seed sources and seed sources grouped by climatic similarity (Figure 1.1) as factors.

A dendrogram summarizing the results of the cluster analysis is presented in Figure 1.5. Four "climate groups" of populations accounted for more than 95% of the total climatic variation (R^2=0.983). The average linkage increased sharply with fewer than four clusters. Of the four groups, 'Nakina' (Arm Lake) has the most severe climate, followed by 'Pickle' (Velos Lake, Saskatchewan), and 'Ignace' (Dollar Lake, Red Lake, Press Lake, and Beaveroo Lake). The 'Kenora' group (Whitedog Lake, Rat River Bay) has the most moderate climate.

Discriminant analysis successfully distinguished the plants in different climate groups from one another. The first two discriminant functions, described in Table 1.4, explained 94.5% of the total variation. Function 1 accounted for 75.7% of the variation and primarily reflected seed weight, seed length, and stem weight per tiller. It separated the Pickle group, with low stem weights and seeds that have a high ratio of weight to length, from the Nakina and Kenora groups (Table 1.5; Figure 1.6). The seed sources in the Ignace group were intermediate, but more similar to plants from the Pickle group than to plants from the Nakina and Kenora groups. Seed length, seed weight, and tiller number were the main discriminating

FIG. 1.5. Hierarchical clustering of wild rice populations represented in the third experiment based on climatic similarity, and mean values of parameters for derived climate groups. Populations: V, Velos Lake; A, Arm Lake; S, Mercer River, Saskatchewan; RL, Rice Lake; D, Dollar Lake; PR, Press Lake; CH, Charnock Lake (=Beaveroo Lake); WD, Whitedog Lake; RR, Rat River Bay.

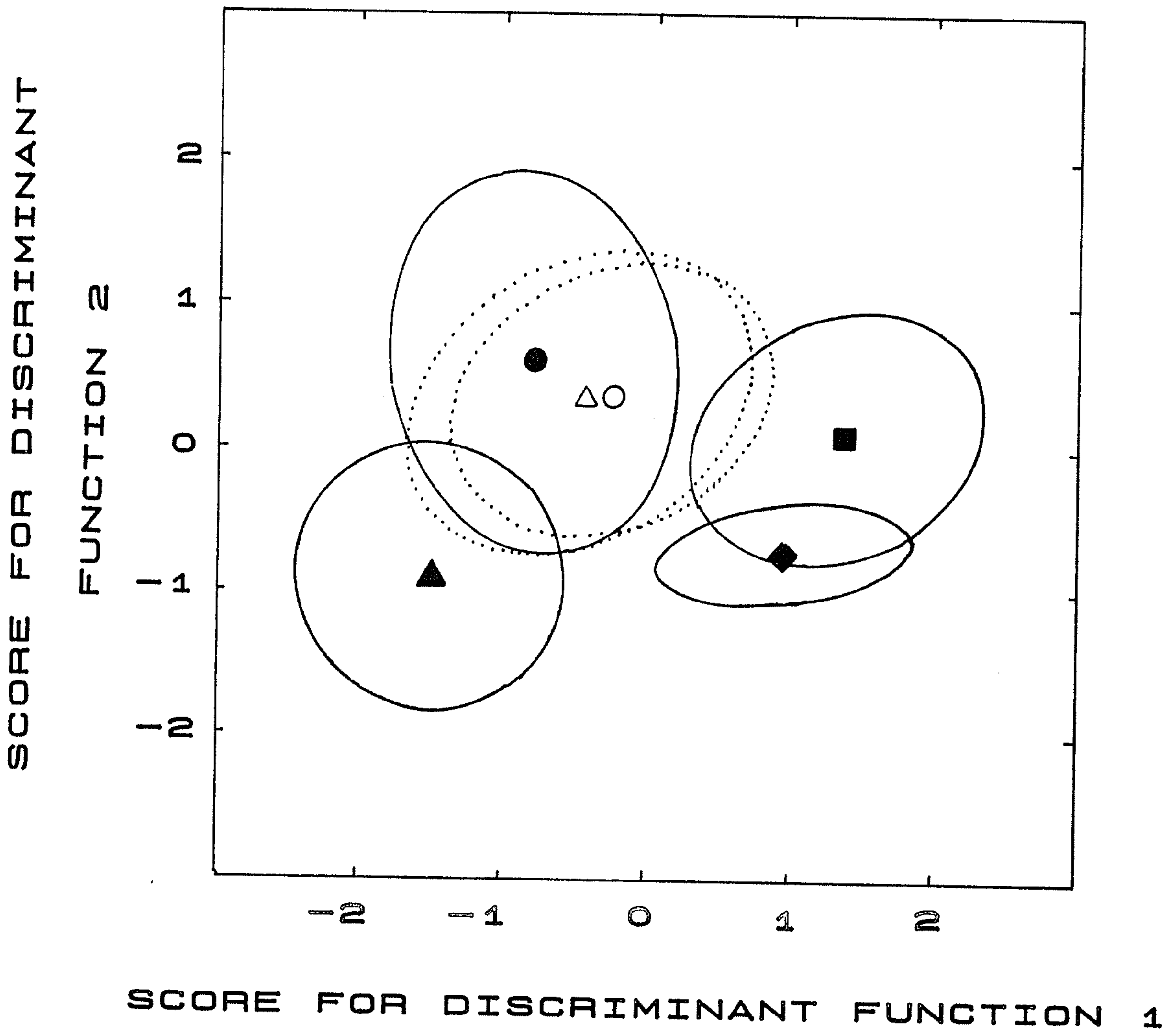


Climate Group	NAKINA	PICKLE	IGNACE	KENORA
Annual Growing• Degree • Days (5 °C)	1166.0	1269.4	1503.0	1649.3
Average Date of First Fall Frost (Year•Day)	241	252	262	261
Probability of Frost before Sept.1 (%)	50	25	4	12.5
Maximum Daylength (minutes)	980	1010	975	970

TABLE 1.4. Discriminant analysis of indigenous wild rice populations grouped by climatic similarity

Discriminant Function	% Variation Explained	STANDARDIZED COEFFICIENTS			
		Seed Weight	Seed Length	Stem Weight per Tiller	Tillers
1	75.71	-1.309	1.245	0.919	-0.003
2	18.75	0.991	-1.662	0.239	0.903

FIG. 1.6. 90% probability ellipses of discriminant scores of wild rice climate groups and introduced populations in experiment 3. Symbols mark group centroids: ▲ , Pickle group; ● , Ignace group; ■ , Kenora group; ◆ , Nakina group; ○ , Beaveroo Lake; △ , Saskatchewan.


SCORE FOR DISCRIMINANT FUNCTION 2
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2
SCORE FOR DISCRIMINANT FUNCTION 1

variables in the second function, which differentiated progeny of Pickle and Nakina plants at one extreme from the Ignace group at the other. Plants from the Ignace seed sources had relatively short, heavy seeds and produced numerous tillers. The intermediate (Kenora) group more closely resembled the Ignace group than it did either the Pickle or the Nakina groups in these respects.

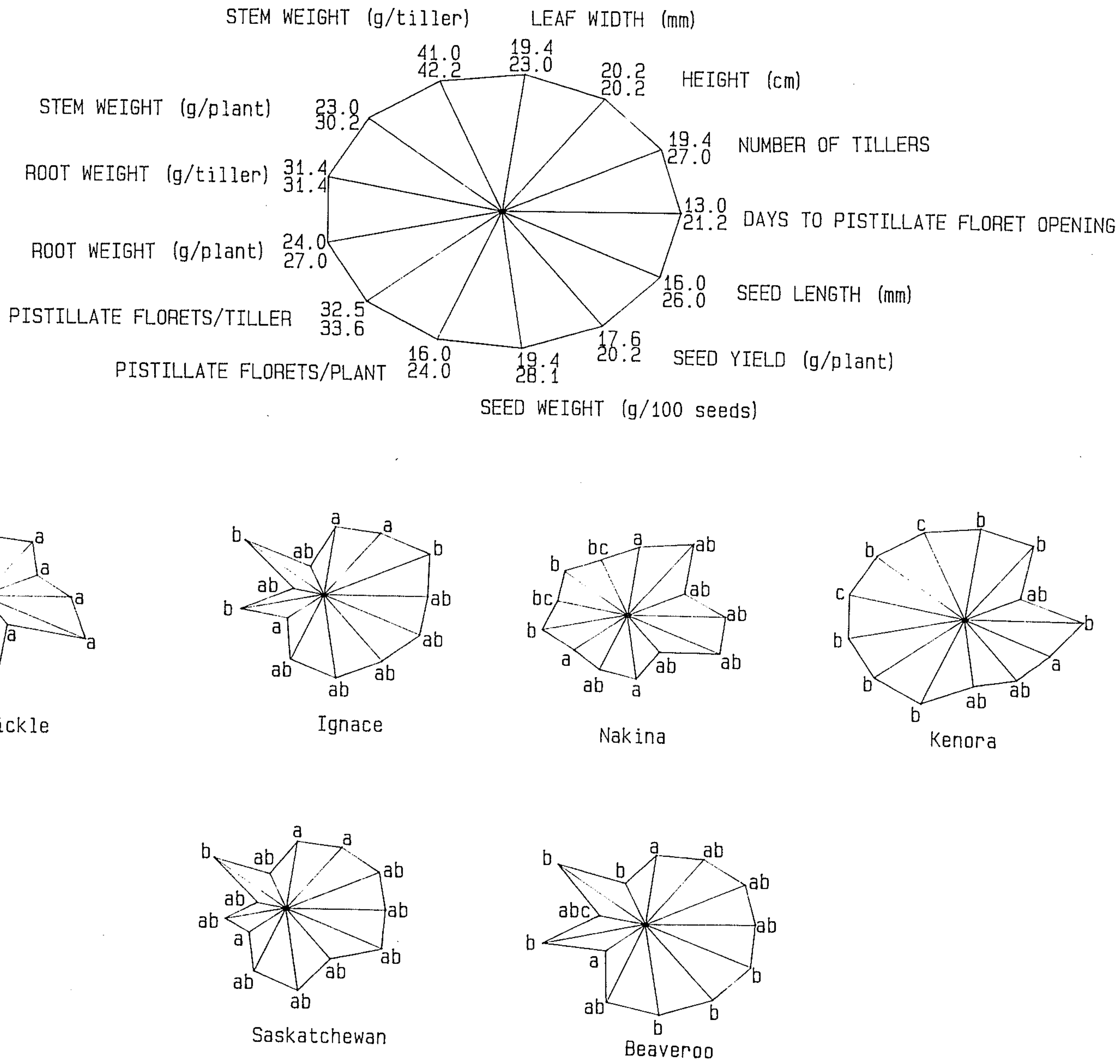
The classification phase of the discriminant analysis placed 66.0% of plants from indigenous populations into the correct climate group. Progenies of the Beaveroo Lake and Saskatchewan populations, which were introduced from a climate similar to the Kenora group (see Appendix 1), were not included in the initial phase of the analysis that defined the discriminant functions, but they were included in the classification phase. Their intermediacy is indicated by the overlap of their probability ellipses with those of the Pickle, Ignace, and Kenora groups in Fig. 1.6. Of the Beaveroo Lake progeny, 44% were placed in the Ignace group, and a further 25% were classified with the Kenora group. The remaining 31% were grouped with Pickle (19%) or Nakina (12%) plants. Plants from Saskatchewan seed were more heterogeneous: as with Beaveroo plants, the majority (59%) were most similar to plants from either the Ignace (35%) or Kenora (24%) groups, but a larger proportion of individuals were grouped with Pickle (24%) or Nakina (17%) plants.

There were significant ($p \leq 0.01$) differences among climate groups for all characters examined. Climate group accounted for a minimum of 13.0% (flowering time) and a maximum of 41.0% (stem weight per tiller) of the total variation in the data set. Fig. 1.7 indicates the relative magnitude of the means for each climate group for all variables; actual means and standard deviations for climate groups and populations are shown in Table 1.5. The Pickle and Kenora groups were at opposite extremes for most plant characteristics; plants from Pickle seed flowered early and were small and low-yielding, while Kenora plants were late to mature but

TABLE 1.5. Mean values (± SD) for characteristics of wild rice progeny from 2 introduced populations and 7 indigenous populations in 4 climatic regions. Region or introduced population means with same letter suffix are not significantly different ($p \leq 0.01$) as determined by a modified LSD test. V, Velos Lake; A, Arm Lake; S, Mercer River, Sask.; D, Dollar Lake; PR, Press Lake; RL, Rice Lake; B, Beaveroo Lake; WD, Whitedog Lake; RR, Rat River Bay.

	Population or Group										
	V	A	S	D	PR	RL	Ignace	B	WD	RR	Kenora
	Pickle	Nakina									
Days to Pistillate Floret Opening	45.8±11.5a	51.2±8.5ab	51.9±8.2ab	51.7±14.5	60.9±12.7	49.8±8.2	54.2±11.4ab	57.5±10.7ab	53.3±18.2	70.4±15.6	62.2±15.2b
Tillers per Plant	14.2±7.1a	16.1±5.1ab	26.4±17.6ab	32.6±14.3	37.4±15.6	21.2±13.7	30.1±17.1b	28.4±15.6ab	16.6±11.3	14.8±4.3	15.8±9.1ab
Height (cm)	113±35a	150±20ab	127±18a	129±22	130±28	135±38	130±30a	134±28ab	155±21	158±30	156±24b
Leaf Width (mm)	8.1±2.6a	9.2±1.7a	9.0±2.4a	7.8±1.3	10.2±1.7	10.5±4.0	9.2±2.7a	9.3±2.2a	11.9±3.4	13.2±3.1	12.3±3.2b
Stem Weight (g/tiller)	0.73±0.70a	2.16±0.94bc	1.34±1.04ab	1.10±0.46	1.43±0.50	1.47±0.85	1.21±0.74ab	1.61±0.65b	3.61±1.67	2.94±1.34	3.38±1.54c
(g/plant)	15.6±15.1a	31.1±6.9b	35.5±15.4b	37.5±22.2	53.4±27.6	30.7±20.1	38.8±24.5b	42.9±23.0b	45.9±10.8	39.9±12.4	43.8±11.3b
Root Weight (g/tiller)	0.13±0.16a	0.50±0.26bc	0.21±0.20ab	0.19±0.14	0.25±0.19	0.32±0.25	0.22±0.20ab	0.33±0.20abc	0.82±0.66	0.83±0.48	0.82±0.57c
(g/plant)	2.5±3.1a	7.2±2.3b	5.1±3.1ab	5.9±4.2	9.2±6.1	6.6±5.3	7.0±5.3b	8.7±5.8b	8.9±4.5	11.3±5.6	9.8±5.0b
Pistillate Florets per tiller	30.6±21.4a	66.1±36.9a	45.8±36.6a	29.5±9.2	54.7±20.6	58.2±54.4	44.6±36.3a	49.4±27.1a	122.2±69.0	94.4±36.0	111.8±57.9b
per plant	466±359a	940±344ab	1078±785ab	937±508	1992±857	1263±922	1116±918ab	1334±798ab	1543±556	1320±397	1462±516b
Seed Weight (g/100)	2.92±0.53b	2.06±0.39a	2.65±0.79ab	3.12±0.85	1.99±0.85	2.77±0.55	2.69±0.86ab	2.93±0.81b	2.13±0.46	2.18±0.47	2.15±0.46ab
(g/plant)	14.5±11.6a	18.6±4.7ab	25.5±19.4ab	28.5±13.5	40.1±25.3	33.9±25.8	33.6±21.6ab	38.5±30.1b	31.8±11.6	28.3±10.0	30.5±11.0ab
Seed Length (mm)	12.3±1.5b	11.0±1.0ab	11.4±1.9ab	13.2±4.8	10.0±2.0	10.7±1.4	11.4±1.9ab	12.5±2.3b	10.4±1.4	10.0±1.3	10.2±1.3a

FIG. 1.7. Characteristics of wild rice plants grown from seed from two introduced populations and from indigenous populations in four climatic regions, and % variance in each characteristic explained by climate group or population in a two-way ANOVA. Ray length is proportional to the relative magnitude of the mean for the population or group for a given variable. Groups or populations with the same letter on corresponding rays were not significantly different ($p \geq 0.01$) for that variable in a modified LSD test. The sample diagram presents ray designations and % variance explained by grouped (above) or ungrouped (below) populations


STEM WEIGHT (g/tiller)
41.0
42.2
LEAF WIDTH (mm)
19.4
23.0
20.2
20.2
HEIGHT (cm)
STEM WEIGHT (g/plant)
23.0
30.2
19.4
27.0
NUMBER OF TILLERS
ROOT WEIGHT (g/tiller)
31.4
31.4
13.0
21.2
DAYS TO PISTILLATE FLORET OPENING
ROOT WEIGHT (g/plant)
24.0
27.0
16.0
26.0
SEED LENGTH (mm)
PISTILLATE FLORETS/TILLER
32.5
33.6
17.6
20.2
SEED YIELD (g/plant)
PISTILLATE FLORETS/PLANT
16.0
24.0
19.4
28.1
SEED WEIGHT (g/100 seeds)
a
a
a a
a
a
a a
a
a a
a
a
Pickle
a
a
b
ab
b
ab
ab
b
a
ab
ab
ab
ab
Ignace
a
ab
bc
b
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bc
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Nakina
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b
a
b
ab
ab
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Kenora
a
a
b
ab
ab
ab
ab
ab
a
ab
ab
ab
ab
Saskatchewan
a
b
ab
b
ab
abc
ab
b
a
b
b
ab
b
Beaveroo

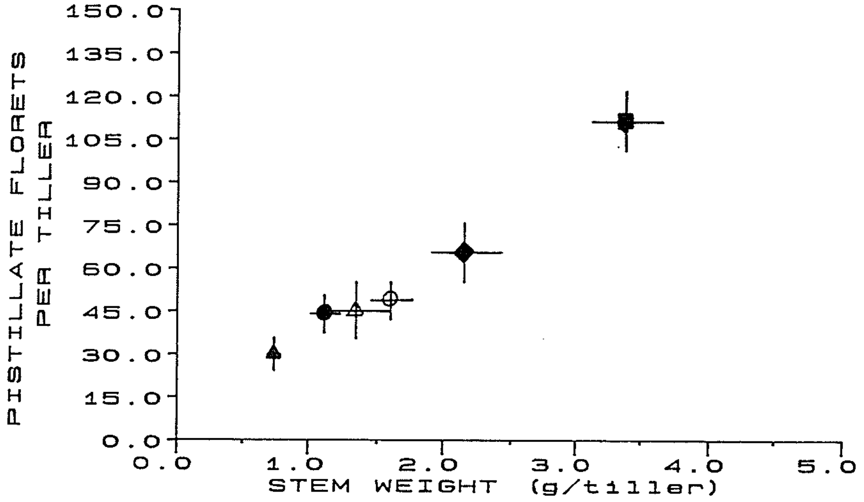
vegetatively and reproductively vigorous. Wild rice plants from the Ignace group, Saskatchewan, Beaveroo Lake, and Nakina formed a continuum between these extremes. Figure 1.8 illustrates the intercorrelations of some of the plant characters and the relative ranks of the population groups; a correlation matrix is shown in Appendix 2.

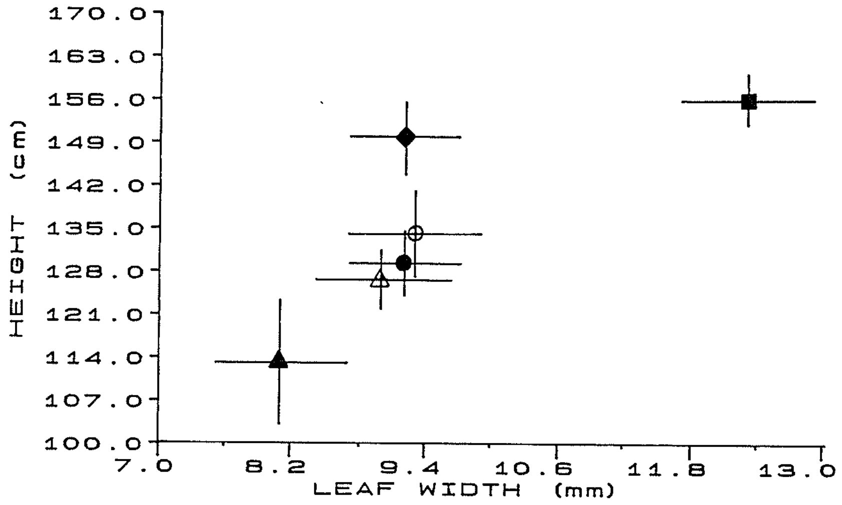
Tiller number and seed variables departed from the typical pattern of continuous variation between extremes demarcated by the Pickle and Kenora groups. These variables displayed striking discontinuities and hence emerged as important parameters in the discriminant analysis. Progeny of the Ignace, Beaveroo Lake, and Saskatchewan populations tillered much more profusely than those from Kenora, Pickle, or Nakina. Plants grown from Beaveroo Lake seed produced long heavy caryopses, while seeds from Nakina had low weights. The high tiller production and large seed size of plants from the Ignace and Beaveroo Lake seed sources outweighed the relatively low floret production per tiller to place them at the high extreme for plant seed yield.

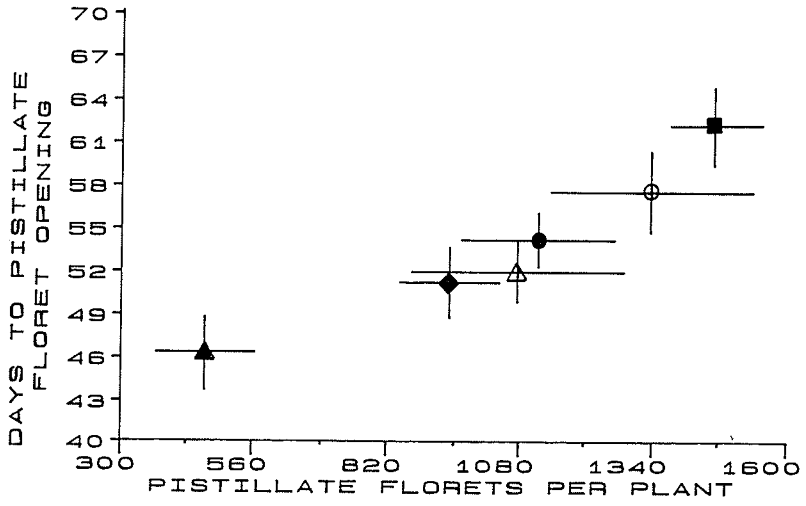
For all variables except seed length and weight, the progeny of the introduced Beaveroo Lake and Saskatchewan populations were intermediate between Kenora plants and those indigenous to the Ignace and Pickle climates that they now inhabit. Although plants from the 2 populations were not significantly different from each other for any variable, those from Saskatchewan were always closer to the Pickle extreme of the continuum than those from Beaveroo Lake (Table 1.5; Figures 1.7 and 1.8).

Little explanatory information was lost in grouping the wild rice populations by climatic similarity. Discriminant analysis was capable of differentiating among ungrouped populations, but required a much more complex set of equations involving ten variables in six functions. The accuracy of classification of wild rice plants was

FIG. 1.8. Intercorrelation of means (±SE) of characteristics of wild rice plants from different climate groups (▲ , Pickle; ● , Ignace; ◆ , Nakina; ■ , Kenora) and transplanted populations (△ , Saskatchewan; ○ , Beaveroo L.). [A]. Tiller floret production vs stem weight; [B]. Heights vs leaf widths; [C]. Flowering time vs plant floret production.


[A] TILLER FLORET PRODUCTION VS STEM WEIGHT


[B] HEIGHT VS LEAF WIDTH


[C] FLOWERING TIME VS PLANT FLORET PRODUCTION

70.1%, only a 4% improvement over the results obtained using grouped populations. When ANOVAs were performed using seed sources grouped by climatic similarity as factors, the fraction of explained variance decreased by an average of only 4.7% compared to the variance explained using ungrouped seed sources. The decrease was greater than 8% for three variables: flowering time, seed weight, and seed length (Fig. 1.7). These parameters were the only ones for which there were significant ($p \leq 0.01$) differences among seed sources within climate groups. Plants from Rat River Bay are later to flower than those from Whitedog Lake; they required an average of 70.5 and 57.0 days respectively for pistillate florets to become receptive. Dollar Lake seeds, with a mean length of 13.9 mm and a mean hundred-seed weight of 3.12 g, were significantly larger and heavier than seeds from Press Lake plants, which were 10.0 mm long on average with a hundred-seed weight of 1.99 g. Red Lake seeds bridged the gap between the two, with a mean length of 10.7 mm and a weight of 2.77 g per 100.

There were significant ($p \leq 0.01$) differences among the two locations (greenhouses) for all variables except tiller number and shoot weight, root weight, and seed yield per plant. Table 1.6 presents overall means and standard deviations for all variables at the 2 locations, and Table 1.7 provides statistics for each population and group at the 2 locations only for those variables having a significant location effect in the ANOVA. Plants at location 1 flowered earlier, were shorter, had smaller stems with narrower leaves, and produced fewer but larger, heavier seeds per tiller than plants grown at location 2. The location factor accounted for a smaller proportion of the total variance for most variables than did climate group: the minimum fraction explained was 0.1% (seed and stem weights per plant), and the maximum was 29.2% (seed length).

TABLE 1.6. Mean values (± SD) for characteristics of wild rice plants grown at two locations and % variance explained by location in a two-way ANOVA. Significant differences between locations indicated by * ($p \leq 0.01$)

	Location		
Characteristic	1	2	% Variation Explained
Days to Pistillate Floret Opening	48.3 ± 10.4	60.8 ± 11.4*	23.0
Tillers	26.2 ± 14.4	19.1 ± 14.3	3.6
Height (cm)	127.6 ± 24.0	147.3 ± 31.3*	9.0
Leaf Width (mm)	8.3 ± 1.7	11.1 ± 3.2*	22.1
Stem Weight			
(g/Tiller)	1.47 ± 0.84	2.11 ± 1.69*	6.2
(g/Plant)	35.91 ± 20.81	38.02 ± 19.09	0.1
Root Weight			
(g/Tiller)	0.24 ± 0.18	0.52 ± 0.51*	13.0
(g/Plant)	5.67 ± 3.92	8.86 ± 5.56	2.2
Pistillate Florets			
per Tiller	41.8 ± 26.4	85.3 ± 58.5*	10.9
per Plant	1043.2 ± 719.2	1333.4 ± 713.4	0.4
Seed Weight (g/100 seeds)	2.91 ± 0.69	2.19 ± 0.60*	21.2
Seed Yield (g/Plant)	37.93 ± 21.96	28.27 ± 15.03	0.1
Seed Length (mm)	12.4 ± 1.8	10.3 ± 1.4	29.2

TABLE 1.7. Mean values (± SD) for selected characteristics of wild rice progeny from nine populations grown in 2 locations. Statistics for groups of indigenous populations in the Ignace and Kenora climatic regions are also shown. Statistics are given only for those variables with a significant location effect (see Table 1.6). G1, Greenhouse 1; G2, Greenhouse 2; V, Velos Lake; A, Arm Lake; S, Mercer River, Sask.; D, Dollar Lake; PR, Press Lake; RL, Rice Lake; B, Beaveroo Lake; WD, Whitedog Lake; RR, Rat River Bay

<table>
<tr><th></th><th></th><th colspan="9">Population or Group</th></tr>
<tr><th></th><th></th><th>V</th><th>A</th><th>S</th><th>D</th><th>PR</th><th>RL</th><th>B</th><th>WD</th><th>RR</th></tr>
<tr><th></th><th></th><th></th><th></th><th></th><th colspan="3">Ignace</th><th></th><th colspan="2">Kenora</th></tr>
<tr><td>N</td><td>G1</td><td>7</td><td>5</td><td>9</td><td>7</td><td>4</td><td>5</td><td>7</td><td>9</td><td>4</td></tr>
<tr><td></td><td>G2</td><td>5</td><td>8</td><td>4</td><td>4</td><td>4</td><td>6</td><td>8</td><td>10</td><td>7</td></tr>
<tr><td>Days to Pistillate Floret Opening</td><td>G1</td><td>44.0±14.9</td><td>46.8±5.5</td><td>49.8±9.8</td><td>43.3±7.8</td><td>59.0±18.9</td><td>45.6±8.0</td><td>49.0±8.8</td><td>46.6±7.9</td><td>58.0±3.5</td></tr>
<tr><td></td><td>G2</td><td>48.4±3.9</td><td>53.4±8.9</td><td>55.0±6.4</td><td>66.5±11.0</td><td>62.8±3.0</td><td>53.3±7.2</td><td>64.9±5.1</td><td>59.4±22.9</td><td>77.6±15.4</td></tr>
<tr><td></td><td>G1</td><td></td><td></td><td></td><td></td><td>47.9±12.6</td><td></td><td></td><td colspan="2">50.1±8.7</td></tr>
<tr><td></td><td>G2</td><td></td><td></td><td></td><td></td><td>59.8±9.3</td><td></td><td></td><td colspan="2">66.9±21.6</td></tr>
<tr><td>Height (cm)</td><td>G1</td><td>89.0±16.4</td><td>145.4±21.5</td><td>132.8±12.2</td><td>125.7±19.6</td><td>137.0±32.8</td><td>128.6±16.2</td><td>127.6±22.4</td><td>138.3±13.4</td><td>134.0±32.1</td></tr>
<tr><td></td><td>G2</td><td>112.2±64.4</td><td>155.9±20.5</td><td>121.8±24.9</td><td>135.2±28.2</td><td>122.2±24.7</td><td>140.8±51.6</td><td>149.0±15.7</td><td>169.7±13.8</td><td>171.7±20.1</td></tr>
<tr><td></td><td>G1</td><td></td><td></td><td></td><td></td><td>129.4±21.5</td><td></td><td></td><td colspan="2">137.0±19.5</td></tr>
<tr><td></td><td>G2</td><td></td><td></td><td></td><td></td><td>133.9±37.6</td><td></td><td></td><td colspan="2">170.5±16.1</td></tr>
<tr><td>Leaf Width (mm)</td><td>G1</td><td>6.7±1.0</td><td>8.2±1.1</td><td>8.4±2.4</td><td>7.3±1.4</td><td>9.1±1.2</td><td>9.7±1.0</td><td>7.8±1.2</td><td>9.1±1.4</td><td>10.0±1.8</td></tr>
<tr><td></td><td>G2</td><td>9.5±3.2</td><td>10.2±1.6</td><td>8.7±1.0</td><td>8.6±0.9</td><td>11.2±1.5</td><td>11.2±5.5</td><td>11.0±1.6</td><td>14.4±2.6</td><td>15.0±2.0</td></tr>
<tr><td></td><td>G1</td><td></td><td></td><td></td><td></td><td>8.5±1.6</td><td></td><td></td><td colspan="2">9.4±1.5</td></tr>
<tr><td></td><td>G2</td><td></td><td></td><td></td><td></td><td>10.5±3.7</td><td></td><td></td><td colspan="2">14.6±2.3</td></tr>
<tr><td>Stem Weight (g/tiller)</td><td>G1</td><td>0.49±0.14</td><td>1.98±0.89</td><td>1.97±0.89</td><td>1.06±0.46</td><td>1.42±0.55</td><td>1.26±0.43</td><td>1.24±0.55</td><td>2.14±0.83</td><td>1.86±0.76</td></tr>
<tr><td></td><td>G2</td><td>1.21±0.62</td><td>2.29±0.94</td><td>1.31±0.55</td><td>1.16±0.53</td><td>1.45±0.50</td><td>1.64±1.11</td><td>2.05±0.44</td><td>4.92±0.93</td><td>3.55±1.23</td></tr>
<tr><td></td><td>G1</td><td></td><td></td><td></td><td></td><td>1.21±0.47</td><td></td><td></td><td colspan="2">2.06±0.79</td></tr>
<tr><td></td><td>G2</td><td></td><td></td><td></td><td></td><td>1.45±0.80</td><td></td><td></td><td colspan="2">4.36±1.24</td></tr>
<tr><td>Root Weight (g/tiller)</td><td>G1</td><td>0.06±0.02</td><td>0.40±0.22</td><td>0.31±0.21</td><td>0.17±0.16</td><td>0.19±0.12</td><td>0.21±0.12</td><td>0.22±0.10</td><td>0.25±0.09</td><td>0.48±0.27</td></tr>
<tr><td></td><td>G2</td><td>0.27±0.19</td><td>0.56±0.26</td><td>0.19±0.13</td><td>0.23±0.10</td><td>0.31±0.25</td><td>0.42±0.30</td><td>0.45±0.22</td><td>1.34±0.48</td><td>1.03±0.46</td></tr>
<tr><td></td><td>G1</td><td></td><td></td><td></td><td></td><td>0.19±0.13</td><td></td><td></td><td colspan="2">0.32±0.19</td></tr>
<tr><td></td><td>G2</td><td></td><td></td><td></td><td></td><td>0.30±0.24</td><td></td><td></td><td colspan="2">1.21±0.48</td></tr>
<tr><td>Pistillate Florets per Tiller</td><td>G1</td><td>18.8±4.4</td><td>45.1±16.4</td><td>45.8±43.9</td><td>26.4±10.0</td><td>47.0±20.5</td><td>44.2±7.1</td><td>31.2±16.0</td><td>59.7±25.0</td><td>72.0±17.2</td></tr>
<tr><td></td><td>G2</td><td>46.0±28.3</td><td>75.4±41.3</td><td>52.6±19.2</td><td>34.9±4.9</td><td>62.4±20.2</td><td>69.9±74.3</td><td>68.0±23.8</td><td>178.4±39.4</td><td>107.2±38.6</td></tr>
<tr><td></td><td>G1</td><td></td><td></td><td></td><td></td><td>37.1±15.3</td><td></td><td></td><td colspan="2">63.5±22.9</td></tr>
<tr><td></td><td>G2</td><td></td><td></td><td></td><td></td><td>57.8±49.6</td><td></td><td></td><td colspan="2">149.1±52.3</td></tr>
<tr><td>Seed Weight (g/100 seeds)</td><td>G1</td><td>3.10±0.43</td><td>2.08±0.21</td><td>3.00±0.66</td><td>3.59±0.62</td><td>2.64±0.69</td><td>2.79±0.40</td><td>3.62±0.65</td><td>2.51±0.32</td><td>2.33±0.28</td></tr>
<tr><td></td><td>G2</td><td>2.94±0.37</td><td>2.22±0.66</td><td>1.91±0.62</td><td>2.32±0.48</td><td>1.35±0.34</td><td>2.74±0.69</td><td>2.34±0.29</td><td>1.79±0.23</td><td>2.10±0.56</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td></td><td>3.10±0.70</td><td></td><td></td><td colspan="2">2.46±0.31</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td></td><td>2.22±0.79</td><td></td><td></td><td colspan="2">1.92±0.41</td></tr>
</table>

The relative growth performance of plants from the various seed sources in the two greenhouses was similar in most cases. Progeny of the Kenora group were more sensitive to location than others for many variables, and were more distinct from other groups at location 2 (Table 1.7). There was a significant ($p \leq 0.01\%$) climate group x location interaction term in the ANOVAs for plant height, leaf width, and stem and root weights per tiller. In all cases the interaction term was attributable to Saskatchewan plants, which had larger, taller tillers and wider leaves at location 1 in contrast to plants from all other populations. The location x population within climate group interaction term was not significant for any variable.

1.4. DISCUSSION

The results indicate that there is substantial genetic heterogeneity within wild rice populations. Standard deviations were large for most variables in most populations; the coefficient of variation (cv) was frequently as high as 0.5, and in some cases approached 1.0 (Tables 1.3 and 1.5). In Table 1.3, for example, the cv of tiller number in the Velos Lake population in experiment 2 was 15.8/16.2, or 0.975. In experiments 2 and 3 more than half of the total variance for almost all variables was "unexplained"; i.e., it was attributable to variation among plants within populations. The much higher proportion of total variance explained in experiment 1 was due to the presence of plants from the Big Creek population, which were very distinct and hence contributed a great deal of variation to the data set. These plants were the only representatives of *Z. aquatica* var. *aquatica*, all others were *Z. aquatica* var. *angustifolia* or *Z. aquatica* var. *interior*.

Such high levels of variability may be expected in a species with a life-history like that of *Zizania aquatica*. The plants are primarily outcrossing and are not known to reproduce asexually (Weir and Dale 1960) - both features that promote genetic heterozygosity and heterogeneity in populations (Grant 1975; Hamrick et al 1979; Loveless and Hamrick 1984). In addition, the natural habitat of wild rice tends to show marked spatial and temporal fluctuation (Moyle 1944; 1967; Lee and Stewart 1981; 1983; 1984; and see chapter 2), resulting in variation in selection pressure on a given wild rice population. Environmental heterogeneity has been shown to be correlated with high genetic variability in populations (Linhart 1974; Abbott 1976). Fluctuations in the environment from year to year together with the prolonged seed dormancy that may occur in wild rice (Moyle 1967; Halstead and Vicario 1969; Atkins 1986) also contribute to variability within stands: a population may comprise offspring of plants that were subjected to different selection pressures in different years.

In spite of high levels of variation within stands, genetic differentiation exists among wild rice populations. This is indicated by the ability of discriminant analysis to distinguish and correctly classify most wild rice plants by their population of origin (Figs. 1.2 and 1.3), and by consistent significant differences among populations revealed by the ANOVAs and modified LSD tests (Table 1.3; Fig. 1.4). There are two major ways that divergence may have occurred: 1) the reproductively isolated populations may have responded, through gradual microevolutionary adaptation, to different selection pressures, or 2) random genetic drift may have caused non-adaptive changes in these relatively small populations (Merrell 1981; Mayr 1982; 1983). While these experiments certainly do not rule out the second mechanism, they do provide some evidence for directed change, and implicate climate as a selective force.

The data from the first two experiments (Table 1.3; Figs. 1.2 to 1.4) suggest that the pattern of variation of wild rice populations in Ontario is correlated with a climatic gradient: increasing climatic severity is associated with a suite of intercorrelated phenological and morphometric characteristics; i.e. earlier flowering, smaller tillers, and the formation of fewer florets per tiller. Data from the third experiment, which included more populations, provides further evidence for clinal variation in response to climate (Table 1.5; Figs. 1.6 to 1.8): indigenous populations from similar climates are similar for all characteristics examined except seed morphology and flowering time, and with the exception of Arm Lake (Nakina climate group), they exhibit the typical clinal trends for all traits except tiller production. Intermediacy is observed in the populations that have been introduced into different climatic regimes, although, since the actual source population was not represented in this experiment, genetic divergence due to climatic influences cannot be inferred. This subject is treated further in chapter 4. The intercorrelations of pairs of plant characters shown in Fig. 1.8a and 1.8b do not necessarily indicate direct relationships with a causal connection to climate. Rather, it is suggested that selection pressures resulting in rapid development and early maturity with increasing restriction on the growing season are a major evolutionary force acting on this annual species. An overall reduction in vegetative and reproductive productivity commonly occurs as a consequence of developmental constraints imposed by accelerated maturation (Allard 1960), but is not necessarily directly adaptive (see Gould and Lewontin (1979) for a discourse on the perils of overenthusiastic adaptationist interpretation). Similar intercorrelation of height, tillering, flowering time, and seed length was observed within a single "domesticated" wild rice population by Foster and Rutger (1980). Increasing severity of climate due to increasing latitude or altitude is associated with precocious reproduction and/or reduced plant size in many species (Clausen et al. 1940; Jennings 1964; McNaughton 1975; Rehfeldt 1978; Hume and Cavers 1982).

There are some discrepancies between the observed patterns of variation and those to be expected if climate were the primary selective force influencing the evolution of wild rice populations. Table 1.1 shows that Arm Lake (Nakina) experiences earlier frosts and has fewer growing-degree-days than Velos Lake (Pickle), and yet plants from this seed source do not display the expected extremes in morphology and phenology. For all characteristics except flowering time, pistillate floret production per plant, and seed weight, plants from Nakina are intermediate between Kenora and Ignace individuals (Table 1.5; Figs. 1.6 to 1.8). Clearly, some factor other than climate has influenced the evolution of this population. The overlapping of continuous (clinal) and discontinuous (ecotypic) patterns of variation within species is common, as different selection pressures take precedence in different populations (Stebbins 1957; Jain and Bradshaw 1966; Antonovics 1971; McNaughton 1975; Grace and Wetzel 1981; Hume and Cavers 1982; Schwaegerle and Bazzaz 1987).

Tiller production is the only variable that shows no clinal trend; plants from Ignace populations appeared to have the highest potential for tillering, while those from regions with more extreme climates exhibited a lower capacity. This character, as shown in studies of field populations discussed in chapter 2, is strongly influenced by local environmental conditions. A tendency towards tillering in *Avena* is associated with environments in which competition, rather than stress conditions, limit growth (Marshall and Jain 1968). It may be that the potential for tiller production is adaptive in wild rice populations that are mainly subject to K-selection; ie. where density-dependent mortality frequently occurs (Gadgil and Solbrig 1972). Alternatively, it is possible that the increased tillering capacity in plants from Ignace populations is an adaptive feature that confers the potential for high reproductive output without the risk associated with delayed maturation. Production of more tillers is probably more costly in terms of the energy required per seed than is the production of fewer larger tillers with more seeds, as is common for progeny of Kenora populations. However, the benefits accruing from increased potential reproductive output may outweigh the costs of tillering in Ignace populations. The shattering phase begins early with the first tillers, ensuring the parent plant some representatives in the next generation, but the time over which seed matures is then extended either until maximum production is realized or until the growing season is curtailed by fall frost. It is logical that populations primarily from intermediate rather than extreme climatic regimes should adopt such a strategy. Under severe conditions with few growing-degree-days, the growing season is rarely likely to continue long enough for the reproductive potential of later tillers to be realized. At the other extreme, a very moderate climate poses little risk and therefore, as suggested previously, it is more efficient for plants to allocate energy to production of larger tillers with many seeds.

Aside from the exceptionally large seeds from Beaveroo Lake, there is a clinal pattern of increasing seed weight and length with increasing severity of climate (Fig. 1.7). Seed characters of plants from Beaveroo Lake appear to have been influenced by local conditions. As with extensive tillering, allocation of resources to the production of large seeds could confer a competitive advantage, particularly if density-dependent mortality is most important early in development (Gadgil and Solbrig 1972; Harper et al 1970; Harper 1977).

Since plants lack mobility to escape from adverse conditions, they require a flexibility of response to environmental changes. This flexibility is achieved on two levels: 1) on the population level, by genetic heterogeneity among individuals; and 2) at the level of the individual, by phenotypic plasticity. The ability of a single genotype to give rise to different phenotypes under different environmental conditions is an important adaptive strategy in many plant species, especially those like wild rice that are frequently exposed to unpredictable environmental fluctuations within a growing season (Lewontin 1957; Bradshaw 1965; 1974; Marshall and Jain 1968; Hickman 1975). The relative ranking of progeny from different populations and climate groups under varying experimental conditions was similar in this study (except for Saskatchewan plants, see above), and in experiment 3 location accounted for a minor proportion of total variation for most characters (Table 1.6). Nevertheless, the variability in growth that was observed among experiments and locations is of interest as it supports earlier reports of plastic responses of wild rice to temperature. Oelke et al. (1982) found that when wild rice was subjected to long (15 hour) daylengths, temperature had a pronounced effect on plant development. At a 22° C daytime temperature, plants flowered earlier, but were shorter and produced smaller tillers with fewer female florets than plants grown at 19° C. A similar pattern was observed for plants grown in the summer vs winter months (Experiment 2 vs Experiment 1; see Table 1.3) except that there was little effect on pistillate floret production. In Experiment 3, plants grown at the cooler location 2 flowered later and produced larger tillers with more florets as expected from Oelke's results. The effect was most pronounced for populations in the Kenora group, and the issue of differential plasticity is considered in more depth in chapter 3.

Plants at the two locations differed in the balance of yield components rather than in whole-plant productivity; the decrease in seed size and tiller production (the latter was not statistically significant) at location 2 offset the increase in individual tiller size and floret production (Table 1.6). Such compensation effects, resulting in an inverse relationship between the number of plant parts and their size, have been described in other species (Palmer 1952; Linhart 1974; Hamid and Grafius 1978), and have been shown to be adaptive in theoretical studies incorporating cybernetic analysis into demographic models (Caswell 1983).

The results of these experiments have several implications regarding the selection of wild rice source populations for commercial cultivation and for breeding. First, in spite of high levels of intra-population variability, wild rice populations in northwestern Ontario are genetically differentiated. It is therefore worthwhile to select among populations as well as among plants within populations for desired characteristics. Furthermore, many characters show clinal variation, so certain traits may be profitably sought in particular climatic areas. For example, if early flowering is desired, a population that has evolved in a severe climate will probably be a suitable seed source. Tillering capacity and seed size are not as readily predicted from the climatic milieu, so particular populations with optimal characteristics must be sought if the goal is to improve these yield components. The intercorrelation of growth characteristics in wild rice makes it unlikely that all desirable traits will be found in a single population; this is common (Allard 1960). However, populations do exist that have unusual combinations of characters, and these may be extremely useful to the grower or plant breeder. Arm Lake, which yielded progeny that matured rapidly and yet produced relatively many florets per tiller, is an example of such a population.

If climate exerts a strong selective pressure on wild rice populations, the stability of populations that are introduced to lakes in areas with different climatic conditions becomes a crucial issue. Evidence from the progeny of the two introduced seed sources considered in this study indicates that the properties of wild rice populations <u>may</u> change over relatively short periods of time, although this is not conclusively indicated since progeny from the actual source population were not included in this study. If rapid directional genetic changes <u>do</u> occur following introduction into a new environment, it may be necessary for growers to monitor introduced wild rice stands closely and upgrade them periodically through artificial selection or addition of new seed stocks. This question is further considered in chapter 4.

If the results of greenhouse evaluations of wild rice populations are to have practical applications, it must be demonstrated that the relative ranking of populations observed under "controlled" conditions are observed when the same populations are compared under the unmanaged natural conditions prevalent in lakes. Chapter 3 discusses an experiment addressing this subject.

These experiments have shown that wild rice populations in northwestern Ontario are genetically differentiated, and that much of the variation among populations is associated with climatic differences. The relative importance of climate and local environmental variables in explaining patterns of morphological variation in field populations of wild rice is the focus of the next chapter.

Chapter 2

RELATIVE CONTRIBUTIONS OF SOME PHYSICAL, EDAPHIC, AND BIOTIC ENVIRONMENTAL FACTORS TO *IN SITU* VARIATION WITHIN AND AMONG POPULATIONS

2.1. INTRODUCTION

Wild rice (*Zizania aquatica* L.) is in some regards quite specialized in its requirements for growth. The emergent aquatic habit itself is restrictive since only a relatively small area of most water bodies is of a suitable depth to permit the production of viable aerial reproductive structures. The disinclination of the species to grow in the presence of moderate currents or under highly saline conditions further limits the number of locations suitable for its establishment. Wild rice has an annual habit and hence is restricted to latitudes with a growing season of sufficient length to allow it to complete its life cycle. Within these limits, however, this species flourishes under a variety of environmental conditions. Wild rice is tolerant of a broad range of water depths, from virtually nil to two or more metres (Steeves 1952; Aiken et al, 1987). It is found in a variety of sediment types, ranging from clay to black organic muck to peat (Chambliss 1940; Steeves 1952; Aiken et al, 1987) and in association with many other plant species (Lee 1979; Aiken et al, 1987). The range of climatic conditions experienced by this species is considerable even within Ontario, as it spans the breadth of the province between the Manitoba and Quebec borders (a longitudinal range of 79° to 95° W), and extends from the southern border (latitude approximately 42° N) to a northern limit at around 53° 30'N.

It is a truism that variability in the environment will create variability in plant morphology (Stebbins 1957; Bradshaw 1965; 1974). Different ramets of clonal organisms respond to variation in the environment by altering their appearance, a phenomenon known as phenotypic plasticity (e.g. see Wu and Jain 1978; Lieffers and

Shay 1982; Turkington 1983). In addition, pronounced and persistent differences in environment may exert sufficient differential selective pressure to cause the genetic divergence of plant populations, particularly if gene flow between them is restricted. The previous chapter showed that wild rice populations in Ontario are genetically differentiated in their morphology and phenology. Climate was implicated as a major influencing factor. The plastic response of wild rice to variation in water depth or sediment nutrient status has also been well-documented (Rogosin 1958; Thomas and Stewart 1969; Lee 1986b).

It is not known whether wild rice plants from all populations respond similarly to variations in their local environments. This may be an important issue for the wild rice grower who seeks a source of seed to introduce to a new lake or to upgrade an existing lake. If very little management of the lake is possible, a population with an equable response across varying environments may be desirable to improve uniformity of performance. Alternatively, if management techniques exist to maintain an optimum environment, a seed source that is capable of exploiting available resources for maximum productivity would be more appropriate. If populations exist that are better able than others to tolerate excessive water depths or deficiencies of specific nutrients, they might be desirable in some circumstances.

This paper reports on a study of seventeen Ontario wild rice populations. The objectives of the study were (a) to determine the relative importance of regional climatic factors versus local environmental parameters (water depth, edaphic characteristics, and plant competition) in determining wild rice morphology and production, and (b) to ascertain whether all populations have a similar plastic response to changes in their local environments.

2.2. METHODS

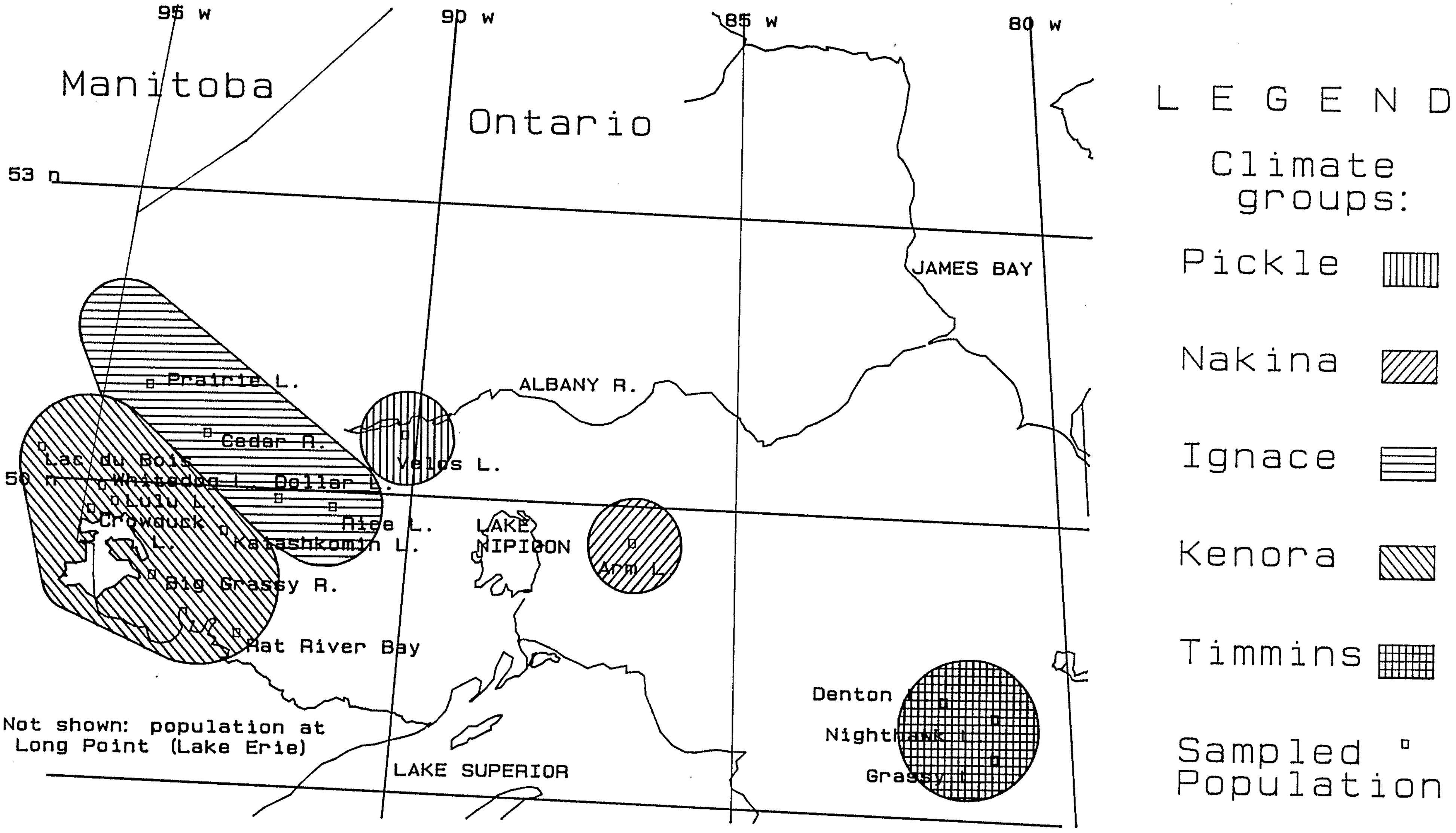
2.2.1. Sampling Procedures

Samples were obtained from seventeen wild rice populations during the summers of 1983 and 1984. Names of the water bodies sampled will be abbreviated in the remainder of this paper as follows: Velos Lake, V; Arm Lake, A; Denton Lake, DT; Grassy Lake, GR; Nighthawk Lake, NH; Prairie Lake, PR; Rice Lake, RI; Dollar Lake, D; Cedar River, CR; Lac du Bois, LDB; Crowduck Lake, CD; Lulu Lake, LU; Whitedog Lake, WD; Rat River Bay, RR; Kaiashkomin Lake, K; Big Grassy River, BG; and Big Creek, BC. All except the BC population, which occurs at Long Point on the north shore of Lake Erie (32° 36'N x 80° 29' W), are shown in Figure 2.1. Sampling commenced in mid-July, when the rice was in full flower, and continued until September.

Since wild rice typically has a patchy distribution, a stratified-random sampling technique was employed. Each subpopulation was randomly sampled at an intensity of 1 sample per 3 ha of wild rice. This frequency was determined as the minimum required to give a 95% probability of sampling all major environmental regions within a population on a highly variable lake described by Lee (1986). To ensure adequate numbers for statistical analyses, a minimum of 10 samples were taken.

At each sample location, all wild rice plants within a randomly placed 0.5 m x 0.5 m quadrat were uprooted. All other emergent vegetation in the quadrat was clipped at the sediment/water interface. Water depth was measured at the centre of the quadrat, and a 50-cm soil sample was taken with a soil corer. All samples were placed in plastic bags and stored on ice for transport to the laboratory, where they were frozen prior to analysis.

FIGURE 2.1. Map of Northern Ontario showing locations of wild rice populations sampled.


95 w
90 w
85 w
80 w
53 n
50 n
Manitoba
Ontario
JAMES BAY
ALBANY R.
Prairie L.
Cedar R.
Lac du Bois
Whitedog L.
Dollar L.
Lulu L.
Velos L.
Crowduck L.
Rice L.
Katashkomin L.
LAKE NIPIGON
Arm L.
Big Grassy R.
Rat River Bay
Denton
Nighthawk L.
Grassy L.
LAKE SUPERIOR
Not shown: population at Long Point (Lake Erie)
LEGEND
Climate groups:
Pickle
Nakina
Ignace
Kenora
Timmins
Sampled Population

2.2.2. Laboratory Procedures

In the laboratory, individual wild rice plants were separated, and the numbers of tillers per quadrat and per plant were recorded. The height from the base of the stem to the flag leaf of the tallest tiller was measured. To obtain a measure of mean potential yield per tiller, the number of pistillate floret pedicels was counted for each tiller in the sample. The mean maximum leaf width was estimated from measurement of 20 aerial leaves. Shoots and roots were separated and dried at 80°C until a constant weight was obtained; weights per tiller were calculated as the total weight for the sample divided by the number of tillers. For samples that contained mature seed, a subsample of 20 oven-dried seeds was used to obtain mean lengths and weights. Potential seed yield per quadrat was calculated as the product of average seed weight, average pistillate florets per tiller, and number of tillers per quadrat. All emergent competing plants were dried until a constant weight was reached for each sample.

Soil analyses were carried out on saturated sediments as described by Lee (1986). The parameters measured included % loss on ignition, pH, and concentrations of extractable nitrogen, phosphorus, potassium, iron, calcium, magnesium, copper, zinc, and manganese.

2.2.3. Data Analyses

Skewness and kurtosis statistics were calculated for all variables to detect departures from the normal frequency distribution assumed for most statistical tests. Where non-normality occurred, it was corrected with a logarithmic or square-root transformation.

A multiple regression procedure with dummy variables (essentially an analysis of covariance, or ANCOVA) was used to analyse effects of climate and local environmental variables on wild rice growth and morphology. The approach is described in detail by Nie et al (1975, pp. 373-383). Plant variables were regressed on three classes of variables. The first group, the covariates, included environmental variables and their squares. The polynomial terms were included to improve the fit of the regression equation, since the growth response of plants to nutrient concentrations is often curvilinear (Etherington 1975; Salisbury and Ross 1985). The second class of predictors in the regression equation comprised dummy variables representing individual populations in one set of analyses, or populations grouped by climatic similarity (see below) in a second set. These constitute the groups or factors in the analysis of covariance. Finally, there were dummy variables representing the differential effects of local environmental variables on different populations - these were the interaction terms in the analysis of covariance.

A hierarchical procedure was used, as suggested by Nie et al (1975): environmental variables were entered first in a stepwise fashion, then the population (or climate group) dummy variables were entered as a block, and finally the interaction dummy variables were entered stepwise. This approach permits an assessment of the effects of local environmental parameters on wild rice growth and morphology, and also permits a direct comparison of wild rice performance in different populations by adjusting for among-population variability in these parameters. Analysis of residuals (normal-probability plots and plots of residuals vs predicted scores) were performed to detect any severe inadequacies in the model or violations of assumptions (Nie et al 1975; Sokal and Rohlf 1981), but none were apparent.

Simple bivariate correlation analyses showed that the local environmental variables (water depth, plant competition, and sediment characteristics) were highly intercorrelated (see Appendix 3). Such multicollinearity of predictor variables creates difficulties in multiple regression analysis Nie et al, 1975; Green 1979). To correct this problem, principal components analysis was performed on the entire field environmental data set (including the introduced populations discussed in chapter 4) to produce a new, uncorrelated set of fewer environmental variables. A "varimax" orthogonal rotation (Nie et al 1975) was used in the analysis to simplify the interpretation of the principal components. Scores for each principal component (PC) were output for each case in the data set, and the PC scores formed the new set of environmental predictor variables in the multiple regression procedure.

Part of the multiple regression procedure involved assessing the explanatory power of groups of populations defined by climatic similarity in the prediction of wild rice performance. An average-linkage, hierarchical agglomerative Q-type clustering procedure like that described for chapter 1 was used to define the population groups shown in Figure 2.1. Appendix 1 presents a dendrogram summarizing the results of the cluster analysis, which included all the populations considered in field studies and experiments. Mean values of the climatic parameters serving as clustering criteria are shown for the derived groups of populations in Table 2.1. The SAS programme package (SAS Institute Inc. 1982a; 1982b) was used for the cluster analysis; all other procedures were performed using the SPSS programme package (Nie et al 1975; Hull and Nie 1981).

TABLE 2.1. Means of selected climatic characteristics for groups of wild rice populations sampled in field surveys, as defined by cluster analysis

Climate Group	Annual Growing-Degree-Days (5° C)	Average Date of First Fall Frost (Year-Day)	Probability of Frost Before Sept. 1 (%)	Maximum Daylength (minutes)
Pickle	1276.4	250	25.0	980
Nakina	1166.0	241	50.0	980
Timmins	1416.8	249	3.3	957
Ignace	1508.6	262	2.5	980
Kenora	1636.6	262	11.1	971
Lake Erie	2093.8	274	0.0	915

2.3. RESULTS

2.3.1. Principal Components Analysis

Scores on the first seven factors derived in the principal components analysis were retained as the local environmental data set in the subsequent ANCOVAs. These seven components accounted for 82.3% of the variance in the original data set, and were interpretable as primary dimensions in the environment (see below). The eighth and subsequent components (thirteen were derived in total) each accounted for less than 5.0% of the variation, and were not easily interpreted.

The coefficients from the rotated factor matrix are presented in Table 2.2. Variables with the highest coefficients for a given component contribute the most to that component. The square of the coefficient is the proportion of variance in that variable accounted for by that component (Nie et al, 1975). The first component (PC1) explained 28.8% of the environmental variation. It had high positive loadings for iron, manganese, calcium, magnesium, potassium and zinc, and a high negative loading for % loss on ignition, and thus may be interpreted as a measure of the ratio of the mineral:organic content of the sediment. PC1 will be referred to as the mineral:organic component, or simply M:O.

Principal component 2 (PC2), which accounted for 12.0% of the environmental variance, was primarily a function of sediment phosphorus, with minor contributions from calcium, magnesium, and zinc. PC2 will be referred to as the phosphorus component, or P.

The third component (PC3) mainly represented pH. The largest (negative) loading for zinc also appeared on this factor. Manganese and calcium, with positive coefficients, and iron, with a negative loading, also made minor contributions to PC3. This component, accounting for 11.2% of the variance, will be designated as pH:Zn.

TABLE 2.2. Coefficients of the rotated factor matrix and variance explained for the first seven principal components of the environmental data set. Coefficients that are underlined account for more than 5% of the variance in a given variable; bold face indicates the largest coefficient for a variable

Environmental Variable	Factor 1	2	3	4	5	6	7
% Loss on Ignition	**-0.79**	-0.01	0.03	-0.06	-0.03	0.04	0.14
pH	0.10	-0.16	**0.86**	0.19	-0.02	-0.10	0.05
Phosphorus	-0.02	**0.91**	-0.08	0.18	0.11	0.01	-0.05
Nitrogen	-0.04	0.20	0.14	**0.87**	-0.11	-0.09	0.13
Iron	**0.82**	0.20	-0.24	-0.05	0.01	-0.06	0.10
Manganese	**0.82**	-0.09	0.26	-0.16	-0.04	-0.12	0.09
Zinc	0.34	-0.24	**-0.56**	0.42	-0.26	-0.23	0.16
Copper	-0.08	-0.04	0.00	0.12	0.00	0.00	**0.96**
Calcium	**0.66**	-0.45	0.30	0.14	0.08	0.22	-0.09
Magnesium	**0.70**	-0.31	-0.08	0.14	0.30	0.27	-0.24
Potassium	**0.60**	-0.13	0.02	0.37	0.45	0.12	-0.13
Emergent Competition	0.00	-0.01	-0.04	-0.09	-0.19	**0.92**	0.01
Water Depth	0.09	-0.13	0.04	-0.16	**0.86**	-0.25	0.02
% Variance Explained	28.8	12.0	11.2	10.5	7.9	6.3	5.5

PC4 explained 10.5% of the variation, and was primarily a function of nitrogen, with potassium and zinc as secondary variables. This will be designated the nitrogen component, or N.

Water depth was the major variable in the fifth component. Zinc again played a minor role, with a negative loading; magnesium also contributed to this factor. PC5 explained 7.9% of the variation, and will be referred to as the depth component, or D.

Principal component 6 accounted for 6.3% of environmental variance, and mainly represented plant competition. Magnesium, with a positive loading, and water depth and zinc, with negative coefficients, were minor contributing variables. The plant competition component, or PC, will refer to PC6.

Sediment copper had the largest loading for component 7, which will be designated the copper component, or Cu. Magnesium, with a negative coefficient, also played a minor role in this final environmental factor. PC7 accounted for 5.5% of the environmental variation.

Preliminary analyses indicated that the mineral:organic, nitrogen, depth, and plant competition components were most important in predicting wild rice productivity. Only these environmental parameters plus the phosphorus component were used in the construction of dummy interaction variables. The P component was included because phosphorus has been implicated as a limiting factor in other wild rice populations (Peden 1982; Lee 1987). Since they were not expected to have much relevance, the pH:Zn and Cu components were omitted to simplify the model: for each environmental component, 16 additional interaction dummy variables were required in the analysis.

The means and standard errors of scores on each component for each population are shown in Appendix 4.

2.3.2. Analyses of Covariance

Total Variation Explained

Figure 2.2 (a-h) shows the partitioning of variation for each plant characteristic examined. In general the analyses were quite efficacious, with 70 to 80% of the total variance in most variables explained by the derived equations. Stem weight was least well explained, with 68.8% of the total variation accounted for by the regression equation (Figure 2.2a). The model most successfully explained plant height (overall multiple R^2=0.847, or 84.7% of variation accounted for; Figure 2.2c) and seed length (R^2=85.8%; Figure 2.2g).

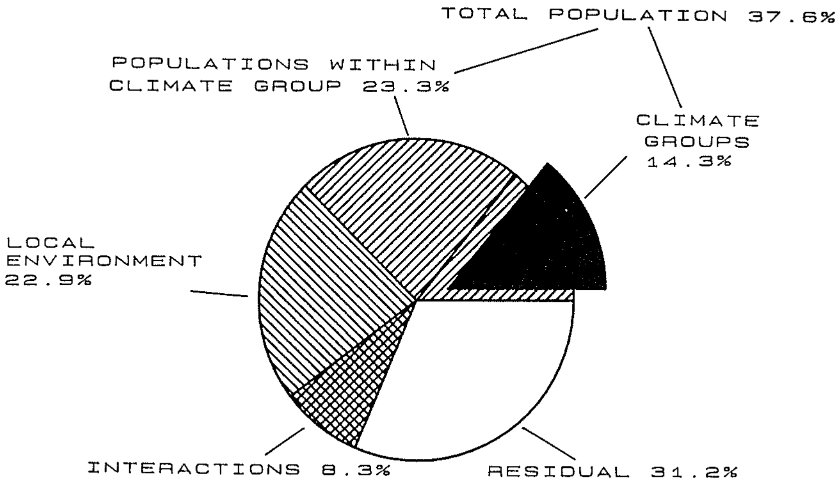
The results of the ANCOVAs are summarized for each variable by a set of predictive equations (one for each population), which are presented in Appendix 5. Some of these equations were applied to the analysis of introduced wild rice populations in chapter 4.

Variation Explained by Environmental Parameters

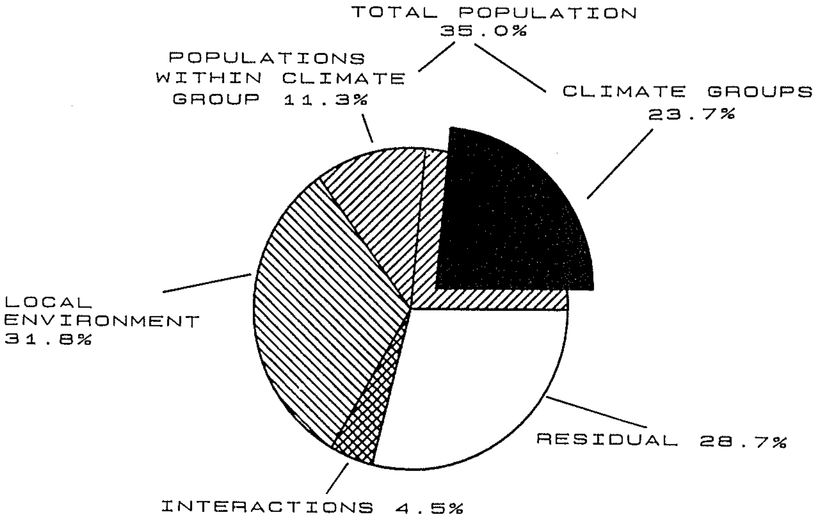
Physical, edaphic, and biotic environmental factors accounted for 20 to 32% of the total variation in most wild rice characteristics (Figure 2.2). Variation in seed length was the most poorly explained by the environmental component of the model, with a multiple R^2 of only 16.7% (Figure 2.2g). By contrast, covariate terms accounted for the majority of the explained variation in plant height, with an R^2 of 61.6% (Figure 2.2c).

Covariate partial regression coefficients significantly different from 0 ($p \leq 0.05$) are shown for all plant variables in Table 2.3. The magnitude of the coefficient indicates the relative predictive efficacy of a covariate for a particular plant variable, while the sign indicates the direction of slope of the partial regression line. All of the environmental components contributed significantly to variation in at

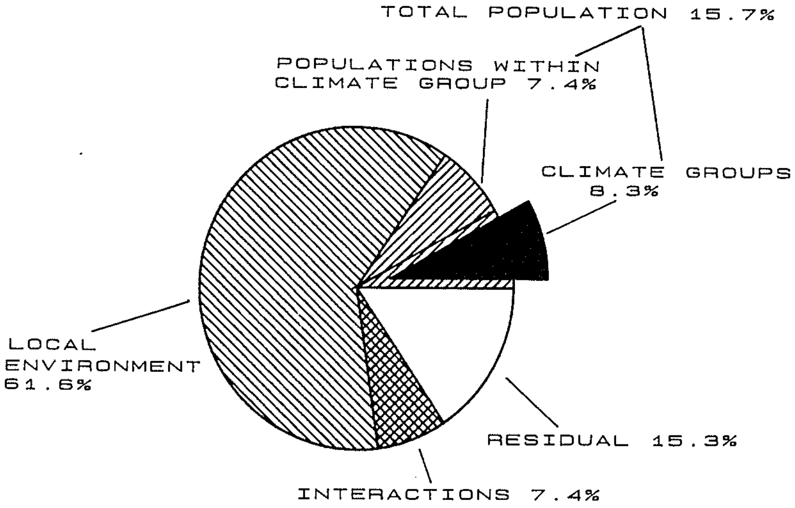
FIGURE 2.2. Partitioning of variation in wild rice characteristics for seventeen populations. Numbers are values of multiple R^2 (expressed as a percentage) for components of the ANCOVA models for each plant variable.



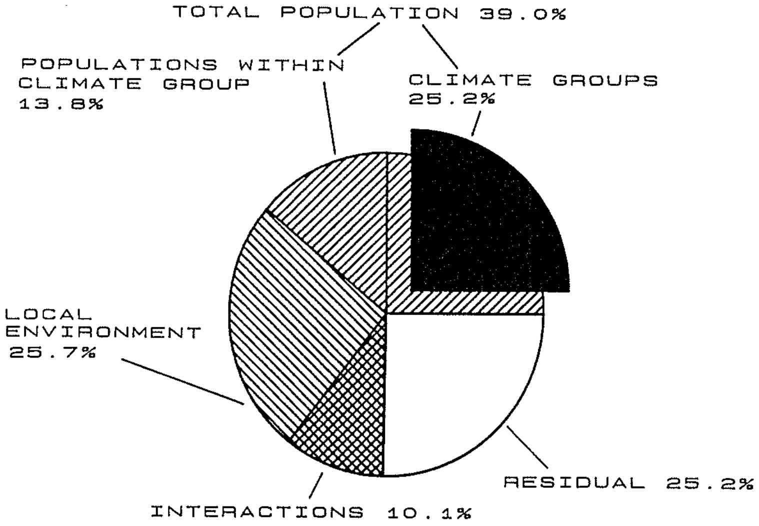
(a) Shoot Weight per Tiller



(b) Root Weight per Tiller

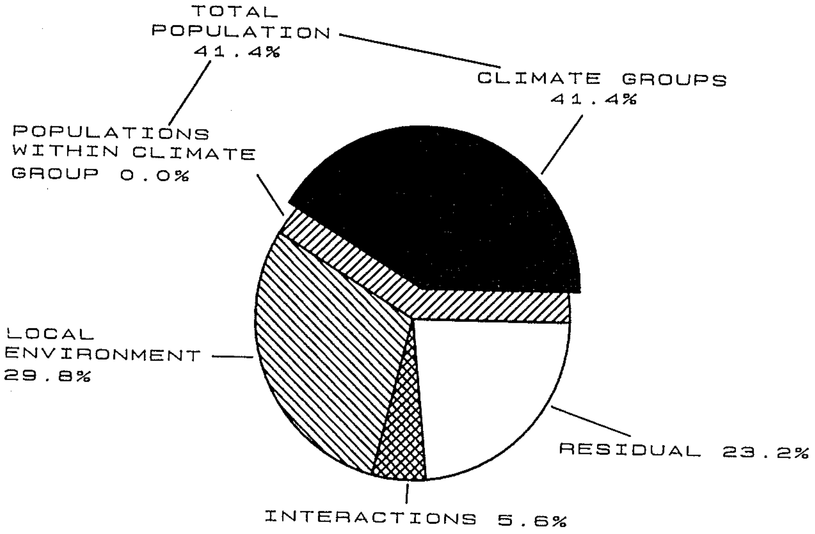


(c) Height

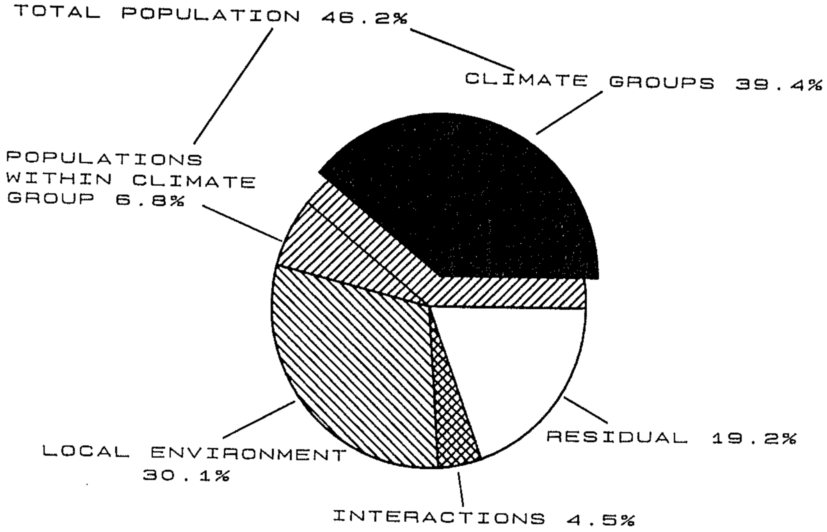


(d) Tillers Per Plant

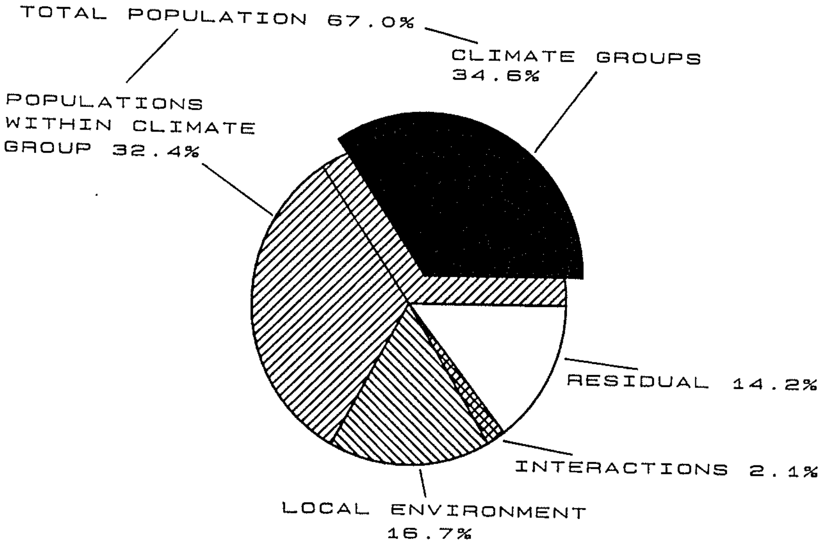
(e) Leaf Width



(f) Pistillate Floret Production



(g) Seed Length



(h) Seed Weight

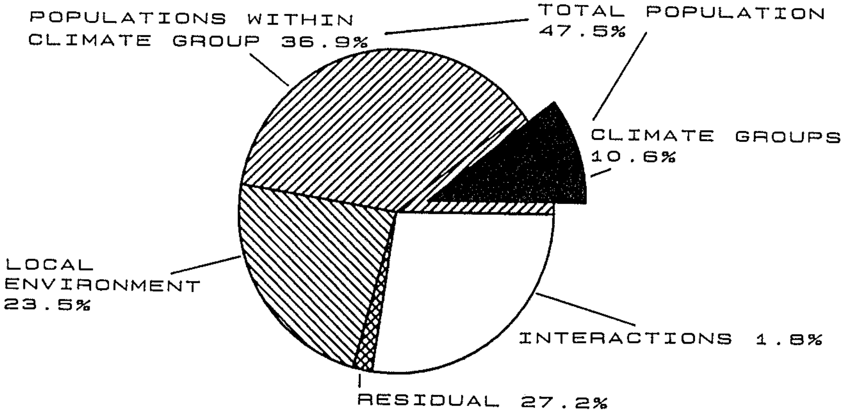


TABLE 2.3. Partial regression coefficients of environmental components contributing to variation in wild rice characteristics. All plant variables except leaf width were converted to natural logarithms prior to analysis. Only coefficients found significant ($p<0.05$ that $B=0$) in t-tests on the final equations are shown; nonsignificant coefficients are indicated by *

Environmental Component	Stem Weight	Root Weight	Height	Tillers per Plant	Leaf Width	Pistillate Florets	Seed Length	Seed Weight
M:O	*	-0.14	*	*	*	0.10	-0.03	*
P	*	*	*	*	-0.35	*	*	*
pH:Zn	*	*	*	0.05	*	*	*	*
(pH:Zn)^2	*	*	*	*	-0.20	*	*	*
N	*	*	-0.09	*	*	*	*	*
(N)^2	*	*	*	0.05	0.16	0.04	*	*
D	*	-0.18	0.22	-0.07	*	*	*	*
(D)^2	*	0.08	0.02	*	*	*	*	*
PC	-0.08	*	*	*	-0.21	*	*	0.03
(PC)^2	*	-0.04	*	*	*	*	*	*
Cu	0.05	*	*	*	*	*	*	*
(Cu)^2	*	*	-0.01	*	*	*	*	*

least two wild rice characteristics, but M:O, N, D, and PC were the most important predictors.

Increases in the sediment mineral:organic ratio were associated with the production of taller plants with smaller root masses that produced more numerous pistillate florets, but shorter seeds. Wild rice plants were shorter, but produced more tillers, broader leaves, and more pistillate florets per tiller as sediment nitrogen concentration was increased. Increasing water depth resulted in taller plants that produced fewer tillers. Root weight was a complex function of D and D^2: at shallower initial depths root weight decreased with increasing water level, but with further increases the effect became positive (Figure 2.7). Increased interspecific competition was generally associated with production of smaller stems and roots, narrower leaves, and heavier seeds by the wild rice plants.

The other covariates had fewer significant effects on wild rice growth. Leaf width was decreased in association with increasing P and increases in the ratio of sediment pH:Zn. The pH:Zn ratio was positively related to tiller production. Increasing sediment copper concentrations positively influenced stem weight, but plant height was decreased in proportion to Cu^2.

Variation explained by Individual and Grouped Populations

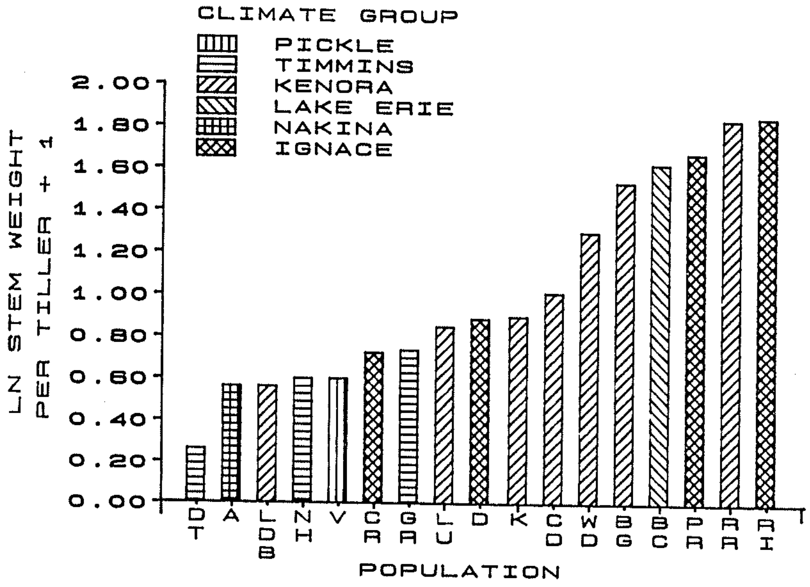
A greater proportion of the variation in most plant characters was explained by individual population factors than by the local environmental components. The exception was plant height, with a total population R^2 of only 15.7%, compared to an R^2 of 61.6% for the environmental covariates (Figure 2.2c). For other dependent variables differences among populations accounted for at least 35.0% of total variation (root weight; see Figure 2.2b), up to a maximum of 67.0% (seed length, Figure 2.2g; the next highest was 47.5% for seed weight, Figure 2.2h).

For all wild rice variables except leaf width, some explanatory power was lost when analyses were performed using populations grouped by climatic similarity (climate groups) as factors. This was indicated by a reduction in the multiple R^2 obtained. Thus variation explained by differences among populations over and above those due to effects of water depth, edaphic conditions and interspecific competition was partitioned into two components: variation among climate groups, and variation among populations within climate groups. The latter was calculated as the difference in the R^2 obtained for grouped and ungrouped populations. The partitioning is shown in Figure 2.2(a-h). Figure 2.3(a-h) presents in ascending order the population intercepts obtained from the ANCOVAs for the different wild rice characteristics (actual observed population means and standard deviations are given in Appendix 6). Populations in the same climate group tend to be contiguous and relatively distinct from populations in different groups for those variables that are strongly influenced by climatic regime. Means of the population intercepts for the various climate groups are shown in Table 2.4

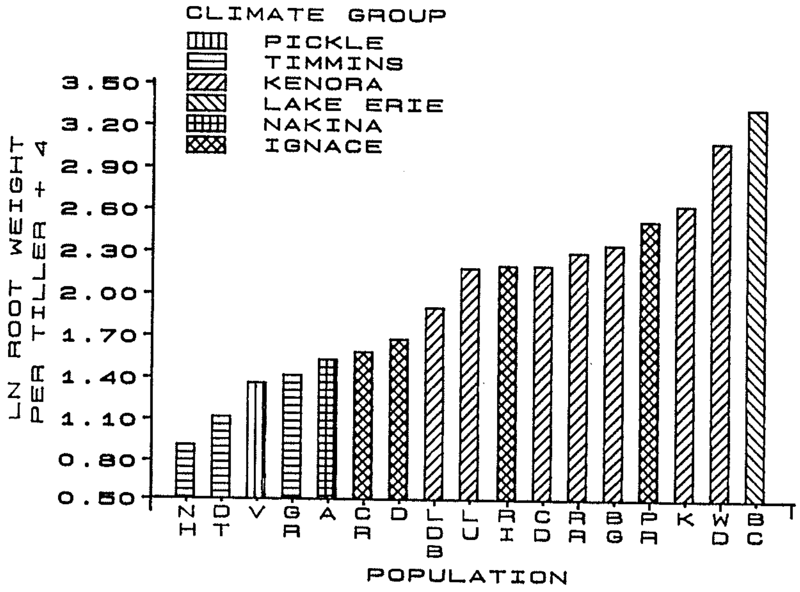
The proportion of information lost when populations were grouped varied widely for the different wild rice characters. Climate group had excellent explanatory power for leaf width and pistillate floret production, with multiple R^2 values of 0.416 and 0.394 respectively (Figures 2.2e and f). All of the information was retained for leaf width (total population R^2=climate group R^2=0.416) when the analysis was performed using grouped populations, indicating that there are no significant differences among populations within climate groups after the effects of the local environment are taken into account. The narrowest leaves are found in wild rice plants from Timmins, Pickle and Nakina populations, followed by Ignace and Lake Erie plants. Kenora plants have the widest leaves in a constant, average environment (Figure 2.3e; Table 2.4). There was a decrease of only 6.8% in the

FIGURE 2.3. Population intercepts of equations for wild rice characteristics: predicted mean values of plant variables when all environmental principal components are held constant at 0 (the average for all populations combined).

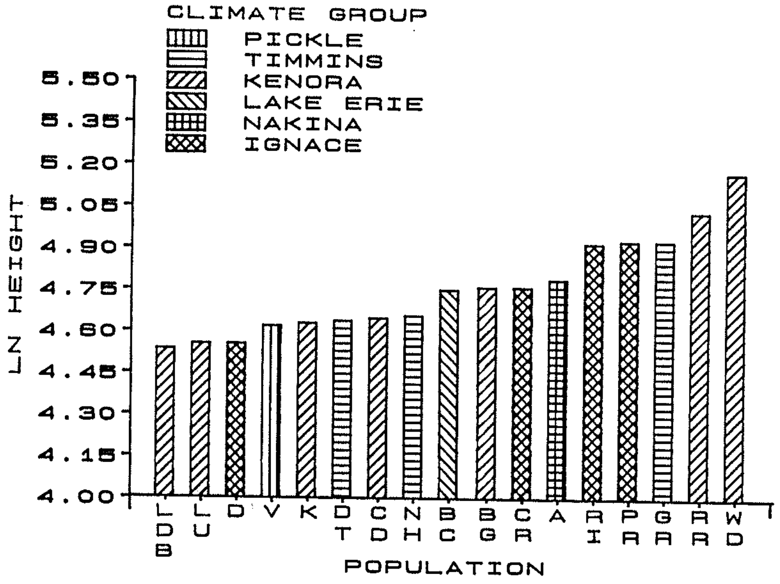
(a) Shoot Weight per Tiller



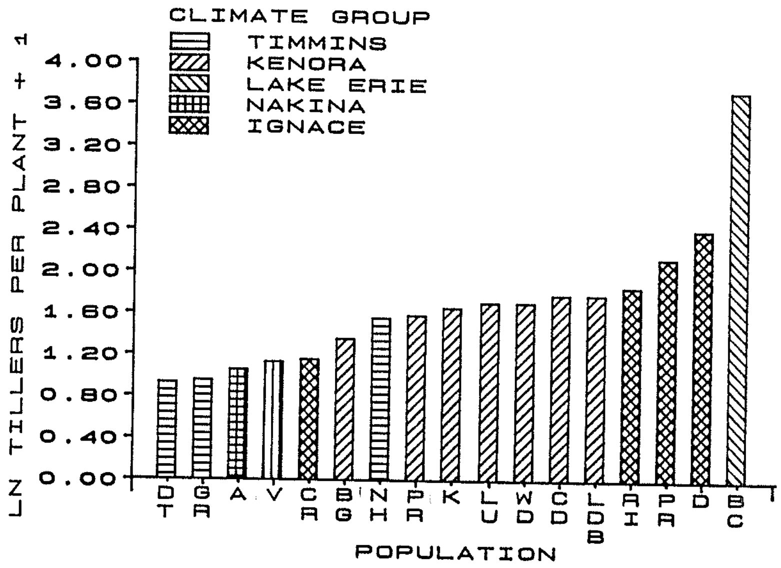
(b)Root Weight per Tiller

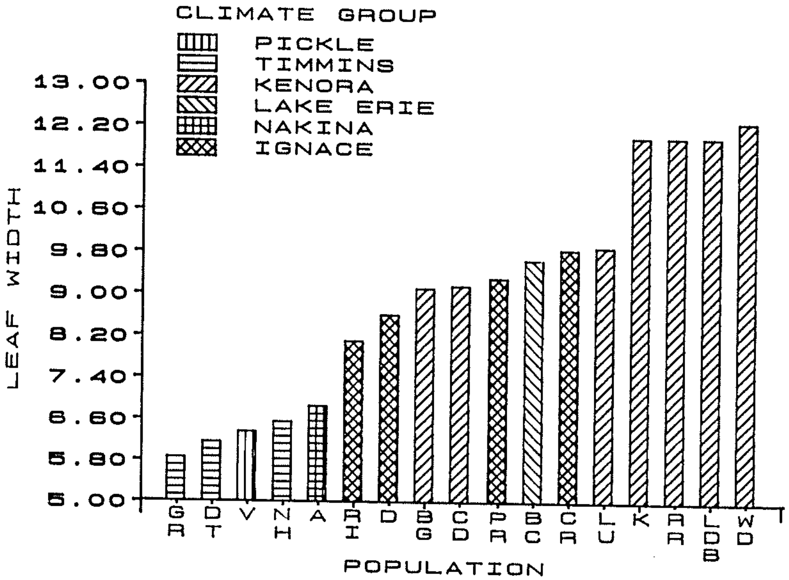


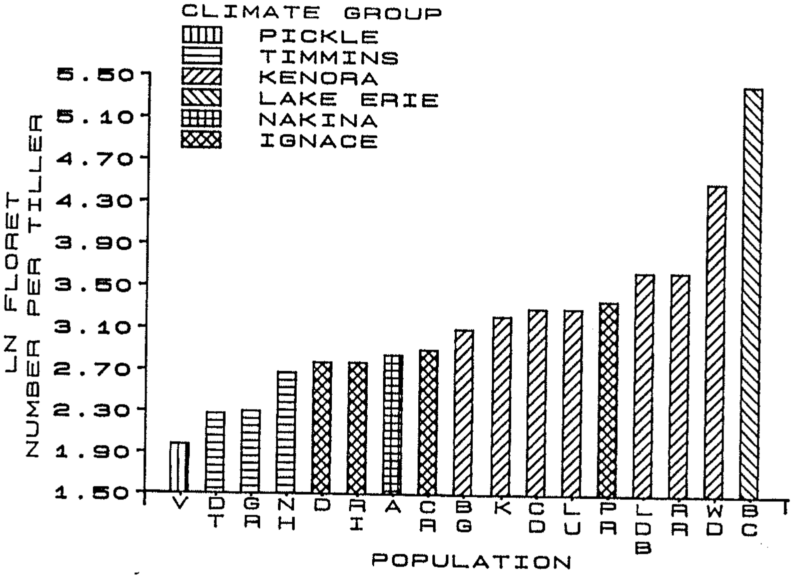
(c) Height

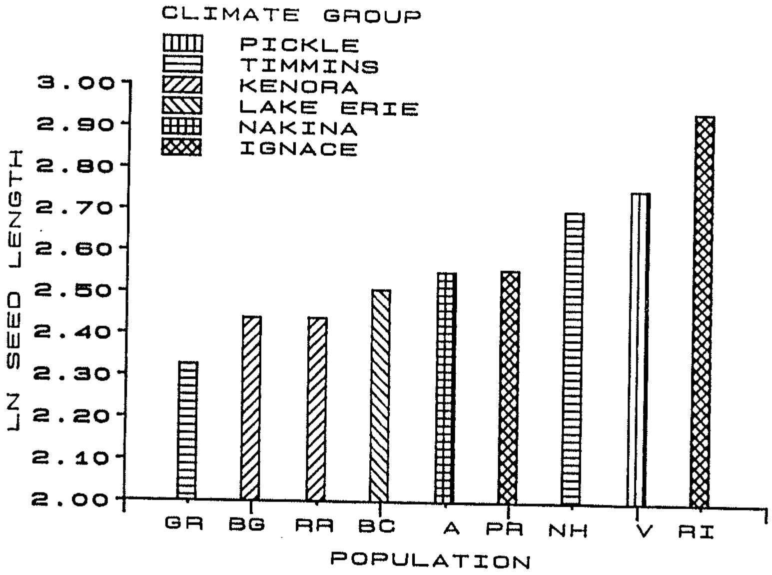


(d) Tillers Per Plant




(e) Leaf Width


(f) Pistillate Floret Production


(g) Seed Length

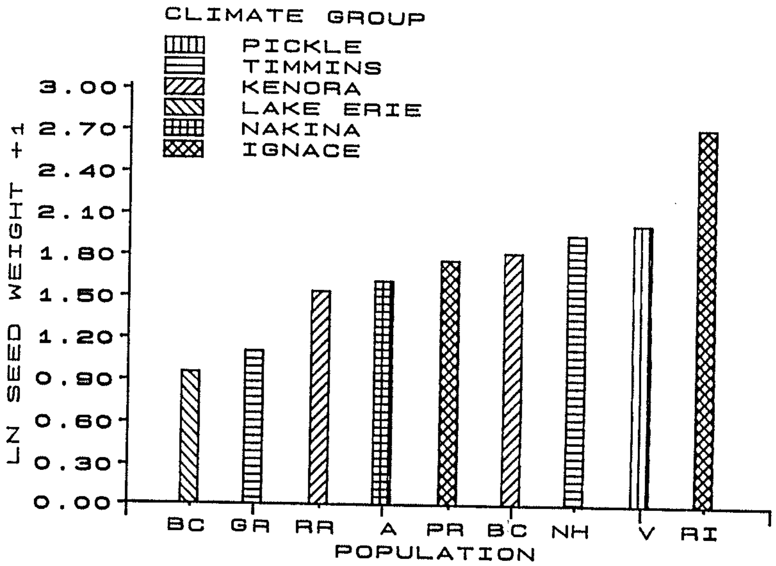

(h) Seed Weight

TABLE 2.4. Means and ranges of intercepts of ANCOVA equations for groups of wild rice populations with similar climates. All plant variables except leaf width are expressed as natural logarithms. Group abbreviations are as follows: P, Pickle; N, Nakina; T, Timmins; I, Ignace; K, Kenora; E, Lake Erie.

		Group					
		P	N	T	I	K	E
Tillers per Plant	minimum			-0.06	0.16	0.36	
	mean	0.13	0.06	0.15	0.89	0.66	2.74
	maximum			0.55	1.40	0.79	
Height	minimum			4.64	4.56	4.54	
	mean	4.62	4.79	4.74	4.79	4.77	4.75
	maximum			4.93	4.93	5.18	
Leaf Width	minimum			5.9	8.1	9.1	
	mean	6.4	6.9	6.2	9.0	10.9	9.6
	maximum			6.6	9.9	12.3	
Stem Weight	minimum			-0.73	-0.27	-0.43	
	mean	-0.40	-0.43	-0.46	0.29	0.15	0.63
	maximum			-0.26	0.85	0.84	
Root Weight	minimum			-3.10	-2.42	-2.10	
	mean	-2.65	-2.47	-2.86	-2.01	-1.63	-0.68
	maximum			-2.59	-1.49	-0.93	
Florets	minimum			2.28	2.78	3.11	
	mean	1.99	2.87	2.43	2.96	3.54	5.43
	maximum			2.69	3.38	4.50	
Seed Length	minimum			2.33	2.56	2.44	
	mean	2.75	2.55	2.51	2.75	2.44	2.51
	maximum			2.70	2.94	2.44	
Seed Weight	minimum			0.09	0.75	0.53	
	mean	1.01	0.60	0.52	1.23	0.67	-0.06
	maximum			0.95	1.71	0.81	

explained variation in pistillate floret production when populations were grouped (R^2=39.4% versus 46.2%, Figure 2.2f); thus 85% of the explanatory power of the model was retained. Figure 2.3f and Table 2.4 show that Pickle and Timmins populations have the lowest yields, followed by Ignace and Nakina, with Kenora and Lake Erie wild rice plants at the upper end of the continuum.

A large proportion of the variation among populations was accounted for by differences among climate groups for wild rice root weight and tiller production as well. The factor multiple R^2 for root weight decreased from 0.350 to 0.237 when populations were grouped (Figure 2.2b), while the analogous decrease was 0.390 to 0.252 for tiller production (Figure 2.2d). Thus 68% of the explanatory power of populations considered individually was retained for root weight, and 65% was retained for tiller production. As with pistillate floret production, Timmins, Pickle and Nakina wild rice populations are at the lower end of the spectrum for root weight, and Lake Erie is at the upper end. Ignace and Kenora populations are intermediate but show more overlap than is observed for pistillate floret production (Figure 2.3b; Table 2.4). A similar pattern is also observed for tiller production except that the relative ranking of Ignace and Kenora populations is reversed: wild rice plants from Ignace populations tend to produce more tillers than those from Kenora.

The multiple R^2 for grouped populations was 0.346 for seed length (Figure 2.2g), a larger absolute value than was observed for root weight or tiller production. However, the proportional decrease in R^2 when populations were grouped was also greater: the total R^2 for ungrouped populations was 0.670, so nearly 1/2 of the explanatory power (48%) was attributable to variation among populations within climate groups (R^2=0.324). Pickle and Ignace populations tended to have larger seeds than Kenora, Lake Erie, or Nakina populations. The two Timmins populations, however, were near the opposite ends of the continuum (Figure 2.3g).

Differences among individual populations explained 37.6% of the total variation in stem weight, but climate group was a poor predictor, explaining only 14.3% of the variation (Figure 2.2a). Figure 2.3a and Table 2.4 show that populations in the Pickle, Timmins and Nakina groups generally had lower stem weights than those from the Ignace, Kenora, or Lake Erie groups, but within these broad categories there was no distinct separation.

Climatic regime also had little explanatory power with regard to seed weight; the multiple R^2 for factors decreased from 0.475 to 0.106 when individual populations were grouped (Figure 2.2h). The high variability among populations within climate groups is illustrated by Figure 2.3h. A similar situation was observed for plant height; there was relatively little variation explained by differences among populations (15.7%; Figure 2.2c), and the proportion accounted for dropped to 8.3% when populations were grouped. Overlap between populations from different climatic regimes is apparent in Figure 2.3c.

Variation Explained by Population-Environment Interactions

Interaction terms explained a minor proportion of variation in all wild rice characteristics. They accounted for less than 6.0% of the total variation in all wild rice characters examined except tiller production, stem weight, and plant height. Table 2.5 summarizes the significant ($p \leq 0.05$) interaction terms, some of which are described below.

The regression equation for stem weight had the second largest interaction component, explaining 8.3% of the total variation (Figure 2.2a). Stem weights of wild rice plants in the typical population were not affected by the mineral:organic component, but plants from the RR and CR populations had contrasting responses:

TABLE 2.5. Partial regression coefficients of population-by-environment interaction terms contributing to variation in wild rice characteristics. All plant variables except leaf width were converted to natural logarithms prior to analysis. Coefficients for populations shown were significantly different ($p<0.05$) from reference coefficients presented in Table 2.3.

	Environmental Component				
	M:O	P	N	D	PC
Stem Weight	RR(-0.18)	A(-0.20)	BC(1.21)	LU(0.35)	BC(0.13)
	CR(0.21)	*	*	D(0.33)	WD(0.21)
	*	*	*	GR(0.33)	*
Root Weight	*	*	BC(1.47)	PR(-0.46)	A(-0.26)
	*	*	*	GR(0.28)	RR(0.18)
	*	*	*	*	WD(0.37)
Height	BC(-0.09)	LDB(0.13)	RR,LDB(0.01)	RR(0.02)	D(-0.30)
	*	WD(0.17)	K(0.04)	BC(0.04)	BG(-0.14)
	*	GR(0.20)	PR(0.05)	*	A(-0.06)
	*	*	D(0.08)	*	RR(-0.05)
Tillers per Plant	LU(-0.47)	WD(-0.19)	PR(0.11)	LU(-0.39)	WD(-0.21)
	LDB(-0.35)	*	*	K(-0.35)	*
	D(-0.26)	*	*	WD(0.41)	*
	BC(0.96)	*	*	BC(0.77)	*
Leaf Width	RR(-0.82)	BG(-1.29)	LDB(1.24)	LDB,CR(-0.81)	BC(0.89)
	*	PR(1.61)	*	*	*
	*	RI(1.80)	*	*	*
Pistillate Florets	LU(-0.38)	BG(-1.29)	GR(-0.62)	CR(-0.37)	CR(-0.30)
	WD(-0.35)	BC(0.48)	*	GR(0.36)	*
	RR(-0.12)	*	*	*	*
Seed Length	NH(0.05)	*	*	*	A(-0.07)
Seed Weight	*	*	*	*	A(-0.17)

those from RR produced smaller stems in association with increased M:O, while CR plants responded positively to sediment mineral content. Wild rice from the A population had a unique negative response to P for this character; other populations did not respond significantly to variation in the sediment phosphorus content. In the typical case there was no significant effect of N or D on stem weight, but BC plants had a strong positive response to N, and plants from the D, LU, and GR populations shared a similar positive response to the depth component. Wild rice plants from the WD and BC populations were positively influenced by competitive pressure, while all others showed decreased stem weight in association with increased interspecific competition. Functions derived from the partial regression coefficients for these populations and some showing the typical negative response to PC are plotted in Figure 2.4. The figure illustrates the dependence of the relative ranks of populations on the environmental conditions in which they are observed. Curves for most of the populations having a 'typical' or reference coefficient have been omitted for clarity in all plots illustrating interaction terms. Only curves for reference populations at the extremes and midranges for the environmental component and plant variable concerned are shown; these serve to place the atypical populations in the context of the overall range of variation in the populations sampled.

The largest contribution of interaction terms was observed for tiller production, with an R^2 of 0.101 (Figure 2.2d). There were diverse responses to M:O. While plants from the typical wild rice population were not affected over the observed range of this edaphic variable, those from LU, LDB, and D produced fewer tillers with a high ratio of mineral to organic sediment content, and BC plants had the opposite response. The functions are plotted in Figure 2.5. WD plants had a unique negative response to P and to the competition component, while tillering in

FIGURE 2.4. Partial regression of stem weight on the plant competition component for selected wild rice populatons. The functions are plotted over the observed ranges of PC scores for each population; mean PC scores are indicated by "+".

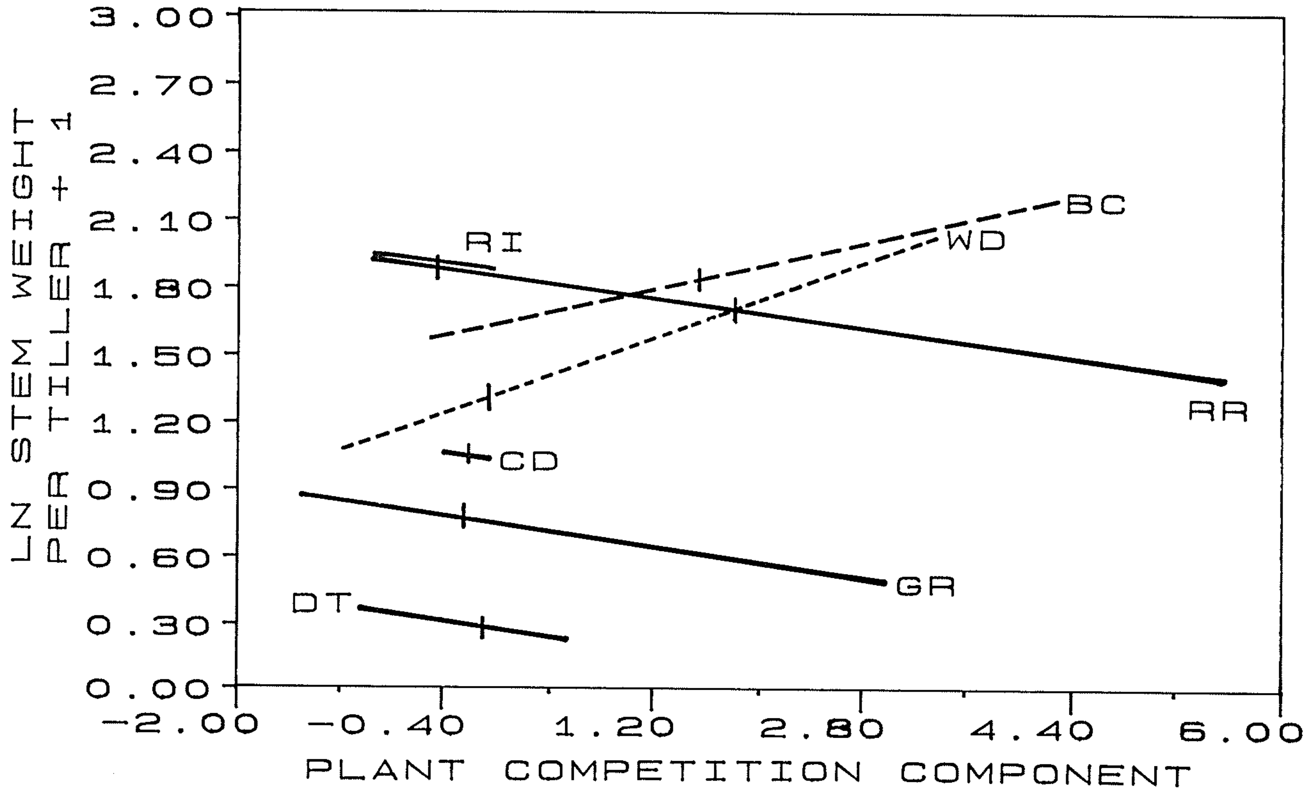
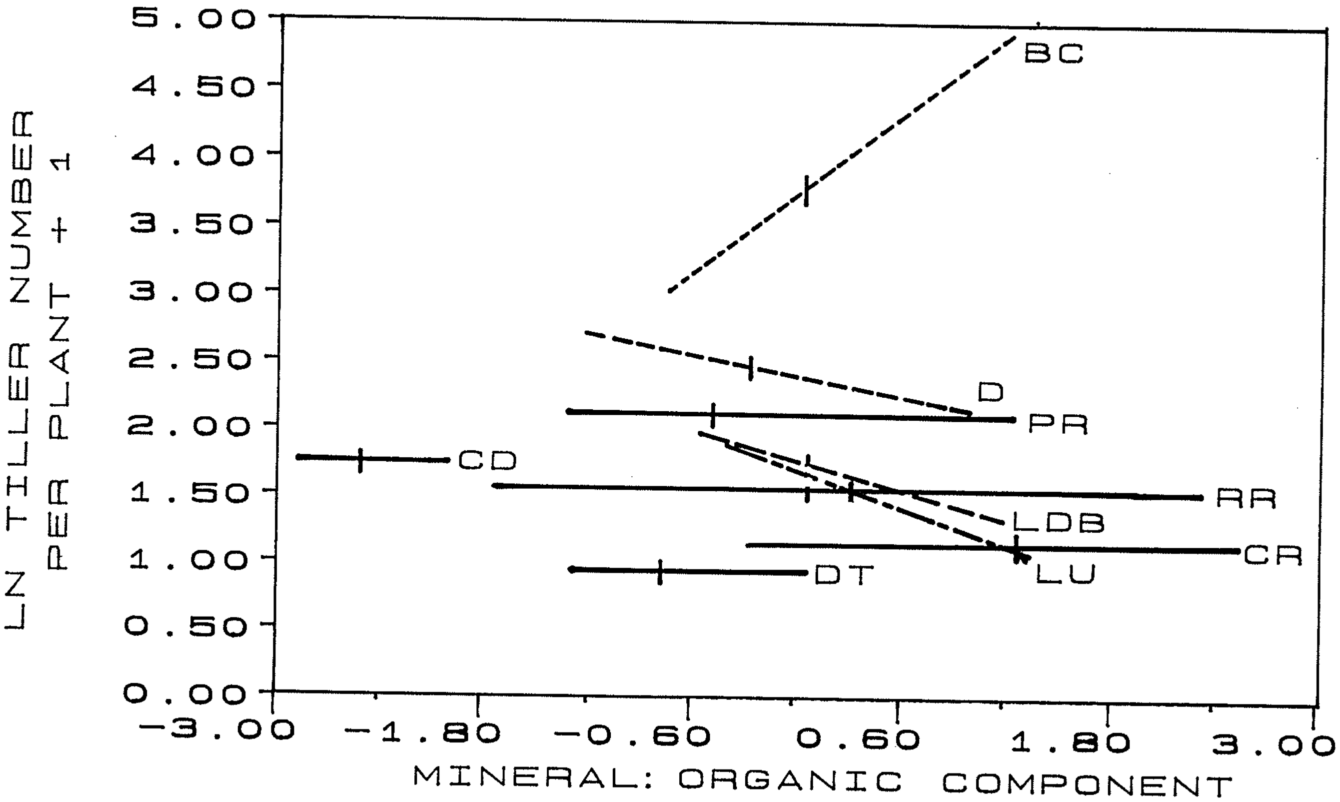

LN STEM WEIGHT
PER TILLER + 1
3.00
2.70
2.40
2.10
1.80
1.50
1.20
0.90
0.60
0.30
0.00
-2.00
-0.40
1.20
2.80
4.40
6.00
PLANT COMPETITION COMPONENT
BC
WD
RI
RR
CD
GR
DT

FIGURE 2.5. Partial regression of tiller number on the mineral:organic component for selected wild rice populatons. The functions are plotted over the observed ranges of M:O scores for each population; mean M:O scores are indicated by "+".


LN TILLER NUMBER PER PLANT + 1
5.00
4.50
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
−3.00
−1.80
−0.60
0.60
1.80
3.00
MINERAL: ORGANIC COMPONENT
BC
D
PR
CD
RR
LDB
CR
DT
LU

PR plants was enhanced by high N more than was typical. The effect of the depth component on wild rice tillering was complex, and is graphically presented in Figure 2.6. Tillering in plants from LU and K was more dramatically reduced than was typical with increased D, while WD and BC plants actually had a positive response.

Plant height was the only other wild rice character with interaction terms accounting for more than 6.0% of total variation (R^2=0.074; Figure 2.2c). BC plants were unique in their negative response to M:O. LDB, GR, and WD plants were all taller at high values of P, but others were not significantly affected by this parameter. Increasing N resulted in taller wild rice plants in the LDB, D, K, PR, and RR populations, but shorter plants in all other cases. All plants increased in height with high values of D, but wild rice from RR and BC was less affected by changes in depth than wild rice from other populations. Competition from other emergent species resulted in shorter wild rice plants in only D, BG, A, and RR populations.

Interaction terms accounted for less than 6.0% of the total variation in all wild rice characters except those discussed above, and therefore will not be described in detail. A few points are of particular interest. The curvilinear response of root weight to water depth (Figure 2.7) was mentioned above. Plants from the GR population had a unique positive response to increasing D both for root weight, and also for pistillate floret production, as shown in Figure 2.8. Increasing M:O was positively associated with pistillate floret production for most populations, but three in the Kenora group (WD, LU, and RR) had higher yields under conditions of lower sediment mineral:organic ratio (Figure 2.9). Finally, pistillate floret production in most populations was not influenced by P, but two populations were exceptional: wild rice from BG was more productive at lower P levels, while BC plants had a positive response to this environmental parameter (Figure 2.10).

FIGURE 2.6. Partial regression of tiller number on the depth component for selected wild rice populatons. The functions are plotted over the observed ranges of D scores for each population; mean D scores are indicated by "+".

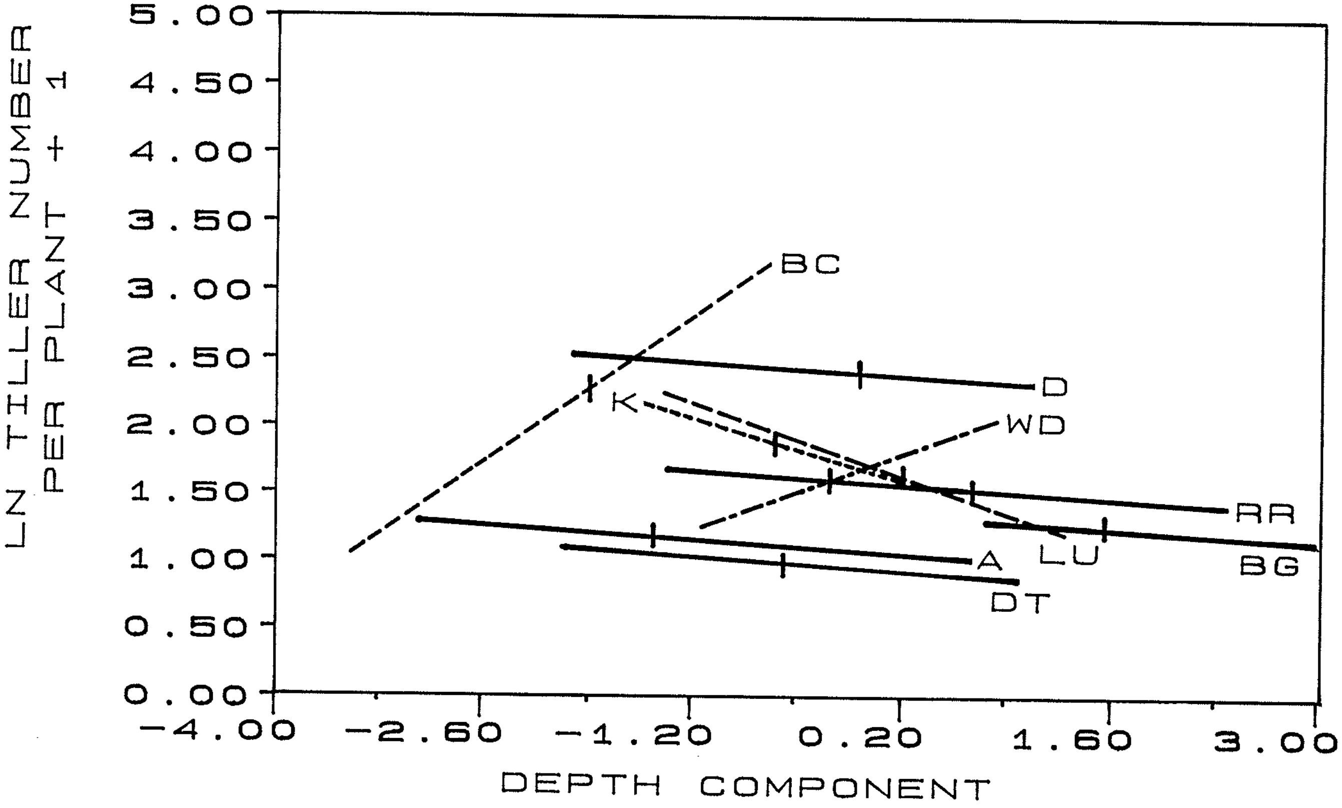

LN TILLER NUMBER PER PLANT + 1
5.00
4.50
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
−4.00
−2.60
−1.20
0.20
1.60
3.00
DEPTH COMPONENT
BC
D
K
WD
RR
LU
BG
A
DT

FIGURE 2.7. Partial regression of root weight on the depth component for selected wild rice populatons. The functions are plotted over the observed ranges of D scores for each population; mean D scores are indicated by "+".

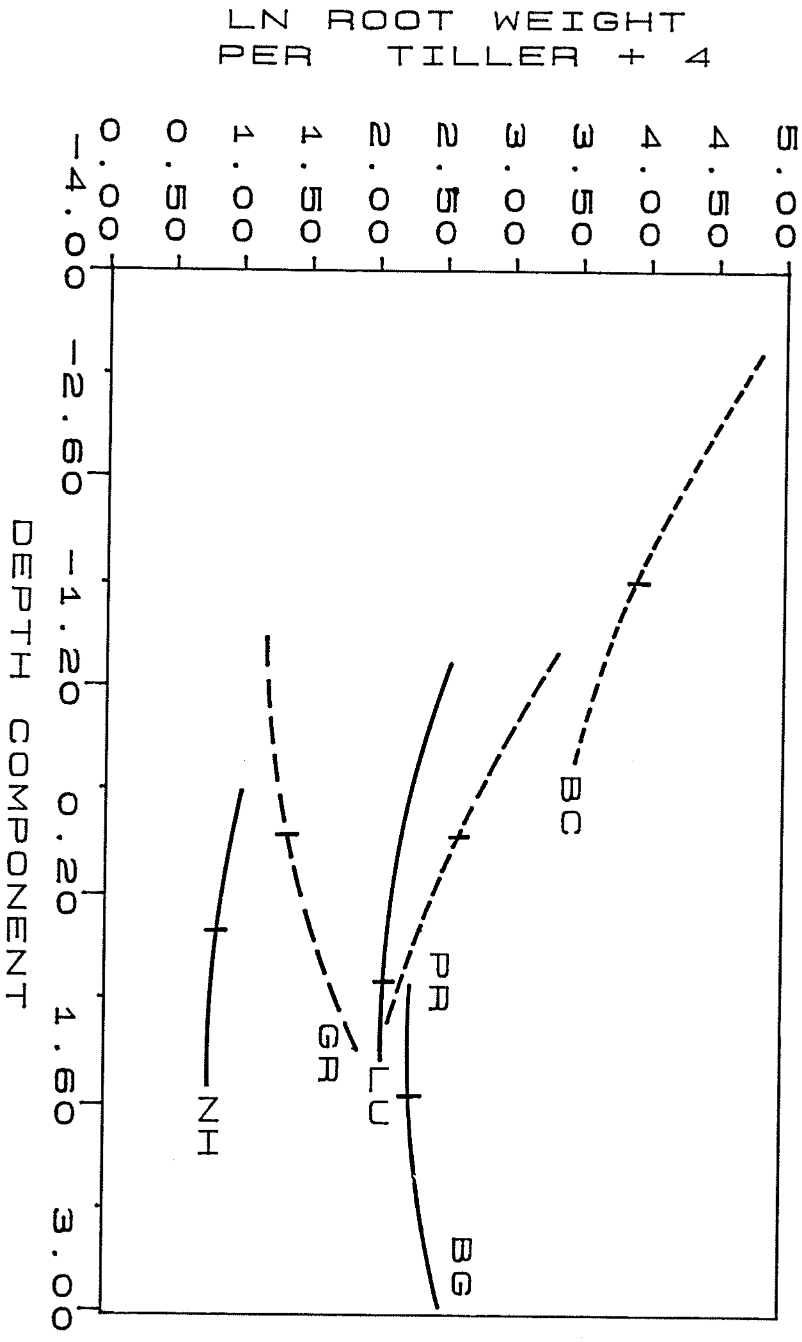

LN ROOT WEIGHT
PER TILLER + 4
0.00
0.50
1.00
1.50
2.00
2.50
3.00
3.50
4.00
4.50
5.00
-4.00
-2.60
-1.20
0.20
1.60
3.00
DEPTH COMPONENT
BC
PR
GR
LU
NH
BG

FIGURE 2.8. Partial regression of pistillate floret production on the depth component for selected wild rice populatons. The functions are plotted over the observed ranges of D scores for each population; mean D scores are indicated by "+".

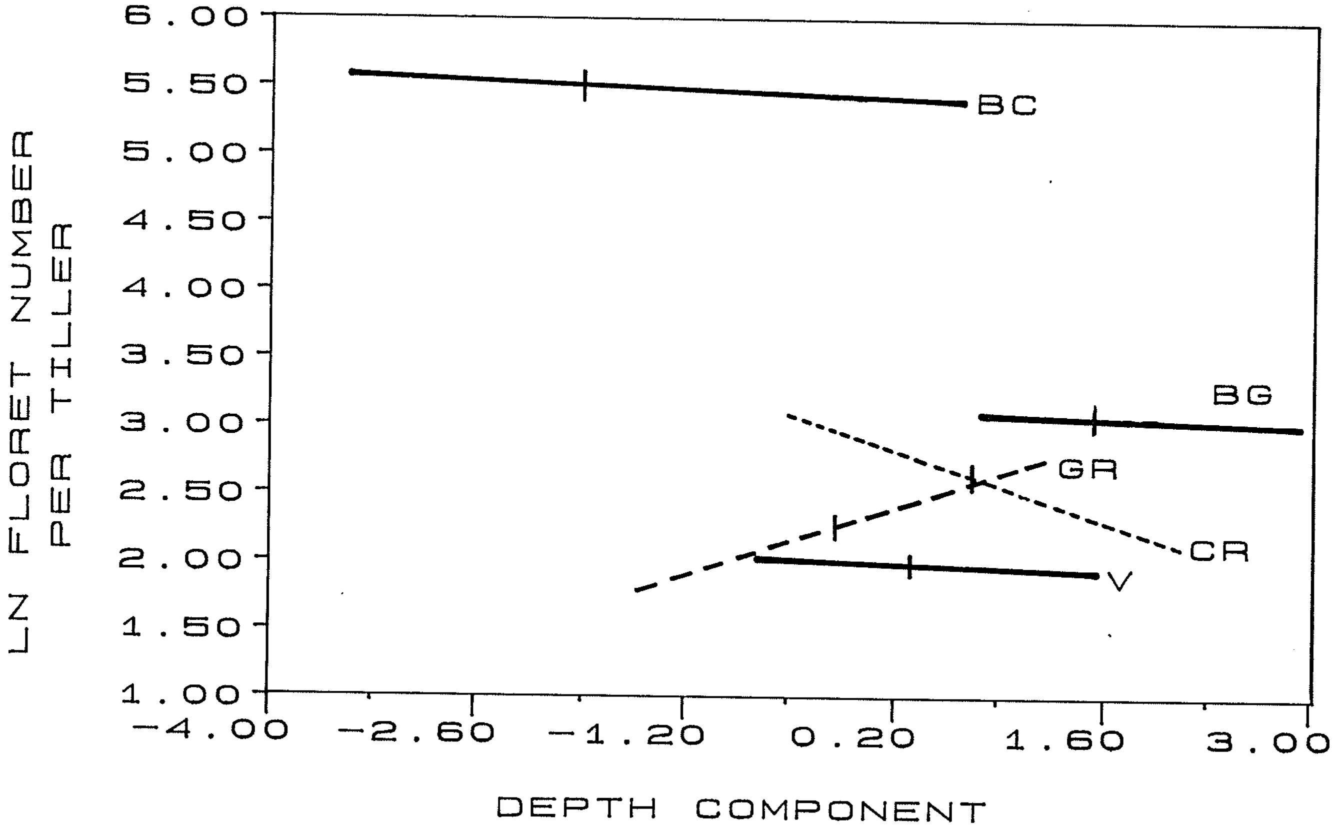

LN FLORET NUMBER
PER TILLER
6.00
5.50
5.00
4.50
4.00
3.50
3.00
2.50
2.00
1.50
1.00
-4.00
-2.60
-1.20
0.20
1.60
3.00
DEPTH COMPONENT
BC
BG
GR
CR
V

FIGURE 2.9. Partial regression of pistillate floret production on the mineral:organic component for selected wild rice populatons. The functions are plotted over the observed ranges of M:O scores for each population; mean M:O scores are indicated by "+".

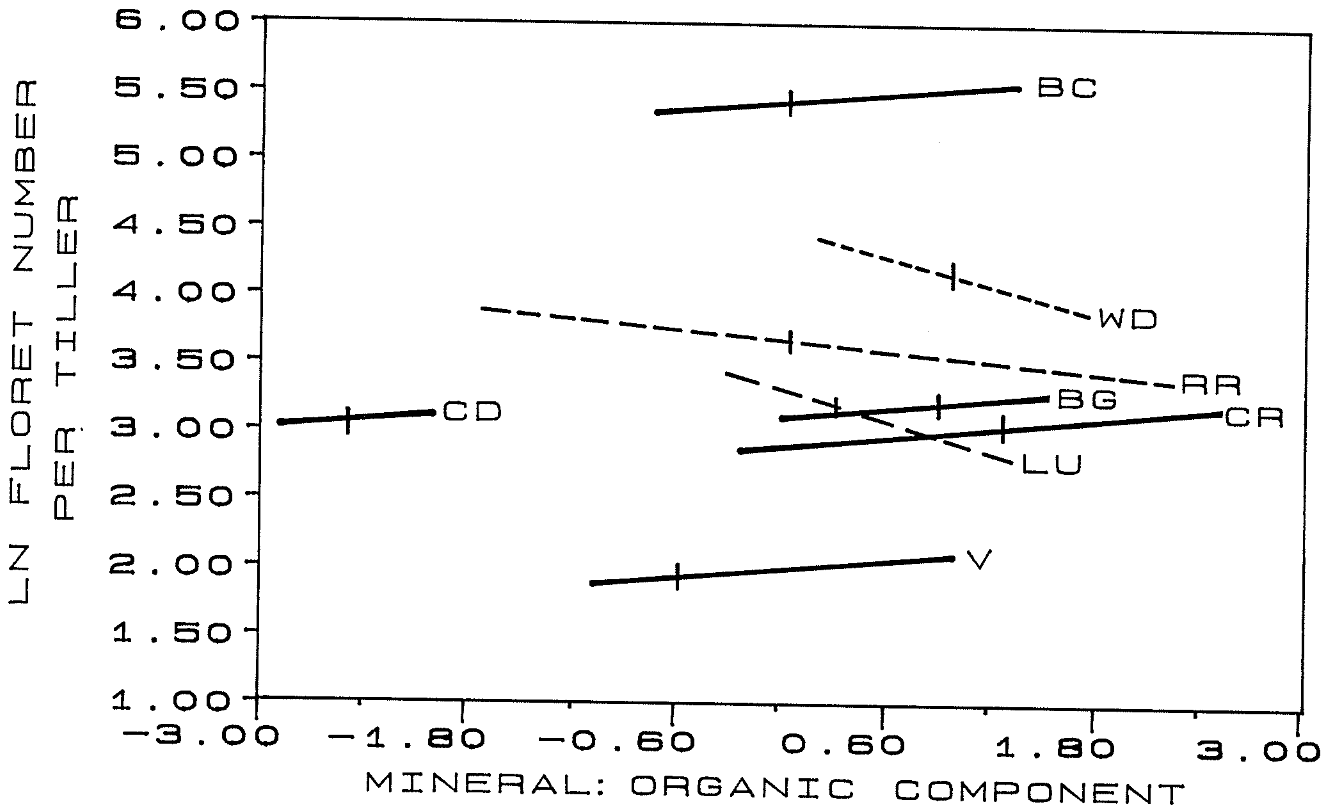
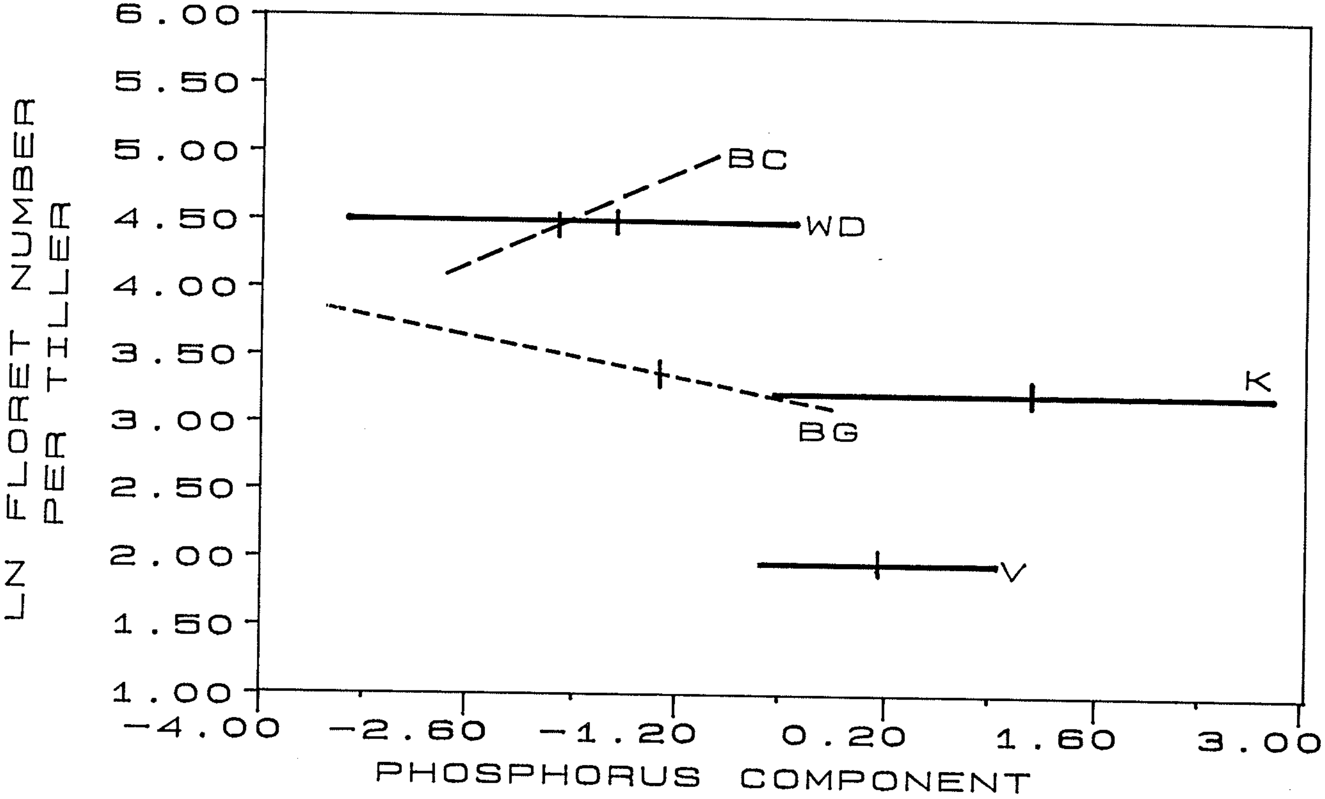

6.00
5.50
5.00
4.50
4.00
3.50
3.00
2.50
2.00
1.50
1.00
LN FLORET NUMBER
PER TILLER
-3.00
-1.80
-0.60
0.60
1.80
3.00
MINERAL: ORGANIC COMPONENT
BC
WD
RR
BG
CD
CR
LU
V

FIGURE 2.10. Partial regression of pistillate floret production on the phosphorus component for selected wild rice populatons. The functions are plotted over the observed ranges of P scores for each population; mean P scores are indicated by "+".



6.00
5.50
5.00
4.50
4.00
3.50
3.00
2.50
2.00
1.50
1.00
LN FLORET NUMBER PER TILLER
-4.00
-2.60
-1.20
0.20
1.60
3.00
PHOSPHORUS COMPONENT
BC
WD
K
BG
V

2.4. DISCUSSION

The equations derived from the analyses of covariance explained a minimum of 68.8% (stem weight) and a maximum of 85.8% (seed length) of the total variance in plant morphology and productivity. Some of the 15-30% residual variation is probably attributable to aspects of the environment that were not considered in this study. However, substantial genetic variation within wild rice populations was demonstrated in experiments described in chapter 1, and this would also contribute to residual variance in the analyses. As noted previously, several features of the life history of wild rice promote within-population variability. The outcrossing breeding system and annual habit are associated with high within-population variability (Grant 1975; Hamrick et al 1979). The potential for prolonged seed dormancy (Halstead and Vicario 1969; Atkins 1986) is particularly important in this regard, since recruits from the seed bank in any given season may represent offspring of parents that grew under differing environmental conditions (Harper 1977; Brown and Venable 1986), and hence were subject to different selective pressures.

In most cases, environmental parameters accounted for 20-30% of the total variation, or 30-40% of the explained variation in plant characteristics. Height was an exceptionally plastic trait: 61.6% of the total variation in this variable was accounted for by the local environment. The mineral-organic, nitrogen, depth, and plant competition components were the most important predictors of wild rice morphology and productivity. The M:O component accounted for nearly 30% of the total environmental variability, and may be considered a measure of general sediment type: high mineral content is typical of clay soils, while muck and peat soils have a greater proportion of organic material. In general high M:O was associated with increased height, decreased root mass, and the production of more numerous, shorter seeds (Table 2.3; Figure 2.9). Nitrogen and water depth are known to be important factors in wild rice growth (Rogosin 1958; Weir and Dale 1960; Thomas and Stewart 1969; Grava 1982; Peden 1982; Sain 1982; Stevenson and Lee 1987), and have been shown to limit the productivity of other aquatic emergent macrophytes (Barko and Smart 1978; 1979; Van der Valk and Davis 1980; Yamasaki and Tange 1981; Lieffers and Shay 1982; De Laune et al 1986; Vermeer 1986). The general nature of the effects observed is consistent with previous reports for this species: high N is associated with decreased height and increased tillering, leaf width, and floret production, and increased water depth is accompanied by the production of fewer, taller stems and has a variable effect on root mass (Table 2.3; Figure 2.7).

Few studies specifically concerned with the effects of interspecific competition on wild rice have been performed. Wild rice is usually found in fairly deep water, being displaced from the shallower margins of a lake or river by perennial emergent species (Aiken et al 1987), and thus appears to perform a fairly early role in the hydrosere (Clements 1916; Van der Valk 1981). Early successional species are typically poor competitors for limiting resources (Grime 1974; Harper 1977). However, there is evidence that in at least some cases a positive correlation exists between wild rice growth and the presence of other plant species (Lee 1987). In these analyses, increases in the plant competition component are generally accompanied by decreases in vegetative productivity and increases in seed weight (Table 2.3). Both of these syndromes are associated in wild rice with rapid development (see chapter 1 and Appendix 2). Rapid seedling establishment and increased seed size at the expense of vegetative vigour are expected to confer a selective advantage when a species having a primarily ruderal or r- strategy is subjected to competitive pressure (Grime 1974; Harper 1977).

Differences among populations (presumably having a genetic basis) generally account for a larger proportion of the variability than does the local environment: 30-50% of the total, or 50-60% of the explained proportion for most plant characters. Differences among populations are particularly important for the "yield" variables of number of pistillate florets per tiller (explains 46.2% of the total), seed length (67.0%), and hundred-seed weight (47.5%) (Figures 2.2f,g,h). It would appear that considerable divergence has occurred among these reproductively isolated populations.

In the experiment comparing wild rice populations in the greenhouse, climatic conditions at the source were found to account for almost all of the variation among populations (see chapter 1), but less congruence was observed in the present field study. This discrepancy is probably due partly to the presence of a larger number of populations in the field study representing a more complete range of variation within the Ignace, Kenora, and Timmins groups, and partly to effects of other, undefined local environmental differences. With the exceptions of leaf width and pistillate florets per tiller, 1/3 to 3/4 of the variation in plant variables explained by differences among populations is lost when populations are grouped into climatic regions. Thus for most plant characters there are substantial differences among populations within climatic groups, even when the local environments are statistically held "constant". Nonetheless, regional factors account for 20-40% of the total variation in most characters, so the climatic factors considered have significant predictive power. With the exception of plant height, the general pattern of association of climatic severity with reduced vegetative and reproductive vigour that was observed in the greenhouse was also evident in the expanded field study. Similar patterns have been observed in other species (Clausen et al 1940; Jennings 1964; McNaughton 1975; Rehfeldt 1978; Christophe and Birot 1979; Hume and Cavers 1982). There appears to be a loose association between maximum daylength and seed size, a plastic relationship reported in a *Desmodium* species (Wulff 1986), although the reduced number of populations sampled for seed characters makes this a tenuous conclusion.

The superior capacity for tiller production by Ignace populations observed in the greenhouse (chapter 1) was also seen in field populations. It was suggested in the last chapter that a genetic potential for extensive tillering might be an adaptive response to environments characterized by a high risk of density-dependent mortality, or an adaptation to increase potential reproductive output with minimal risk. The results of the field study tend to support the latter proposed explanation: 3 of the 4 Ignace populations surveyed were at the high extreme for tiller production (Figure 2.3d). Measured levels of intra- and interspecific competition were not particularly high in these stands (Appendices 4 and 6). However, competition from submerged and floating species was not considered in this study, nor was a demographic analysis performed, so the evidence is insufficient to discard the first hypothesis. A much higher relative tillering capacity was observed for the BC population in the field than in the greenhouse, possibly because a) conditions prevailing in the greenhouse during experiment 1 were not conducive to expression of a genetic potential for high tillering capacity, and/or b) high intra- and interspecific competition observed in the field (see Appendix 4) resulted in differential survival of individuals with higher tillering capactity.

Wild rice in the A population had a poorer relative performance in the field than was observed in the greenhouse, where it fell between plants from the Ignace and Kenora groups for most characters. Its greater similarity to Pickle and Timmins wild rice in the field is more consistent with the relative severity of the climate prevailing at this location (Table 2.1). The performance of BC plants was also relatively poorer in their growth performance in the field than in the greenhouse (except with regard to tiller production), although they were still at the extremes for most vegetative characters. The relative increase in vigour of these populations in the greenhouse vs. *in situ* may indicate a superior ability to take advantage of improved light and nutritional conditions.

The interaction terms in the ANCOVAs accounted for only a small proportion (2-8%) of the variance in most variables. Tiller production and stem weight per tiller were the only variables with an interaction component explaining more than 8% of the total variation. Nevertheless, some interesting patterns emerged when interactions were considered over all populations and all environmental variables.

The typical wild rice plant was taller and produced fewer tillers when depth was increased. Wild rice from the GR population, however, appeared to be more vegetatively and reproductively vigourous as D increased (see Tables 2.3 and 2.5, and Figures 2.7 and 2.8). The depth component for the GR population was in an intermediate range, and it is not legitimate to extrapolate the regression line beyond values of D actually observed in this population (Sokal and Rohlf 1981). Nevertheless, it is possible that this wild rice population is physiologically adapted for improved productivity in deeper water, and could serve as an interesting subject for further study.

Four of the five populations in the Kenora climate group had at least one interaction term involving M:O (Table 2.5). Increases in the value of the mineral:organic component were associated with decreased tillering in LU and LDB populations (Figure 2.5), and with reduced pistillate floret production in Lu, RR, and WD populations (Figure 2.9). Leaf width and biomass variables were also negatively influenced in RR wild rice. It appears that these populations, with M:O values in the intermediate to high-intermediate range, are relatively intolerant of highly mineral sediments. The opposite effect was seen for BC wild rice; this population had increased tillering in association with increased M:O, which was in the intermediate range.

Two Kenora populations, BG and WD, had values of the phosphorus component in the low range, and appeared to be positively influenced by low P levels (Table 2.5). Increased pistillate floret production and leaf width was associated with decreases in P for the BG population (Figure 2.10), while WD wild rice produced more tillers with low P. By contrast, the BC population, which was also at the low end of the range for the P component, had a decreased pistillate floret production in association with lower P. BC wild rice would appear to require higher levels of P for optimum productivity than is the case for BG or WD wild rice.

In summary, this study has related wild rice morphology and productivity to local environmental conditions, climatic conditions, and differences among populations not accounted for by these factors. 70 to 85% of the total variation was explained by these parameters. The largest proportion of variation in most variables was explained by differentiation of populations; 1/2 to 2/3 of the explanatory power was retained for most variables when populations were grouped by climatic similarity. The previously observed pattern of reduced vegetative and reproductive vigour with increasing climatic severity persisted, although more overlap was apparent. The local environment accounted for 20-30% of variation in most plant variables. Plant height was the exception, and was primarily a function of local conditions, especially water depth. Interaction terms made only minor contributions to the predictive equations, but some interesting patterns suggesting particular sensitivity or adaptive advantage under specific environmental conditions were observed for some populations.

Chapter 3

DIFFERENTIAL RESPONSES OF POPULATIONS TO VARYING CULTIVATION CONDITIONS

3.1. INTRODUCTION

The harvesting of wild rice (*Zizania aquatica* L.) has historically been an important facet of the economies of Northwestern Ontario and Eastern Manitoba (Jenks 1900; Chambliss 1940). Interest in the commercial lake production of wild rice has recently expanded to other regions of Ontario and to other provinces (Aiken et al 1987). As new stands are developed, demand is increasing for information regarding preferred seed sources and management techniques to maximize and stabilize production.

Results presented in chapter 1 indicated that substantial genetically-based differentiation for plant characteristics such as potential seed production, maturity, and seed size exists among Ontario wild rice populations. However, direct comparisons have been made only in the greenhouse under conditions as close as possible to optimum: consistently high light levels and temperatures, adequate sediment nutrients, and shallow, unvarying water levels prevailed. Effects of average water depth, edaphic conditions, and plant competition can be statistically corrected for in comparisons of populations *in situ* (chapter 2), but the relative contribution of such environmental factors as temperature, light availability, water depth fluctuations, predation, and disease to observed differences in wild rice growth in the field is not readily quantified. Thus, it is not known if the relative ranking of populations observed under controlled conditions persists when they are compared in common natural environments. This information is essential to the development of efficient procedures for the identification and selection of superior commercial wild rice strains.

In this study, wild rice from four populations previously compared in the greenhouse was introduced into a lake that was deemed suitable for wild rice growth but had not formerly supported wild rice. The purpose of the experiment was to ascertain if the relative performances of these populations observed under controlled conditions persisted when they were compared in a natural environment.

3.2. METHODS

3.2.1. Seed Sources

Wild rice seed from four populations was planted in the spring of 1984. The seed sources and abbreviations used throughout the remainder of this paper are as follows: Dollar Lake, Ontario (D: 49° 40' N, 91° 53' W); Beaveroo Lake, Ontario (B: 49° 41' N, 91° 19' W); Whitedog Lake, Ontario (W: 50° 08' N, 94° 53' W) and Mercer River, Saskatchewan (S: 55° 05' N, 105° 30' W). Some field data pertaining to the regional and local environments of the source stands are presented in Table 3.1. Wild rice plants from these populations were grown from seed in two greenhouses from June to October 1984 as part of experiment 3 discussed in chapter 1. One greenhouse (G1) was located at Lakehead University in Thunder Bay, Ontario, and the other (G2) was situated 3.3 km north of the campus. Conditions in the greenhouses differed in two important respects. G1 was shaded by adjacent buildings, so the ambient natural light level was lower at that location. However, G1 was not as well ventilated as G2, with the result that maximum daytime temperatures were higher.

3.2.2. Study Site and Experimental Design

The experimental lake "E" is located in the Ignace District of Northwestern Ontario (49° 39' N, 91° 22' W), and covers approximately 25 ha. Prior to the initiation of this experiment, the water was 150 to 175 cm deep throughout most of

TABLE 3.1. Selected environmental parameters for wild rice seed source populations and the experimental lake.

	Location				
	S	D	B	W	E
North Latitude	55°05'	49°40'	49°41'	50°08'	49°39'
West Longitude	105°30'	91°53'	91°19'	94°53'	91°22'
Growing-Degree-Days (5°C)*	1262.4	1497.4	1497.4	1670.2	1497.4
Mean Date of First Frost (year-day)**	253	262	262	270	262
% Probability of Frost before September 1**	25	5	5	0	5
Water Depth (cm)+	100	84	68	73	107
Sediment Nitrogen++	-	1.08	1.14	1.79	0.57
Sediment Phosphorus++	-	1.79	0.94	1.28	2.00
Sediment Potassium++	-	2.71	2.00	10.16	2.83
Sediment Iron++	-	59.8	56.3	115.2	73.9

*Source: Environment Canada (1982a)

**Source: Environment Canada (1982b)

+Depth for S estimated from Archibold and Weichel (1984)

++Values given in $g \cdot m^{-2} \cdot 0.2m^{-1}$; see Lee (1986) the lake, so the outlet was cleared to achieve a lower level suitable for growing wild rice. Salient climatic data, the mean water depth, and the mean sediment macronutrient and iron concentrations measured in August 1984 are presented in Table 3.1.

One 10 kg bag of seed from each population was broadcast by hand in a single north-south strip across the lake (Figure 3.1). Although it would have been more desirable for statistical purposes to have a randomized arrangement of the four populations over the entire lake (Cochran and Cox 1957), such an approach was not logistically feasible in this case. Since seed must be broadcast into the water, it is subject to lateral drift as it travels from the water surface to the surface of the substrate. It was thus necessary to leave large empty spaces between the populations to ensure that they remained discrete. Preliminary studies showed that the lake was fairly uniform for those environmental parameters important for wild rice productivity, but as a precaution, edaphic conditions for each population were measured in the experiment (see below).

The harvest was carried out in August 1984, when wild rice was in the grain-filling stage. For each population, 10 (0.5 m x 0.5 m) quadrats were sampled at regular intervals on a north-south transect across the lake. A sample unit consisted of all the wild rice plants in the quadrat, a water depth measurement, and a 20 cm column of sediment. Plants and sediments were placed in plastic bags and transported on ice to the laboratory for processing. Laboratory procedures were as described in chapter 2. Wild rice morphometric variables obtained were as follows: tiller and plant density (stems or plants per m^2), maximum height, mean maximum aerial leaf width, mean number of tillers per plant, mean shoot dry weight per tiller, mean root dry weight per tiller, and mean number of pistillate floret pedicels per tiller. In addition the following sediment characteristics were recorded for each

FIGURE 3.1. Seeding pattern on the experimental lake near Ignace, Ontario

sample: % loss on ignition (LOI), bulk density (BD; in $g \cdot cm^{-3}$), pH, and extractable concentrations of nitrogen (N), phosphorus (P), potassium (K), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), calcium (Ca), and magnesium (Mg). Nutrient concentrations are expressed in units of $g \cdot m^{-2} \cdot 0.2m^{-1}$ (Lee 1986).

3.2.3. Data Analyses

Subprogrammes in the SPSS statistical package (Nie et al 1975; Hull and Nie 1981) were used for all tests. When necessary (as indicated by skewness and kurtosis statistics) variables were normalized by natural logarithm (*ln*) transformations prior to analysis.

One-way analyses of variance (ANOVAs) by population were conducted for all variables. The assumption of homogeneity of variance among groups was tested using Cochran's "C" statistic, which was nonsignificant ($p>0.01$) for all variables. A modified least significant difference (LSD) ranges test (Nie et al 1975) at the 0.01 significance level was performed using all variables that were significant ($p \leq 0.01$) in the ANOVA.

The initial ANOVAs revealed significant differences among populations for 3 of the edaphic variables: Fe, Mn, and Ca. The modified LSD test indicated that the west end of the lake, where W wild rice was planted, had significantly lower sedimentary concentrations of these elements than the eastern part, where B and D plants were grown (Table 3.2). Consequently it was possible that some of the differences in wild rice productivity among the experimental populations were due to edaphic rather than genetic factors. An ANCOVA by multiple regression with dummy variables was required in order to examine this possibility.

This method was described in detail in the previous chapter. Briefly, the procedure was as follows: 1. Principal components (PC) analysis was performed on the edaphic variable set to derive new, uncorrelated variables that summarized the

TABLE 3.2. West-east gradient in edaphic characteristics of the experimental lake. Means with different suffixes were significantly ($p \leq 0.01$) different in a modified LSD test.

	Population Seeding Location			
	W	S	D	B
Fe	51.9a	75.7ab	84.6b	81.2b
Mn	1.64a	2.10ab	2.45b	2.48b
Ca	157.8a	185.0ab	205.5ab	254.0b
PC1	-0.96a	-0.06ab	0.37b	0.55b

environmental data. 2. A new data matrix containing wild rice variables and principal component scores for each case was generated. 3. Hierarchical multiple regressions were conducted for each plant characteristic. Independent (predictor) variables were entered in 3 steps. First, PC scores and their squares were entered stepwise to account for variation in plant growth caused by edaphic factors. Second, dummy variables representing the four populations were entered as a group to show their relative performances after correction for edaphic differences. Finally, interaction terms for each population-by-PC combination were entered stepwise to detect any differences among the populations in response to variation in edaphic factors.

3.3. RESULTS

3.3.1. Principal Components Analysis

The first seven factors derived accounted for 93.3% of the total environmental variation measured. The eighth and subsequent components (thirteen were derived) each accounted for less than 3% of the variation, and were omitted from the remainder of the analysis.

Table 3.3 summarizes the results of the principal components analysis. For each component, the % variance explained and the coefficients of the rotated factor matrix are given. The square of a coefficient gives the proportion of the variation in that variable accounted for by the PC it is loading on. For ease of interpretation, the major contributing variables are identified for each component, and each is given a descriptive designation.

ANOVAs by population on the PC scores were performed as a check. As expected from the ANOVAs on the original environment variables, only M1, which was primarily a function of Mg, Mn, Fe, and Ca, was significantly different among

TABLE 3.3. Summary of principal components analysis on experimental lake environmental parameters: coefficients of the rotated factor matrix and interpretation.

	Principal Component						
	1	2	3	4	5	6	7
Designation	Mineral 1	Mineral 2	Nitrogen	Phosphorus	Depth	Potassium	Organic
Rotated Matrix Coefficients							
Bulk Density (BD)	0.210	0.702	0.028	-0.217	-0.165	0.018	0.500
Loss on Ignition (LOI)	-0.150	0.338	0.118	-0.420	0.017	-0.302	0.716
pH	0.186	0.161	0.942	-0.004	0.014	0.027	-0.089
Phosphorus (P)	0.176	-0.158	0.100	0.917	0.185	-0.031	-0.175
Nitrogen (N)	-0.111	0.007	0.763	0.172	-0.157	0.302	0.443
Iron (Fe)	0.905	0.233	0.036	0.169	-0.104	0.167	-0.104
Manganese (Mn)	0.954	0.048	-0.075	0.016	0.103	0.083	-0.028
Zinc (Zn)	0.172	0.920	0.199	0.072	0.064	-0.119	0.074
Copper (Cu)	-0.188	0.787	-0.017	-0.303	0.332	0.073	0.028
Calcium (Ca)	0.877	0.069	0.146	-0.030	-0.329	0.001	0.138
Magnesium (Mg)	0.774	-0.354	0.204	0.257	-0.201	0.144	-0.147
Potassium (K)	0.222	-0.040	0.166	-0.022	0.020	0.940	-0.098
Water Depth (WD)	-0.217	0.162	-0.087	0.174	0.926	0.012	-0.037
% Variance Explained	30.7	23.7	12.8	12.0	7.4	3.5	3.1
Important Variables	Mg,Mn,Fe,Ca	Zn,Cu,BD	pH,N	P	WD	K	LOI,BD,N

populations ($F_{(3,36)}=5.92$; $p<0.01$). The modified LSD test confirmed the existence of an east-west gradient in sediment mineral concentrations, with W sediment at the low end (Table 3.2; Figure 3.2).

3.3.2. Analyses of Covariance

Environmental and Interaction Effects

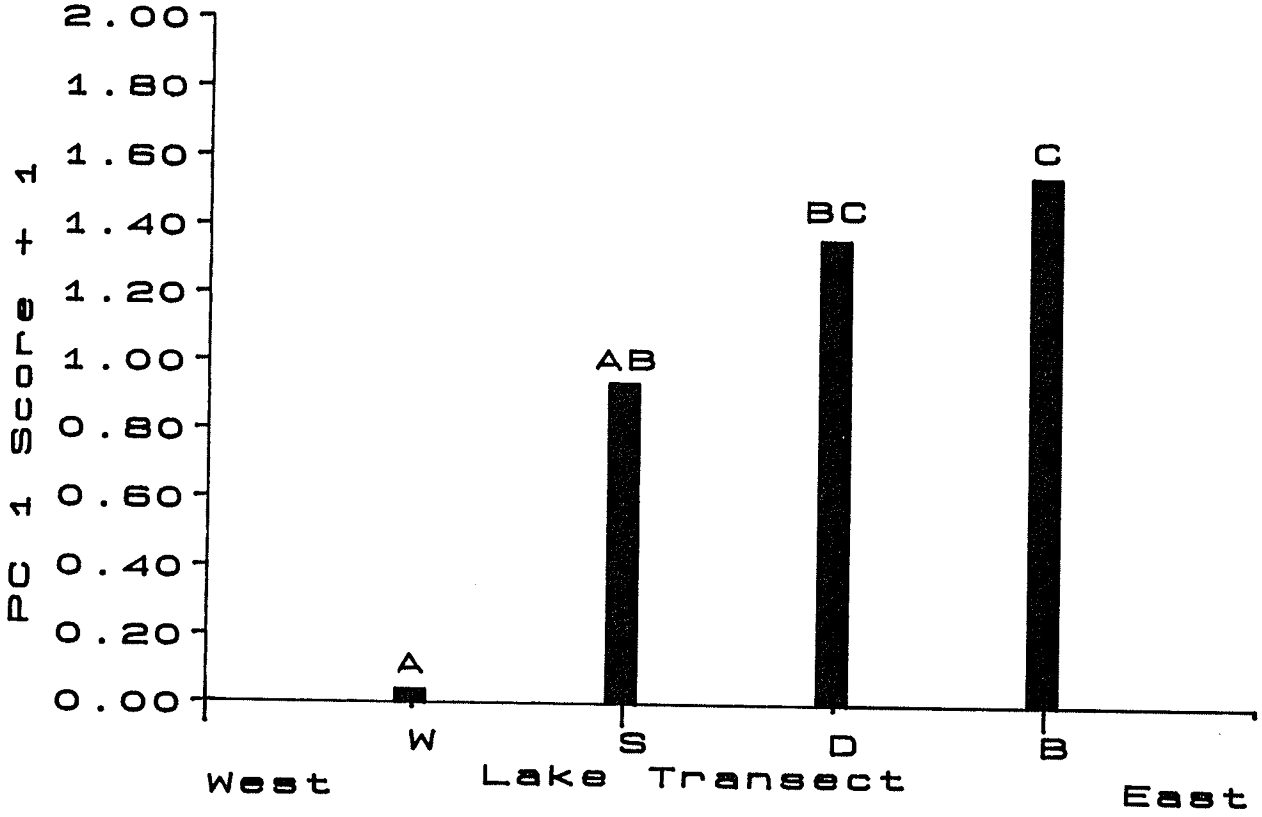
The water depth component was the only covariate with a significant slope in the regression equations. Tiller and plant density (natural logarithms) were a linear function of the depth component, with partial regression coefficients of -0.316 and -0.258 respectively. Leaf width and (*ln*) stem weight, with coefficients of -0.368 and -0.086, were functions of the square of the depth component. No other significant covariates emerged in the analyses; in particular, the first mineral component did not influence wild rice plant characteristics in the lake. There were no significant interaction terms in any of the analyses, indicating that wild rice plants from all populations responded similarly to the range of environmental variation encountered in the experimental lake.

Variation among Populations

Since variation in the first mineral component did not significantly affect any of the wild rice characteristics measured, observed differences among populations were not attributable to the east-west gradient in Fe, Mn, and Ca. Consequently, the "corrected" population means obtained in the ANCOVAs were virtually identical to the observed means that were not corrected for environmental variation, and ranges tests of pairs of means were valid.

Wild rice populations were better differentiated in the lake than in G1, and more poorly differentiated than in G2. In the lake, significant ($p \leq 0.01$) differences were observed for stem weight, root weight, pistillate floret production, and leaf

FIGURE 3.2. East-west gradient in mean score for the first principal component across the the experimental lake. Bars with different associated letters were significantly different ($p \leq 0.01$) in a modified LSD test



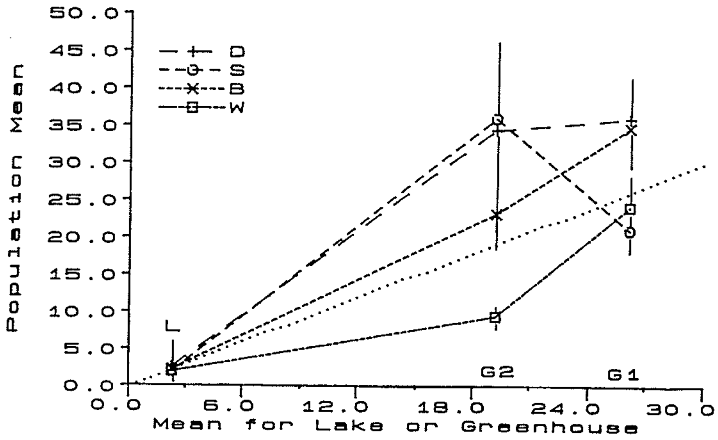
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
PC 1 Score + 1
A
AB
BC
C
W
S
D
B
West
Lake Transect
East

width. There were no significant differences for plant or tiller density, tiller production, or plant height. Figure 3.3(a-f) shows individual population performance under each of the three different cultivation regimes in the context of the mean performance for all populations. In the experimental lake, plants from the B population were the most vigourous in terms of stem weight, root weight, leaf width, and pistillate floret number. D wild rice plants were at the low extreme for these characteristics, with S and W intermediate.

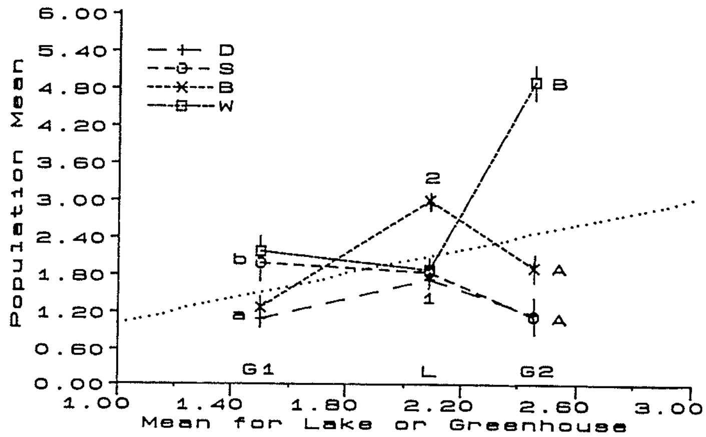
When progeny from the same populations were grown in G1, no significant differences at the 1% level were observed for any variable except stem weight (Figure 3.3b). Wild rice from W produced the largest stems and most florets per tiller, and D plants were again at the low extreme. On the average, wild rice plants in the lake produced many fewer tillers (Figure 3.3a) and slightly smaller roots (Figure 3.3c) and fewer florets (Figure 3.3f) than in G1. Only plants grown from B seed had larger roots and more numerous pistillate florets in the lake. Overall average stem weights (Figure 3.3b), heights (Figure 3.3d), and leaf widths (Figure 3.3e) were greater in the lake than in G1. The increase in height was fairly uniform for all populations, while B and D progeny showed the greatest increase in leaf width in the lake. B and D plants produced larger stems in the lake, but there was a slight decrease in the stem weights of plants from S and W in the lake compared to G1.

A different pattern again emerged when progenies were raised in G2. There were significant ($p \leq 0.01$) differences among populations for all variables, and plants from W had the highest mean values for all characters except tiller production, for which the D and S populations were superior. On the average, wild rice plants produced larger stems and roots with broader leaves and more pistillate florets in G2 than in G1 or the lake, but this overall mean increase was entirely due to the

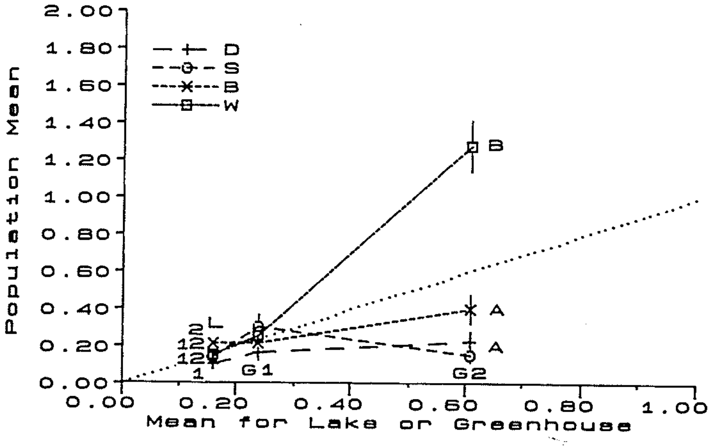
FIGURE 3.3. Means (± SE) of wild rice characteristics for four populations in three environments relative to overall mean performance in each environment. Means with different letter or number designations for a given environment were significantly different ($p \leq 0.01$) in a modified LSD test. L, Lake; G1, Greenhouse environment 1; G2, Greenhouse environment 2



[a] Tiller Number

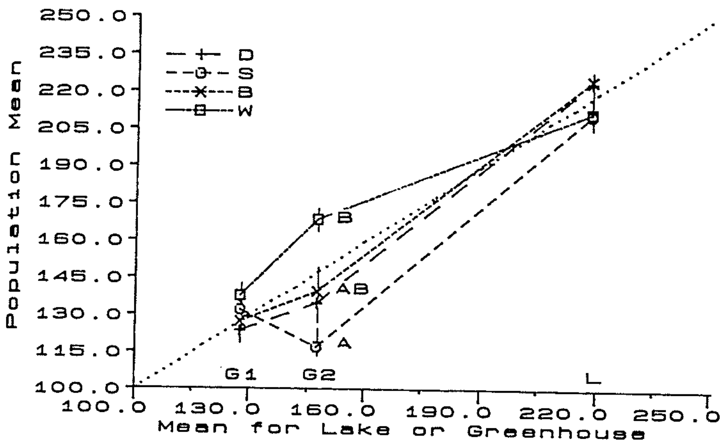


[b] Stem Weight

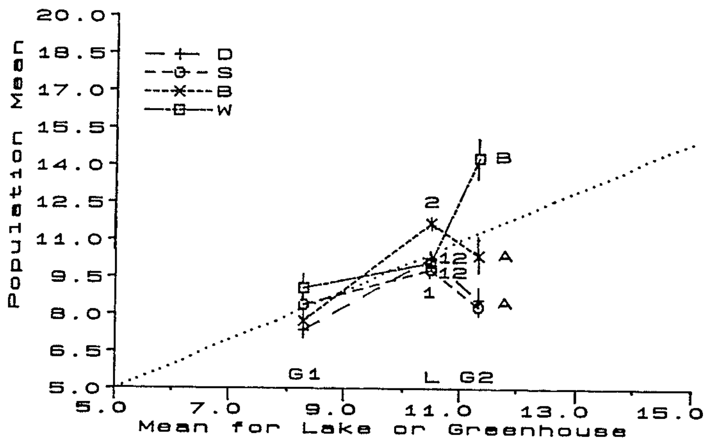


[c] Root Weight

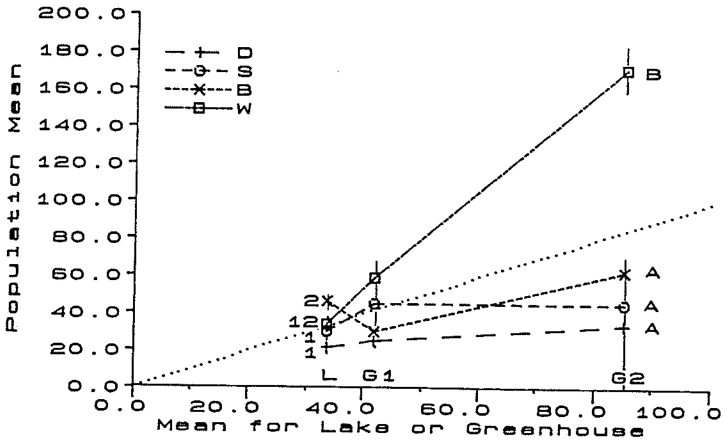
[d] Height



[e] Leaf Width



[f] Pistillate Floret Number



response of W plants: progeny of the other three populations were either essentially unchanged or decreased in productivity. Mean plant height in G2 was slightly greater than in G1, and much less than in the lake; again the increase relative to G1 was due to the response of W plants. Tiller production was also intermediate in G2, and for this character alone W wild rice exhibited a smaller than average change.

3.4. DISCUSSION

This study has demonstrated unequivocally that superior performance of wild rice populations evaluated in the greenhouse does not guarantee superior performance in the field. Genotype-by-environment interactions are very commonly observed in experiments comparing genetically homogeneous cultivars of crop plants (Finlay and Wilkinson 1963; Allard and Bradshaw 1964; Eberhart and Russell 1966). The population-by-environment interactions observed here may be considered analogous, with the distinction that the average responses of different distributions of genotypes to varying environments are under consideration rather than the specific responses of different individual genotypes.

The relative performances of progeny of the four populations were similar in all three environments for tiller number and plant height. These two characteristics were primarily affected by the difference in water depth between the greenhouse (30 cm) and lake (mean 107 cm) environments. The sensitivity of these traits to water level is well-documented (Rogosin 1958; Weir and Dale 1960; Thomas and Stewart 1969; Stevenson and Lee 1987), and the significance of the depth component in the ANCOVAs suggests that it was a limiting factor for wild rice growth in this particular lake.

For other variables, productivity of the D and S wild rice populations was not dramatically different in the three environments. Plants had similar or slightly larger stems with similar or broader leaves, but smaller or similar roots and floret numbers in the lake versus the greenhouses (Figure 3.3). The B population was notable for its superior performance in the lake, but the magnitude of the difference in plant size and productivity between the lake and the greenhouses was not great. It is possible that this wild rice is better adapted to deep water than the others, although water depths measured at the source in 1984 were not greater for this population (Table 3.1).

The performance of the W population was most profoundly influenced by environment. In G2 these plants were substantially more vigourous than the others for all characters considered except tiller production, but they were similar to D and S and slightly less productive than B plants in the lake (Figure 3.3). Some factors appeared to be limiting W productivity in G1 and in the field experiment. In chapter 1, significant differences between the two greenhouses in wild rice growth were attributed to poorer ventilation in G1 and shading of G1 by neighboring buildings, resulting in lower natural light levels and higher (supra-optimal) maximum daytime temperatures relative to G2.

It appeared that the capacity of W progeny to exploit the (presumably) more favourable temperature and light conditions in G2 was not equalled by plants from the D, B, or S seed sources. Plants derived from the W population seemed to have a greater magnitude of response, and those from the other three seed sources a greater equability of response (*sensu* Garbutt and Zangerl, 1983) to varying environments. Potential yield capacity is often positively correlated with environmental sensitivity in crop plants (Finlay and Wilkinson 1963; Eberhart and Russell 1966; Perkins and Jinks 1973; Schwagerle and Bazzaz 1987). The ability of individuals in natural (i.e. undomesticated) populations to exploit favourable conditions could arise by either or both of two mechanisms (Lewontin 1957). First, it could arise through genetic heterogeneity in the population as a whole, by flexibility at the population level of organization. A superior capacity to utilize available resources could also arise through differential developmental flexibility of individuals, or phenotypic plasticity. Genetic variability for direction and degree of developmental plasticity has been reported within and among other species (Marshall and Jain 1968; Bradshaw 1974; Hickman 1975; Brown 1983; Marshall et al 1986; Schwagerle and Bazzaz 1987).

All species must achieve a compromise between maximizing fitness for a specific environment and maintaining the flexibility to respond to environmental changes. The role of life-history and niche (in the broadest sense of the term; see Hurlbert 1981) characteristics in determining adaptive strategies for different species has been a subject of considerable interest (Harper 1967, 1977; Stearns 1977; Zangerl et al 1977; Hamrick et al 1979; Caswell 1983; Morisset and Boutin 1984). Some of the concepts used in these studies, most of which focus on intraspecific patterns, may be extended to the interpretation of comparisons of populations within species. Jennings (1964) reported on genetic differences among temperate and tropical varieties of *Oryza* in yield response to management practises such as fertilizer application, water depth control, and plant spacing, and rationalized the differential sensitivities in terms of adaptation to generally prevailing environmental conditions for the two groups. Differences in climate may be an important factor in the differential sensitivities of W and the other populations observed in this experiment. Zangerl et al (1977) argue that increased variability (in the form of plasticity and/or genotypic and/or allelic diversity) is expected in populations that are subject to relatively less stressful conditions, or more spatial and/or temporal heterogeneity. The W source population is located in the Kenora climatic region, which has a more moderate climate than the other source lakes or the experimental lake (see Table

3.1 and Appendix 1), and climatic conditions may be considered a measure of persistent stress on a population. It was noted in chapter 1 that plants from populations in the Kenora region (Whitedog L. and Rat R. Bay) were more sensitive than others to varying greenhouse location. Kenora populations also appeared to be more sensitive to variation in local environmental parameters in the field studies discussed in chapter 2; they appeared in a disproportionately large number of interaction terms in the ANCOVA (see Table 2.4).

It is logical that extreme flexibility (on the individual or population level) would be non-adaptive for wild rice populations in relatively severe climates, since the production of large tillers with more pistillate florets is generally accompanied by delayed reproduction (see Appendix 2). The potential to suspend maturation in favour of luxurious growth, or an early selective advantage for large, late-maturing individuals under favourable conditions would be strongly selected against in locations with a short growing season. A similar explanation for differences in temperature sensitivity among montane and lowland frogs has been advanced by Smith-Gill (1983).

To confirm the hypothesis that intra-population variation in phenotypic flexibility of wild rice is systematically related to climatic severity, further experiments using more populations and a more diverse array of environments should be performed. It would also be of interest to determine whether differential environmental sensitivity is associated with levels of within-population genetic variability as well as developmental plasticity.

In conclusion, this study has demonstrated that wild rice populations differ in the magnitude and direction of their sensitivity to environmental variation. This observation raises questions regarding the evolutionary significance of such differences and the mechanisms by which they are manifested, but it also has some practical implications for wild rice breeding. Artificial selection should be carried out in environments that resemble the targeted ones as much as possible. It might be possible to deliberately select for high or low environmental sensitivity as described by Jinks and Connoly (1973; 1975) and elaborated by Falconer (1981), to obtain cultivars tailored for use in managed or unmanaged wild rice stands. Finally, it will be absolutely essential to adhere to the standard plant breeding practise of field-testing prospective new varieties in several locations and over several years to ensure that their desired characteristics are fairly stable before they are released for commercial use.

Chapter 4

DIVERGENCE AMONG SOURCE AND INTRODUCED POPULATION PAIRS

4.1. INTRODUCTION

Wild rice (*Zizania aquatica* L.) is the only cereal that is indigenous to North America. Its historical importance to the aboriginal peoples and early European settlers of the Great Lakes region is well established (Jenks 1900; Chambliss 1940), and man has probably been a primary agent of dispersal of this species. More recently, wild rice has been exploited commercially as a cash crop, leading to the establishment of many new populations. In Canada most of these introduced populations are unmanaged and reseed themselves every year. As a result, they are subject to the same natural selection pressures as natural, indigenous populations.

The stability of introduced populations for parameters affecting productivity is a question of concern both to wild rice breeders and to growers. If evolutionary change is rapid in this species, management practises to maintain desirable traits in newly established populations may be required. New wild rice stands are usually small and reproductively isolated, both features that facilitate relatively rapid stochastic shifts in the genetic architecture of populations (Falconer 1981; Merrell 1981). Differences in the direction and/or degree of selection pressure would increase the probability of divergence between introduced and source populations.

Many aspects of the environment may exert directional selection pressure on wild rice populations. In chapter 2, climatic conditions, water depth, sediment nitrogen concentration, and the ratio of mineral to organic components in the sediment were found to be very important in determining the characteristics of wild rice populations. However, the most important environmental parameters influencing evolution of the species will be those that operate consistently over many generations. Edaphic conditions and water depth can fluctuate markedly from season to season, and may also show directional change as a given lake or river passes through different phases of the hydrosere (Sain 1982; Keenan and Lee 1987). Work discussed in previous chapters has indicated that climate is an important factor influencing the phenology, morphology, and plasticity of wild rice plants from different populations. Further, the analysis in chapter 1 of progeny derived from populations that were introduced into climatic regimes different from their native ones suggested that climate may exert sufficient selective pressure to rapidly alter the characteristics of wild rice populations.

This chapter reports on studies of introduced wild rice stands. Changes in introduced populations were examined using two approaches: 1)comparison of progenies derived from a source and two introduced populations cultivated over a common range of depth and fertilizer treatments; and 2)comparison of introduced and source population pairs *in situ*. The objectives of the studies were to determine if significant shifts in the productivity and/or plasticity of the introduced wild rice populations have occurred, and if so, whether the changes follow trends that would be expected if climate is a major selective force directing evolutionary change in this species.

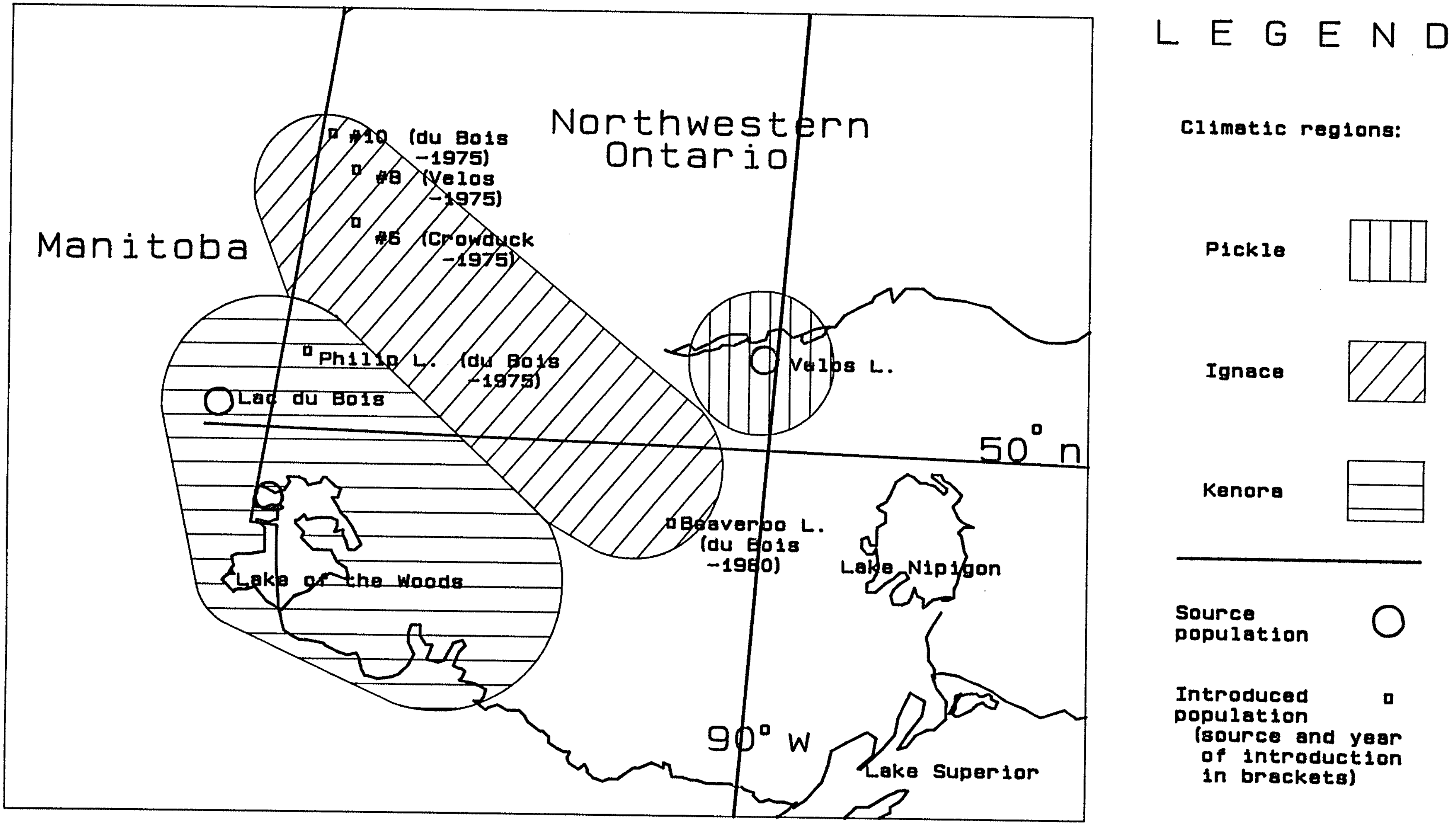
4.2. METHODS

4.2.1. Raft Experiment

Cultivation Conditions

Wild rice seed was obtained from 2 introduced populations (Mercer River, Saskatchewan and Beaveroo Lake, Ontario) and their source (Lac du Bois, Manitoba). Locations of the Ontario stands and the year of introduction are shown in Figure 4.1. The locations were assigned to the climate groups shown using the Q-type clustering procedure described in chapter 1 (see Appendix 1), and climatic data for

FIGURE 4.1. Map of Northwestern Ontario showing wild rice populations studied. For introduced populations, source location and year of introduction are shown. Not shown: Mercer River, Saskatchewan.



Northwestern Ontario
Manitoba
#10 (du Bois -1975)
#8 (Velos -1975)
#5 (Crowduck -1975)
Philip L. (du Bois -1975)
Lac du Bois
Velos L.
50° n
Beaverbo L. (du Bois -1980)
Lake Nipigon
Lake of the Woods
90° W
Lake Superior
LEGEND
Climatic regions:
Pickle
Ignace
Kenora
Source population
Introduced population (source and year of introduction in brackets)

each population are shown in Table 4.1. Two weeks after germination was initiated (June 1985), seedlings were planted in a tub containing greenhouse loam alone or with slow-release fertilizer (Sierra Blend Osmocote (18-6-12), Sierra Chemical Company, Milpitas, California) applied at a rate to give 0, 200, 400, or 800 kg N ha^{-1}. The tubs were suspended at a depth of 25 or 50 cm below the water surface from 2 rafts floating on a sheltered pond (see Stevenson and Lee (1987) for details of the raft design). There were 2 tubs with 5 plants each (10 plants total) for each of the 24 seed source by depth by fertilizer treatment combinations. All of the tubs on each raft were suspended at the same depth, but the positions of the seed source-fertilizer treatment combinations were randomized within each raft. Plants were grown to maturity and harvested in September 1985.

Laboratory Procedures

At the time of harvest, mature seed was collected, and morphometric plant variables recorded as follows: tiller number per plant, height from the base of the stem to the flag leaf of the tallest tiller, maximum width of the flag leaf of the main tiller, mean dry shoot weight per tiller, mean dry root weight per tiller, and number of pistillate floret pedicels on the main tiller. After drying at 80°C, the total weight and mean length of 20 mature caryopses per plant were recorded.

Data Analyses

A considerable amount of material was lost to predation, probably by ducks and/or muskrats. To keep the design of the experiment balanced, each seed source/depth/fertilizer cell was represented by only 5 plants in the analysis instead of the 10 originally planned. For cells with more plants available, 5 cases were chosen at random.

TABLE 4.1. Locations and climates of introduced and indigenous source wild rice populations studied.

Population	Region*	Source	North Latitude	West Longitude	Annual Growing-Degree-Days (5° C)	Average Date of First Fall Frost (Year-Day)	Probability of Frost before Sept. 1 (%)	Maximum Daylength (minutes)	Study**
Velos Lake	Pickle	-	50° 50'	90° 08'	1276.4	250	25	0	F
Mercer River	Pickle	Lac du Bois 1935	55° 05'	105° 30'	1262.4	253	25	40	R
#8	Ignace	Velos Lake 1975	51° 28'	94° 15'	1519.9	263	0	990	F
#6	Ignace	Crowduck L. 1975	51° 22'	94° 15'	1519.9	263	0	990	F
#10	Ignace	Lac du Bois 1975	51° 47'	95° 07'	1519.9	263	0	990	F
Beaveroo Lake	Ignace	Lac du Bois 1980	49° 41'	91° 19'	1497.4	262	5	970	F,R
Lac du Bois	Kenora	-	50° 16'	95° 42'	1611.4	266	10	980	F,R
Crowduck Lake	Kenora	-	49° 40'	95° 01'	1670.2	270	0	970	F
Philip Lake	Kenora	Lac du Bois 1975	51° 22'	95° 09'	1611.4	266	10	970	F

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*Climatically-similar regions defined by cluster analysis (see text).
**F, Field; R, Raft.

Two main analytical approaches were employed. First, factorial analyses of variance (ANOVAs) of plant characteristics were performed using seed source, depth, and fertilizer level as the main factors (3x2x4 design). All variables were tested for normality by inspection of skewness and kurtosis statistics, and transformed where appropriate for use in the ANOVAs. Significant ($p \leq 0.01$) seed source and fertilizer factors were examined using contrasts suggested by inspection of the data (Sokal and Rohlf 1981).

The second approach taken was to examine differential sensitivity of the seed sources to varying environmental conditions, following the methods described by Finlay and Wilkinson (1963) and extended by Garbutt and Zangerl (1983). The performance of plants from each seed source with a given treatment was regressed against the mean performance of all seed sources for that treatment. In order to determine the significance of differences among seed sources for the regression coefficients and intercepts, the analysis was performed using source population (Lac du Bois) progeny as the reference category for comparison with the introduced populations' (Mercer R. and Beaveroo L.) progeny (the latter were represented by dummy variables).

4.2.2. Field Study

Sampling and Laboratory Procedures

Plant and soil samples were obtained from 5 introduced and 3 source wild rice populations in August of 1984. Information regarding these locations is presented in Figure 4.1 and Table 4.1. The 3 source populations were Velos Lake (Pickle region), Crowduck Lake (Kenora region), and Lac du Bois (Kenora region). The introduced populations included lakes #8 (Ignace region; source: Velos L.), #6 (Ignace region; source: Crowduck L.), #10 (Ignace region; source: Lac du Bois), Beaveroo Lake (Ignace region; source: Lac du Bois), and Philip Lake (Kenora region; source: Lac du

Bois).

The sampling design and methodology, as well as laboratory procedures, have been described in chapter 2. Plant variables were obtained as in the raft experiment, except that the mean maximum aerial width of 20 aerial leaves and the mean number of pistillate floret pedicels per tiller were calculated. Insufficient material was obtained to determine mature seed weights and lengths. Environmental variables measured for each sample included water depth, emergent plant competition (dry weight of above-ground vegetation) and the following edaphic parameters: % loss on ignition, pH, and concentrations of extractable nitrogen, phosphorus, potassium, iron, calcium, magnesium, copper, zinc, and manganese.

Data Analyses

The analytical procedures used in this study were based on the ANCOVAs described in chapter 2. To compare wild rice plants in the source and introduced populations, it was first necessary to correct for differences in the "local" environment (edaphic characteristics, water depth, and interspecific competition), which has been shown to account for a significant proportion of the variability in plant productivity. Environmental principal component scores were generated for the introduced populations at the time of the analysis of the indigenous field populations. These environmental variables were used with multiple regression equations previously derived for the source populations (see Appendix 5) to obtain predicted values for each plant variable. If there had been no divergence, it was expected that equations derived for the source populations should accurately predict plant morphology in the introduced populations, such that observed and predicted values would be similar. Observed and predicted values for each sample were compared using the nonparametric Sign test (Hull and Nie 1981). Parametric tests were inappropriate since the data were extremely heteroscedastic; observed values were much more variable than predicted values.

Interpretation of the results of the analysis described above is predicate on the assumption that the regression equations derived for the source populations are efficacious predictors of wild rice morphology and productivity. To test this assumption, a similar procedure was performed using 5 indigenous wild rice populations (Arm Lake, Cedar River, Dollar Lake, Velos Lake, and Whitedog Lake) that were sampled in both 1983 and 1984. Environmental principal component scores for samples obtained in 1984 were applied to equations derived from 1983 data to generate predicted values for each plant variable, and the predicted 1984 values were compared by the Sign test with those actually observed.

4.3. RESULTS

4.3.1. Raft Experiment

Analyses of Variance

The level of fertilizer applied was a significant ($p \leq 0.01$) main effect for all plant variables except tiller number and seed weight and length. Plant size, weight, and potential seed number increased with increasing soil fertility (Table 4.2). Water depth was a significant factor for plant height, stem and root weights, and seed length; mean values for all except root weight were greater for plants grown at the 50 cm depth than at the 25 cm depth (Table 4.3).

The population factor was a significant main effect only for plant height. Plants from Lac du Bois seed were shorter than those from either Beaveroo L. or Mercer R. seed; the latter were not significantly different from each other (Figure 4.2a).

TABLE 4.2. Effect of fertilizer level on wild rice plant growth parameters[*].

	Fertilizer Level			
	0	200	400	800
Tillers per Plant	1.00	1.10	1.07	1.20
Height (cm)	63.3^a	69.5^b	73.4^c	81.2^d
Leaf Width (mm)	6.9^a	7.9^a	9.5^b	9.8^b
Stem Weight (g/tiller)	1.48^a	1.79^a	2.47^b	3.10^c
Root Weight (g/tiller)	0.69^a	1.01^b	1.26^c	1.44^c
Pistillate Florets/Tiller	31.7^a	36.7^a	52.2^b	57.4^b
Seed Weight (g/100)	2.34	2.52	2.52	2.74
Seed Length (mm)	12.1	12.4	12.1	12.5

[*] Numbers followed by different superscript letters were significantly different ($p \leq 0.01$) in an ANOVA.

TABLE 4.3. Effect of water depth on wild rice plant growth parameters*.

	Water Depth (cm)	
	25	50
Tillers per Plant	1.08	1.10
Height (cm)	58.5^{a}	82.5^{b}
Leaf Width (mm)	8.5	8.5
Stem Weight (g/tiller)	1.95^{a}	2.47^{b}
Root Weight (g/tiller)	1.38^{a}	0.82^{b}
Pistillate Florets/Tiller	41.6	47.3
Seed Weight (g/100)	2.46	2.60
Seed Length (mm)	11.9^{a}	12.7^{b}

*Numbers followed by different superscript letters were significantly different ($p \leq 0.01$) in an ANOVA.

Regression Analyses

The lack of differentiation among the 3 wild rice populations indicated by the ANOVAs was also apparent in the results of the regression analyses. When mean performance of individual populations was regressed on grand mean performance, there were significant ($p \leq 0.05$) differences among the source and introduced population intercepts only for plant height, seed weight, and number of pistillate florets per tiller. Progeny grown from Lac du Bois seed were shorter than those from Mercer R. or Beaveroo L., as shown by the ANOVA (Figure 4.2a). Seeds of Mercer R. plants tended to be shorter than others (Figure 4.2b), although the trend was not consistent enough over the different treatments to emerge as significant in the ANOVA.

When the regression lines were extrapolated to the origin, Mercer R. progeny were found to produce more numerous pistillate florets per tiller than Lac du Bois progeny (Figure 4.2c). This variable was the only one with significant heterogeneity of slope among the populations. As shown in Figure 4.2c, the regression lines for both Mercer R. and Beaveroo L. progeny had slopes of less than 1 (0.78 and 0.80 respectively; the average slope for the 3 populations is equal to 1 by definition), while the regression line for Lac du Bois progeny had a slope of 1.41. This variation in sensitivity to change in soil fertility and water depth was responsible for the distinctness of the Lac du Bois and Mercer R. intercepts; it is apparent that over most of the range of mean plant performance observed, Mercer R. progeny were similar to or less than Lac du Bois progeny in potential seed production per tiller.

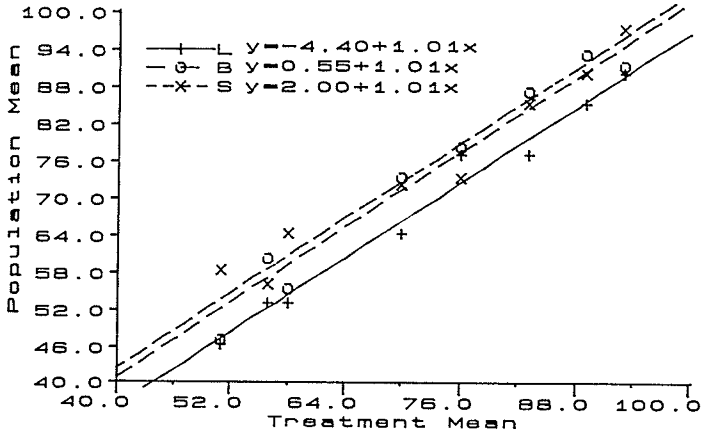
4.3.2. Field Study

Predictive Efficacy of Regression Equations

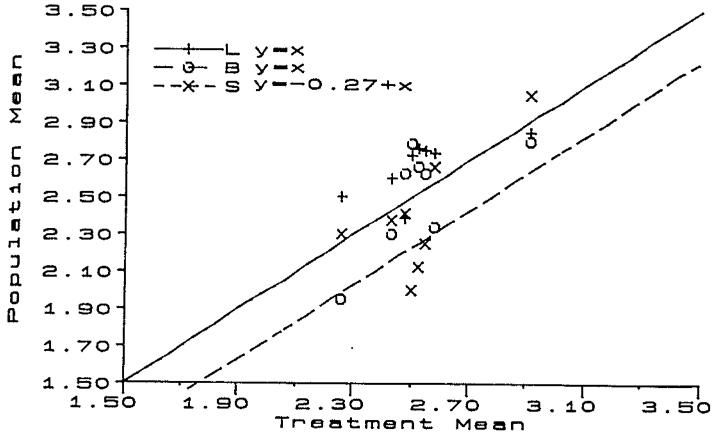
The ability of the equations based on 1983 data to predict wild rice plant performance in 1984 varied among the 5 populations, but, as shown in Figure 4.3,

FIGURE 4.2. Relative sensitivity of progeny from an indigenous and two introduced wild rice populations to different water depths and fertilizer concentrations as indicated by regression analysis.

[a] Height



[b] Hundred-Seed Weight



[c] Pistillate Florets

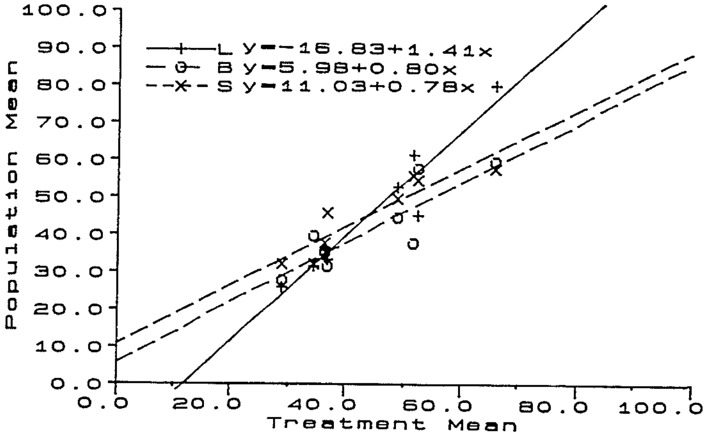
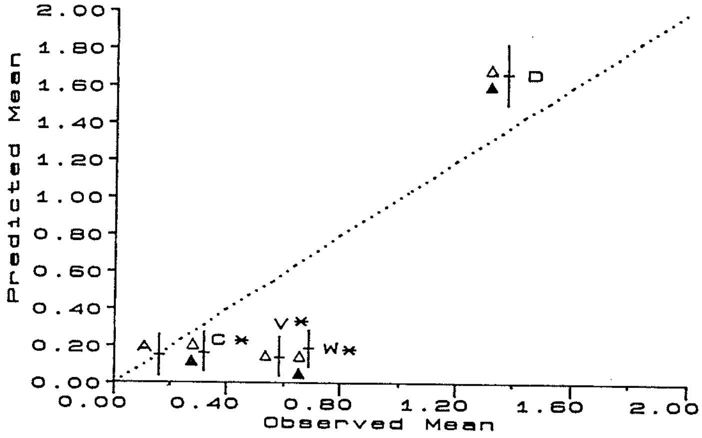
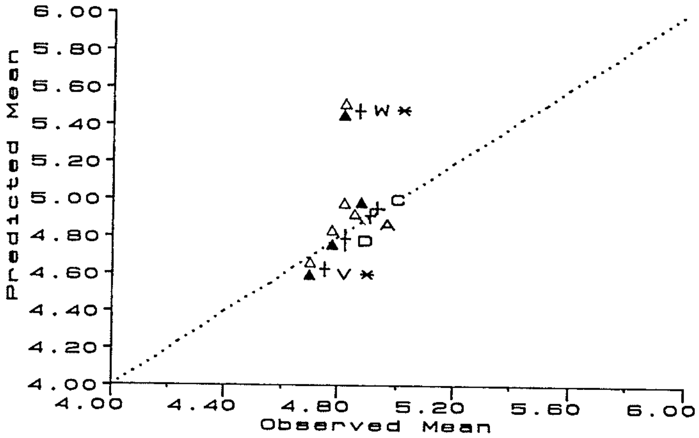


FIGURE 4.3. Predictive efficacy in 1984 of regression equations describing morphometric characteristics of wild rice plants in 1983. The error bars show the 95% confidence interval for the predicted means; the reference diagonal indicates the distribution of points when predicted and observed means are equal. Populations are identified by upper-case letters: A, Arm L.; C; Cedar R.; D, Dollar L.; V, Velos L.; W, Whitedog L. Asterisks (*) indicate that observed and predicted means were significantly different in the Sign Test. Triangles indicate differences in predictor variables between 1983 and 1984: open triangles indicate a significant difference in the mean value of at least one predictor variable, and closed triangles indicate that the range for at least one predictor was more extreme in 1984 (see Appendix 8).

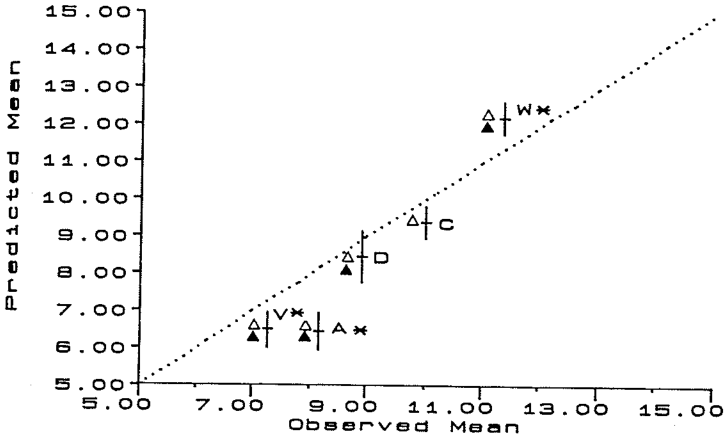
[a] Tillers per Plant (ln)

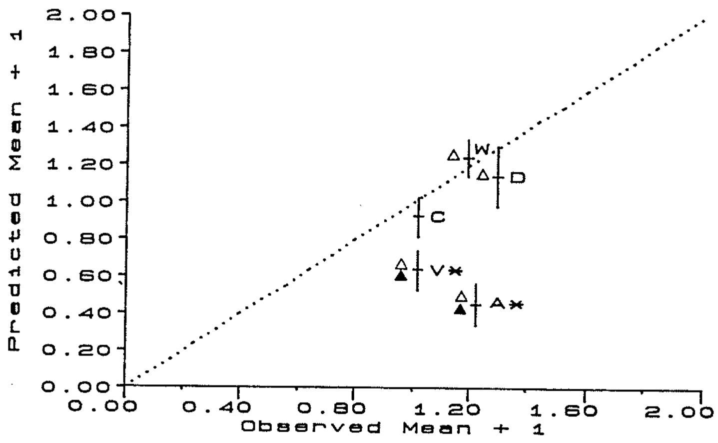


[b] Height (ln)

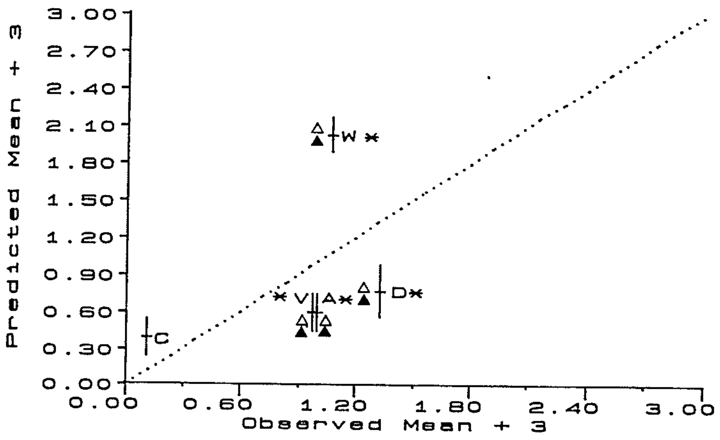


[c] Leaf Width

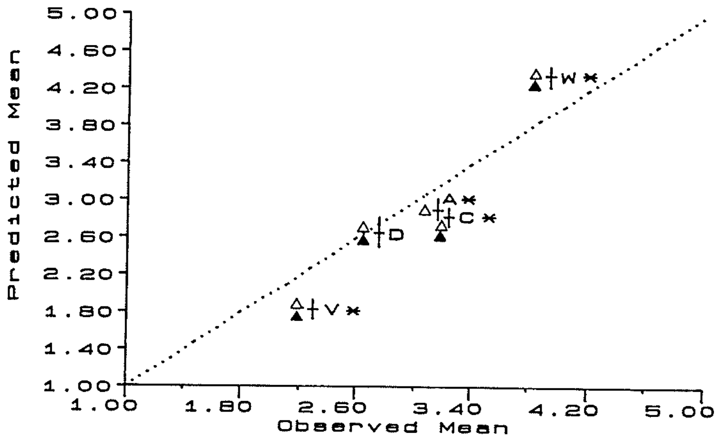




[d] Stem Weight (ln)



[e] Root Weight (ln)



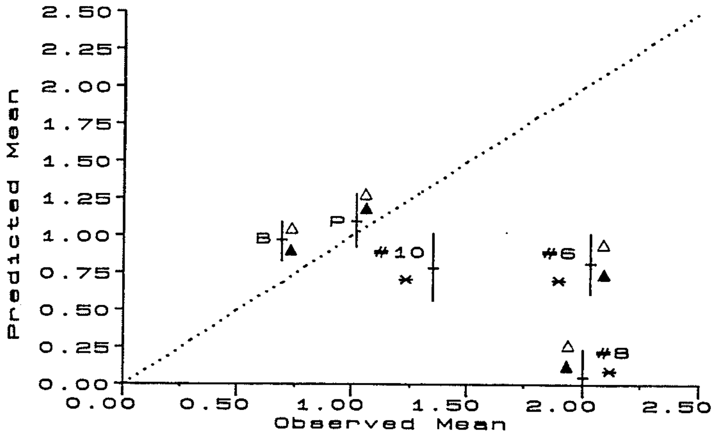
[f] Pistillate Florets (ln)

there was incongruity of predicted and observed values for at least one variable in each population. (Appendix 7 shows the method used to estimate the standard errors associated with predicted means that are shown in Figures 4.3 and 4.4). The uncertainty of values predicted from regression equations sharply increases outside the range of predictor variables originally used to derive the equations; i.e., it is not legitimate to extrapolate (Sokal and Rohlf 1981). In 15 of the 17 instances of poor fit, there was such an incongruence between years in the range of one or more predictor variables (Figure 4.3; and see Appendix 8 for the means and ranges of the PC scores used as predictor variables for each population in 1983 and 1984). There was dissimilarity in the environmental ranges for 6 of the 13 cases with no significant difference between observed and predicted values, indicating that similar ranges are not necessarily prerequisite for adequate predictive power. However, for the purposes of analysis of the introduced populations a conservative approach was taken: where the range of variation in predictor variables extended beyond the range found in the source population, it was assumed that poor fit between predicted and observed wild rice morphology was attributable to inadequacy of the predictive equation rather than divergence of the populations.

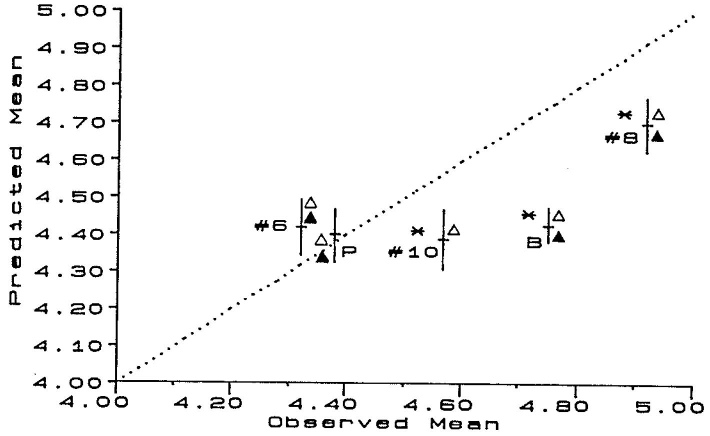
In 2 cases, poor fit of predicted and observed values was not associated with dissimilarity in the ranges of predictor variables (tiller number in the Velos Lake population, Figure 4.3a; and pistillate floret number in the Arm Lake population, Figure 4.3f). In both cases, ANOVA's by year indicated that there was a significant ($p \leq 0.01$) difference in the mean of at least one predictor variable between 1983 and 1984. For these plant variables lack of fit of predicted and observed values was attributed to inadequacy of the equation if the means *or* ranges of predictor variables were not similar for the source and introduced populations.

FIGURE 4.4. Divergence between source and introduced population pairs for morphometric characteristics of wild rice plants. The error bars show the 95% confidence interval for the predicted mean; the reference diagonal indicates the distribution of points when predicted and observed means are equal. Populations are identified by capital letters where applicable; B, Beaveroo L.; P, Philip L. Asterisks (*) indicate that observed and predicted means were significantly different in the Sign Test. Triangles indicate differences in predictor variables between the source population for which equations were derived and the introduced population to which they were applied: open triangles indicate a significant difference in the mean value of at least one predictor variable, and closed triangles indicate that the range for at least one predictor was more extreme in the introduced population (see Appendix 8).

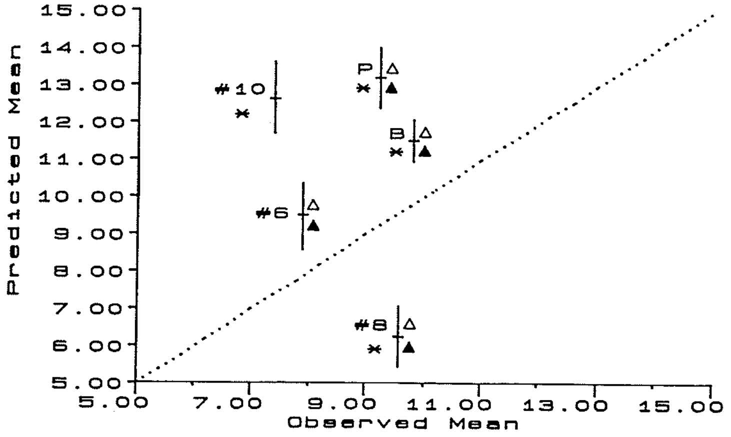
[a] Tillers per Plant (ln)



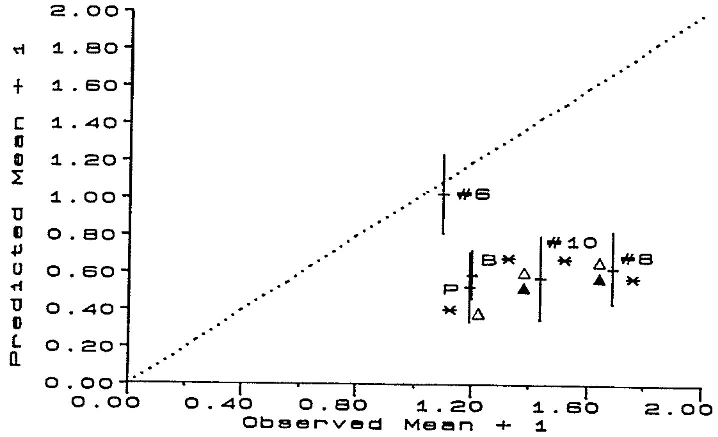
[b] Height (ln)



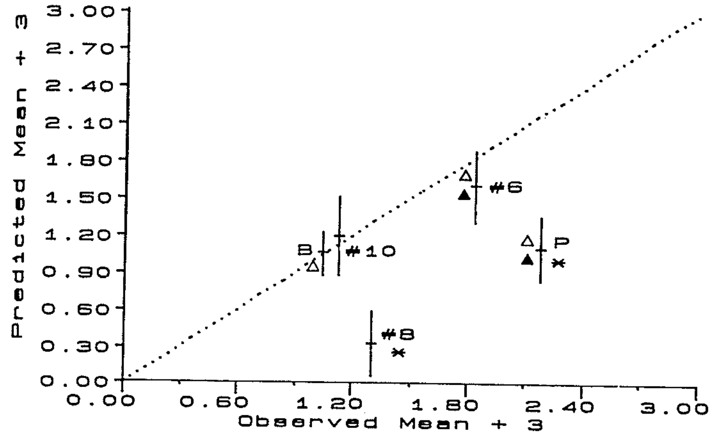
[c] Leaf Width



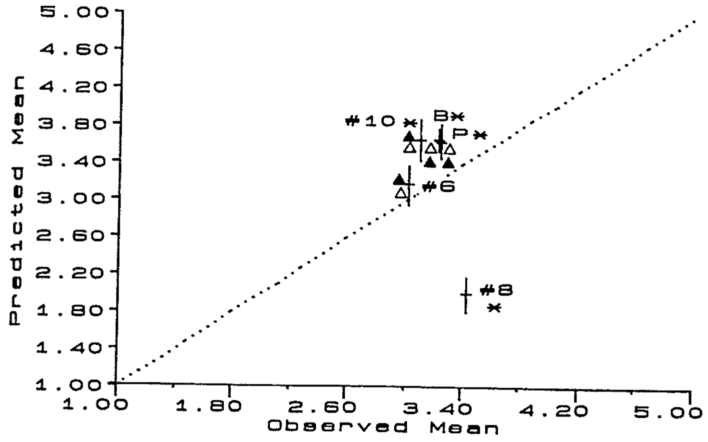
[d] Stem Weight (ln)



[e] Root Weight (ln)



[f] Pistillate Florets (ln)



Introduced Populations

The introduced wild rice populations varied widely in the extent to which observed values for plant variables agreed with those predicted from environmental data (Figure 4.4). There was good agreement for all wild rice variables except tiller number in lake #6, indicating no significant divergence between this population and the source population at Crowduck Lake. The observed tiller number of wild rice plants in #6 was greater than would be predicted for Crowduck L. plants in a similar environment, but the difference may have been due to a different environmental range (Figure 4.4a; Appendix 8).

There was no significant difference between observed and expected tiller numbers for wild rice plants in the Philip L. and Beaveroo L. populations; there was also a good fit for height in Philip L. and for root weight in Beaveroo L. plants. Observed leaf widths were narrower than would have been predicted for Lac du Bois wild rice plants in both Philip and Beaveroo lakes, stem weights were greater than predicted, and floret numbers were fewer. Wild rice plants in the Beaveroo L. population were taller, and those in Philip L. had larger root masses than expected. However, for all variables except stem weight in both populations (Figure 4.4d), the possibility that differences between observed and predicted values was due to inadequacy of the equation could not be ruled out.

Introduced wild rice populations in lakes #10 and #8 appeared to be most distinct from their sources. There was a good fit between observed and predicted values only for root weight in #10, and for no variables in #8. The high observed tiller number, plant height, leaf width, and stem weights of wild rice plants in lake #8 may have been a consequence of the substantial differences between the environmental component scores of lake #8 and the source (Velos L.) environment, but no such discrepancies accounted for the high observed root weights and pistillate floret numbers of #8 plants (Figure 4.4e and f). Environmental parameters were very similar in #10 and Lac du Bois, such that the high tiller production, height, and stem weight, and the low leaf width and pistillate floret production observed at #10 compared to that predicted appear to be the result of divergence.

DISCUSSION

These studies have detected little evidence of climate-influenced divergence between introduced wild rice populations and their seed sources. Progeny of the 3 populations in the raft experiment differed significantly across 8 treatments only for plant height, which has been found to be more strongly a function of local environmental conditions than of climatic factors (chapter 2). The regression analysis suggested that seed weights were somewhat lower for Mercer R. progeny, but the trend was not consistent enough to emerge as significant in the ANOVA.

The observed differences among populations in equability of pistillate floret production across fertilizer and water depth treatments in the raft experiment may be related to a selective effect of climate. Progeny of both of the populations that had been introduced to more severe climates were less sensitive to nutritional status than plants grown from seed from the source population; they exhibited smaller increases in floret production with high soil fertility, but also maintained a more stable potential yield at low applied nutrient concentrations. This result is consistent with the hypothesis put forth in chapter 3 that increasing severity of climate is associated with a less extreme plastic response to variation in the environment. It was argued that extreme developmental flexibility could have an adaptive advantage in moderate climates where reproductive precocity is not essential to survival, but that a more canalized developmental sequence confers greater fitness in environments with a high risk of premature curtailment of the growing season. Since pistillate floret production and ultimately grain yield is strongly correlated with maturation rate in this species (chapter 1; Appendix 2), this trait may be expected to be subject to strong selection pressure for reduced plasticity.

One intriguing result of the raft experiment was the similarity of the Mercer R. and Beaveroo L. progeny. The few differences from the Lac du Bois progeny are common to both of the introduced populations, even though the Mercer R. population was established about 50 years before this experiment was conducted compared to only 5 years of establishment for the Beaveroo Lake population. Lack of differentiation of these 2 populations was also observed in the 2 greenhouses (except for stem weight in G1 (S>B)), although more was apparent in the experimental lake (B>S for stem weight, leaf width, and pistillate floret number; see Figure 3.3). Although both populations were established in locations with more severe climates than the source, Mercer R. is clustered with the "Pickle" region, which is more extreme than the "Ignace" region where Beaveroo L. is located. The wild rice in Mercer R. has therefore been subject to a greater climate differential for a much longer period of time than the wild rice in Beaveroo L., and yet there is no significant difference between these two introduced populations in the degree of their divergence from the source population. It appears that there has been a rapid initial response to selection pressure for reduced plasticity in pistillate floret production, followed by a prolonged plateau when little or no change occurred. A rapid initial response to selection is characteristic of traits governed at least in part by genes with major effects on the phenotype. The protracted period of little or no response may indicate that selection is operating on a large number of genes with minor phenotypic effects, and/or that the trait in question is governed in part by a balanced system of tightly linked genes that must be disrupted by a strategic recombination event before natural selection can operate (Allard 1960).

Aside from plant height and sensitivity of pistillate floret production to fertilizer concentration, none of the traits examined had changed in the introduced populations. In particular, there was no difference in overall mean leaf width, root weight, or pistillate floret production between the 3 populations, although these characteristics appear to be strongly influenced by climatic factors when indigenous wild rice populations are compared in the greenhouse or *in situ.* These results suggest that the climatic factors considered do not exert sufficient directional selection pressure to dramatically alter the genetic constitution of wild rice populations for these morphometric characteristics after half a century of reproductive isolation.

It is possible that populations are buffered from the effects of directional selection by phenotypic plasticity in response to some of the same environmental factors that contribute to that selection pressure, such as temperature and/or daylength. If these factors alter phenology and/or morphology such that potentially non-adaptive genes and gene combinations are protected from selective effects, then evolution will proceed very slowly. Such a conservative mechanism has been postulated in other species (Bradshaw 1965; Smith-Gill 1983). Genes affecting plasticity itself would then logically be the initial targets of selection, as suggested by Smith-Gill (1983).

These studies do not provide direct proof in support of the above hypothesis, but there is some indirect evidence. Studies by Oelke et al (1982) have indicated that wild rice morphology is affected by temperature and daylength. The much greater apparent divergence of source and introduced populations in the field survey, particularly the differences observed in comparison of Beaveroo L. and Lac du Bois, also lends limited support, although there are difficulties in interpretation. It has been stated that most of the apparent changes in the morphometric characteristics of wild rice plants in the introduced populations surveyed in the field could have resulted from inadequacy of the regression equations used to obtain predicted values over the observed environmental range. However, the putative shifts in the properties of plants in the introduced populations have almost all occurred in the direction that would be predicted if climate is a major influencing factor. The wild rice in lake #8 was introduced to a more moderate climate in the "Ignace" region from the severe climate of the "Pickle" region, and values for all measured characters were higher than those that would be predicted for Velos Lake plants under similar environmental conditions. By contrast, wild rice in Beaveroo L. and lakes #6 and #10 was introduced to the more severe climate of the "Ignace" region from the moderate climate of the "Kenora" region. In these populations, where there was incongruity between observed and predicted plant characteristics, observed leaf width and pistillate floret production was lower than predicted and tiller production was higher. Shoot weights and heights were greater than predicted; however these characteristics, though somewhat influenced by climatic regime, were found to be more strongly a function of local environmental effects and tended to differ markedly among populations within climatic regions (chapter 2). Wild rice in Philip L., which originated in the "Kenora" region and was not introduced to a different climatic regime, had narrower leaves and fewer pistillate florets but larger root and shoot weights than was predicted: a mixture of effects.

In conclusion, these studies have found little evidence for genetic divergence of source and introduced population pairs in different climatic regions. This is an encouraging result from the wild rice grower's perspective, since it permits some confidence that the genetic integrity of introduced seed stocks will be maintained over relatively long periods of time. There is the possibility, however, that genetic potential for superior productivity may be masked to some extent by a plastic response to differing climatic conditions. This subject deserves further critical investigation utilizing ranges of environmental parameters encountered under field conditions.

SUMMARY AND CONCLUSIONS

Studies of wild rice plants in the field and of progeny of various populations in the greenhouse, in experimentally-seeded lakes, and on cultivation rafts have demonstrated high variability within and among populations for a number of phenological and morphometric traits. High intra-population variability is expected in this species, which has an annual habit, no vegetative reproduction, a breeding system promoting outcrossing, and the potential for prolonged seed dormancy. The patchy spatial distribution and the consequent virtually complete reproductive isolation of wild rice stands are features that permit genetic differentiation of populations. The occurrence of genetic differentiation of wild rice populations was indicated by significant differences in morphometric characters of progeny evaluated under common environmental conditions.

The majority of the variation observed among progeny of different populations in the greenhouse could be attributed to climatic conditions prevailing at the source. The climatic parameters considered to be of importance in these studies included growing-degree-days, time of first fall frost, risk of early fall frost, and maximum photoperiod during the growing season. When populations were clustered according to these criteria, the proportion of variation explained by the groups was nearly as high as the proportion explained by differences among individual populations. In general, increasing climatic severity was associated with early flowering, short stature, narrow leaves, and low pistillate floret production and shoot and root biomass per tiller. These characteristics showed continuous variation over the climatic gradient. By contrast, tiller production was discontinuous over the geographic range: progeny of populations from intermediate climatic regimes had the highest tillering capacity, while those from the extremes of the range studied produced relatively few tillers. Seed characters were generally less variable than other parameters measured, and were not as clearly related to the climatic gradient: progeny of populations in severe and intermediate climates tended to produce larger seeds than those in moderate climates, but the relationship was not direct. These general trends were also apparent in the analysis of a broader range of populations in field studies, although there were more pronounced differences among populations in similar climates.

The above results suggest that climate has acted as an important selective force influencing the evolution of this species. It is proposed that the length of the growing season acts as a limiting factor controlling the viable range of maturation schedules in wild rice populations. Populations constrained by short growing seasons, low summer temperatures, and high risk of early frosts reach the reproductive phase rapidly, and hence bypass the period of luxuriant vegetative growth that is permissible in more moderate climates. The superior tillering capacity of populations in intermediate climates may be an adaptation permitting high potential reproductive output per plant without the risks associated with delaying maturation to achieve increased seed production per tiller.

Wild rice progenies displayed differential sensitivity to varying cultivation conditions, and consequently the apparent distinctness of populations was dependent on the environment in which they were compared. Climatic conditions at the source appeared to influence stability. When morphometric characteristics of progeny from four wild rice populations were compared in 2 greenhouses and in an experimental lake in the Ignace district, it was observed that the population originating in the region with the more moderate climate was characterized by greater phenotypic plasticity: the superior potential productivity indicated by its performance in one of the greenhouses was not realized in the other greenhouse or in the natural test environment used. Consideration of the other 5 populations represented in the 2 greenhouses also indicated that increasing climatic severity at the source was associated with lower *average* productivity but higher phenotypic stability under variable growing conditions. Similarly, in the analysis of populations *in situ* it was found that those in regions with moderate climatic conditions tended to be more sensitive to local environmental factors. It was suggested that a superior capacity to exploit optimum temperature and/or light and/or nutrient conditions by increasing vegetative and reproductive growth would confer a competitive advantage to plants in an area where risk of premature curtailment of the growing season is minimal. Such extreme developmental flexibility would, however, be non-adaptive and hence subject to negative selection pressure in populations in more severe climatic regions, since luxuriant growth is generally accompanied by delayed reproduction.

Analysis of field data from 17 wild rice populations indicated that the relative importance of the contributions of genetic differences and plastic effects to observed patterns of variation depends on the character under consideration. From 20 to 35% of the total variation in most morphometric plant characteristics could be attributed to "local" environmental parameters (water depth, emergent interspecific competition, and edaphic variables). Plant height was most strongly influenced by the local environment; 61.6% of the total variation was explained by a combination of local factors. The ratio of mineral to organic components in the sediment, sediment nitrogen concentrations, and water depth were the most important predictors of wild rice productivity in the populations surveyed; this is consistent with other findings for this species and other emergent aquatic macrophytes. Differentiation among populations after statistical correction for differences in local environmental parameters accounted for 30 to 50% of the total variation in most plant characteristics. For most characters less than half of the total variation attributed to differences among populations was attributable to differences among populations with similar climates. Climate was a particularly good predictor of leaf width and pistillate floret production per tiller. Most populations responded similarly to variation in local environmental conditions over the ranges observed, although there were a few that appeared to be particularly tolerant of deep water, low sediment nutrients, or high interspecific competition.

The importance of climate in determining morphometric characteristics and levels of developmental plasticity of wild rice has been stressed in this dissertation, and is a logical consequence of this species' annual habit and inability to propagate vegetatively. Successful completion of the life cycle by most individuals in a population is essential for its continued survival, and the length of the growing season is one of the major factors limiting reproductive success in lakes of the Boreal region under consideration in this study. It might be expected, then, that the genetic constitution of populations introduced to different climatic regimes would change fairly rapidly in response to directional selection pressures. The morphometric characteristics of two introduced wild rice populations examined in the greenhouse were intermediate between the mean characteristics of indigenous populations in the climatic regions of the original and new locations. However, studies examining source and introduced population pairs did not find conclusive evidence of genetic differentiation. There were difficulties in interpretation of the field study, since in many cases the local environmental parameters were quite different for the source and introduced populations. Average characteristics of progeny of a source source and two introduced populations grown with a range of depth and fertilizer treatments were similar. However, pistillate floret production of progeny of the source population, which was located in a moderate climatic region, was more plastic in response to the different treatments than it was for progeny of the 2 introduced populations, which had been established in more severe climatic regions. This observation coupled with the lack of apparent substantial differentiation of the 2 introduced populations from one another suggested that plastic responses to differing climatic conditions of temperature and daylength buffer populations from the selective effects of these parameters, retarding the rate of evolutionary divergence of populations. Further, it was proposed that the degree and type of developmental flexibility itself (which is a character under genetic control) is an initial target of natural selection pressures in populations newly established in locations with novel climatic regimes. More critical work is required to confirm this hypothesis.

The results accruing from these experimental and field studies have several implications for breeding wild rice for Canadian lake cultivation. These have been discussed in the individual chapters, but to conclude this thesis, the more important points emerging will be briefly summarized below.

1. There is sufficient genetically-based variation among wild rice populations to warrant selecting among as well as within them for desired characteristics.

2. Much of the variation in commercially-important characteristics (potential grain yield, tillering capacity, maturity) is associated with climatic characteristics, so populations having particular desired traits may profitably be sought in particular regions.

3. Populations exist that have novel combinations of characters, and that appear to have unusual, and possibly useful, responses to variation in edaphic parameters, water depth, and interspecific competition.

4. Populations differ in their sensitivity to environmental variation. It is therefore necessary to evaluate progenies for selection in environments as similar as possible to those in the target area(s) where selected strains will be used. It may

also be desirable to utilize different sources of genetic material and/or selection methods to develop strains tailored for stress or nonstress environments, or for use in managed or unmanaged stands.

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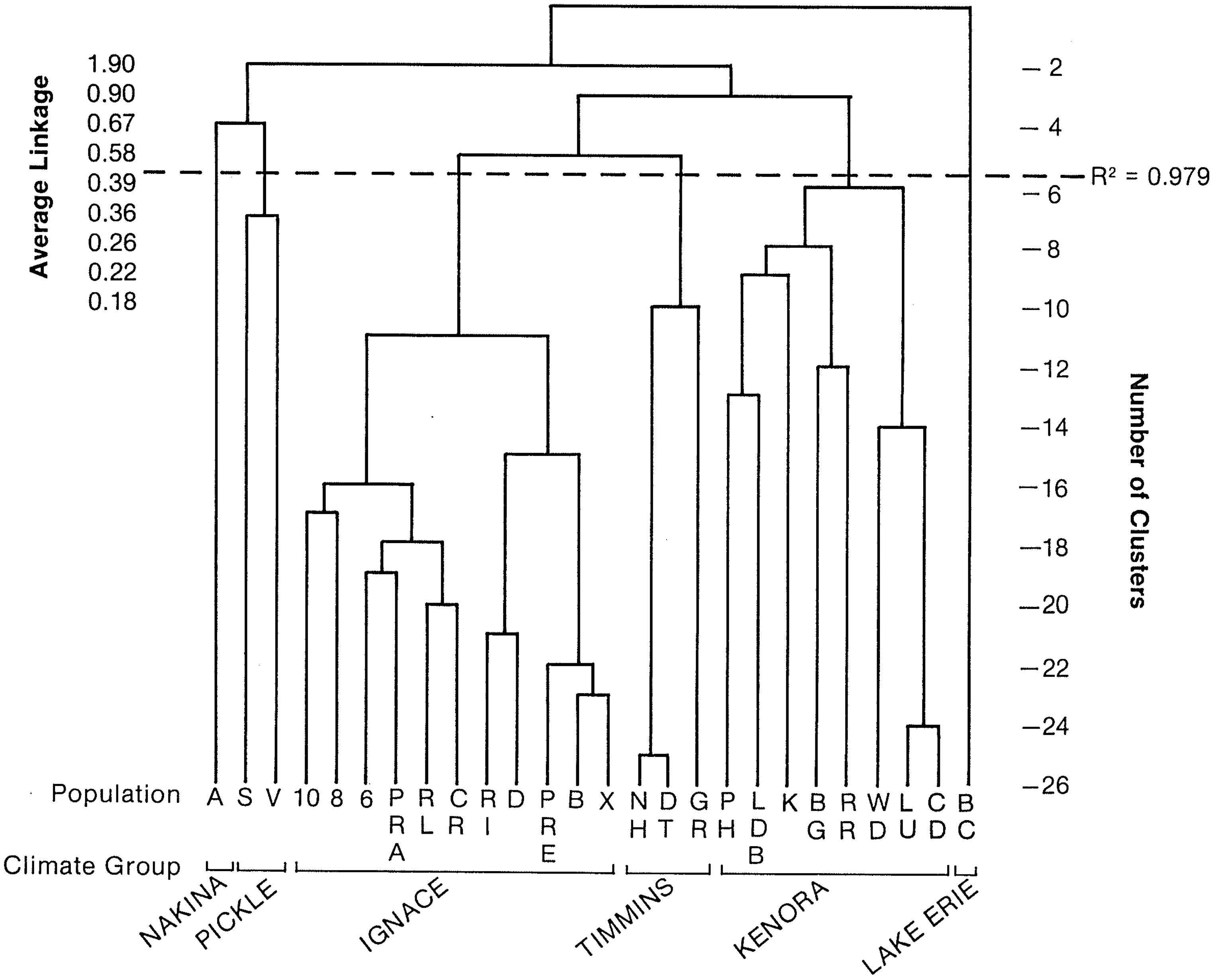
APPENDIX 1. Summary of cluster analysis of all wild rice populations sampled in the field and used as seed sources for progeny tests. Populations were clustered on the basis of selected climatic variables as discussed in chapter 1 (p. 16). The results of this analysis were used to define the "climate groups" of populations and geographic "climatic regions" referred to throughout the text. A, Arm Lake; S, Mercer River, Saskatchewan; V, Velos Lake; PRA, Prairie Lake; RL, Rice Lake (Red Lake District); CR, Cedar River; RI, Rice Lake (Ignace District); D, Dollar Lake; PRE, Press Lake; B, Beaveroo Lake (=Charnock Lake); X, Experimental Lake (Ignace District); NH, Nighthawk Lake; DT, Denton Lake; GR, Grassy Lake; PH, Philip Lake; LDB, Lac du Bois, Manitoba; K, Kaiashkomin Lake; BG, Big Grassy River; RR, Rat River Bay; WD, Whitedog Lake; LU, Lulu Lake; CD, Crowduck Lake; BC, Big Creek.


Average Linkage
1.90
0.90
0.67
0.58
0.39
0.36
0.26
0.22
0.18
R² = 0.979
Number of Clusters
2
4
6
8
10
12
14
16
18
20
22
24
26
Population
A
S
V
10
8
6
PRA
RL
CR
RI
D
PRE
B
X
NH
DT
GR
PH
LDB
K
BG
RR
WD
LU
CD
BC
Climate Group
NAKINA
PICKLE
IGNACE
TIMMINS
KENORA
LAKE ERIE

APPENDIX 2. Correlation matrix of wild rice variables measured for 9 populations in 2 locations (greenhouse experiment 3; n=150). Only significant ($p \leq 0.05$) Pearson correlation coefficients are shown. DFO, days to pistillate floret opening; TILL, tillers per plant; HT, height; LW, leaf width; SWT, stem weight; RWT, root weight; FEM, pistillate florets per tiller; PFEM, pistillate florets per plant; SDL, seed length; SDWT, seed weight.

	DFO	TILL	HT	LW	SWT	RWT	FEM	PFEM	SDL
TILL	-0.22								
HT	0.29	-0.20							
LW	0.52	-0.20	0.51						
SWT	-	0.60	0.32	0.36					
RWT	0.29	0.32	0.35	0.60	0.77				
FEM	0.42	-0.22	0.48	0.83	0.36	0.60			
PFEM	0.17	0.54	0.22	0.51	0.78	0.78	0.57		
SDL	-0.31	-	-	-0.60	-0.26	-0.47	-0.60	-0.53	
SDWT	-0.31	-	-	-0.46	-0.20	-0.41	-0.55	-0.46	0.88

APPENDIX 3. Correlation matrix for environmental variables measured in wild rive stands in 1983 and 1984 (n=584). For clarity, only significant ($p \leq 0.05$) Pearson correlation coefficients are shown. LOI, % loss on ignition; P, Phosphorus; N, Nitrogen; Fe, Iron; Mn, Manganese; Zn, Zinc; Cu, Copper; Ca, Calcium; Mg, Magnesium; K, Potassium; PC, plant competition; D, water depth.

	LOI	pH	P	N	Fe	Mn	Zn	Cu	Ca	Mg	K	PC
pH	-											
P	-	-0.16										
N	-	0.18	0.20									
Fe	-0.52	-0.08	0.08	-								
Mn	-0.52	0.21	-0.17	-	0.56							
Zn	-0.24	-0.16	-0.09	0.22	0.37	0.15						
Cu	0.12	-	-	0.20	-	-	0.14					
Ca	-0.51	0.32	-0.32	-	0.29	0.59	0.13	-0.09				
Mg	-0.56	-	-0.16	-0.09	0.48	0.44	0.20	-0.21	0.72			
K	-0.47	0.14	-	0.12	0.43	0.45	0.19	-0.12	0.49	0.62		
PC	-	-0.08	-0.08	-0.13	-	-	-0.08	-	0.13	0.10	-	
D	-0.11	-	0.13	-0.12	0.15	0.12	-0.16	-0.08	-	0.13	0.22	-0.26

APPENDIX 4. Wild rice population mean (± SE) scores on the first seven principal components of the environment data set. Only data for indigenous populations are shown; see Appendix 8 for information regarding environmental parameters of introduced populations.

Population	Principal Component						
	1	2	3	4	5	6	7
V	-0.58±0.10	0.14±0.08	-0.72±0.12	0.06±0.12	0.30±0.13	-0.38±0.11	-0.28±0.08
A	0.69±0.16	-1.37±0.14	-0.32±0.17	-0.19±0.14	-1.44±0.22	-0.56±0.17	0.46±0.27
DT	-0.76±0.14	-0.66±0.20	1.31±0.42	-0.10±0.17	-0.60±0.33	-0.09±0.17	1.10±0.67
GR	0.08±0.13	-0.46±0.14	1.22±0.11	-0.69±0.11	-0.19±0.17	-0.25±0.17	0.82±0.47
NH	1.11±0.12	-0.18±0.19	1.34±0.06	0.45±0.07	0.46±0.11	0.02±0.09	0.56±0.46
PR	-0.48±0.09	0.71±0.12	-1.00±0.09	-0.55±0.16	-0.19±0.14	0.01±0.15	-0.62±0.13
RI	0.14±0.08	0.61±0.10	0.03±0.07	-1.03±0.10	0.55±0.12	-0.47±0.04	-0.56±0.06
CR	1.27±0.11	0.09±0.12	0.50±0.13	-0.56±0.10	0.74±0.14	-0.14±0.14	-0.48±0.15
D	-0.27±0.11	0.30±0.14	-0.27±0.15	1.65±0.11	-0.07±0.14	-0.38±0.04	0.38±0.16
LU	0.33±0.24	-0.38±0.12	-0.92±0.09	-0.82±0.19	0.20±0.33	1.18±0.58	1.02±0.28
CD	-2.49±0.06	-1.19±0.13	0.06±0.06	-0.41±0.08	0.75±0.10	-0.21±0.03	0.37±0.10
K	-0.30±0.08	1.16±0.15	0.88±0.08	2.17±0.10	-0.64±0.08	-0.10±0.08	0.09±0.14
LDB	0.06±0.07	0.80±0.09	-0.80±0.08	-0.34±0.08	-1.00±0.12	-0.12±0.20	-0.02±0.14
BG	0.92±0.18	-1.32±0.30	0.70±0.27	0.26±0.11	1.56±0.18	0.05±0.28	-0.68±0.23
RR	0.07±0.20	0.32±0.14	-0.68±0.06	-0.22±0.12	0.66±0.13	1.84±0.32	-0.67±0.13
WD	0.98±0.06	-1.61±0.11	-1.32±0.18	1.20±0.12	-0.30±0.08	-0.05±0.13	-0.52±0.20
BC	0.04±0.22	-1.99±0.20	1.63±0.33	-0.40±0.08	-1.90±0.31	1.55±0.63	0.11±0.56
ALL	0.00±0.04	0.00±0.04	0.00±0.04	0.00±0.04	0.00±0.04	0.00±0.04	0.00±0.04

APPENDIX 5. Predictive equations for morphometric characteristics of wild rice plants in 17 populations. Equations were derived from analyses of covariance of data from field surveys. Chapter 2 should be referred to for details regarding the populations and the analytical procedures followed, as well as the partial regression coefficients used in constructing the equations. The reference equation is given for Velos Lake (V). For clarity, only unique coefficients arising from significant interaction terms are specified for other populations; when the coefficients are the same as for V, they are indicated by ".

ln Tillers per Plant

V:	0.133+0.014(M:O)	+0.054(pH:Zn)	−0.046(N)	$+0.046(N)^2$	−0.072(D)
DT:	−0.062 "	"	"	"	"
GR:	−0.044 "	"	"	"	"
A:	0.055 "	"	"	"	"
CR:	0.156 "	"	"	"	"
BG:	0.363 "	"	"	"	"
NH:	0.547 "	"	"	"	"
RR:	0.576 "	"	"	"	"
K:	0.659 "	"	"	"	−0.349(D)
LU:	0.707−0.466(M:O)	"	"	"	−0.393(D)
WD:	0.720 "	"	"	"	+0.414(D)−0.189(P)−0.214(PC)
CD:	0.777 "	"	"	"	"
LDB:	0.794−0.349(M:O)	"	"	"	"
RI:	0.874 "	"	"	"	"
PR:	1.127 "	"	+0.11(N)	"	"
D:	1.395−0.258(M:O)	"	"	"	"
BC:	2.739+0.955(M:O)	"	"	"	+0.769(D)

ln Height

V:	4.621+0.044(M:O)	−0.092(N)	$-0.006(N)^2$	+0.224(D)	$+0.021(D)^2$	$-0.008(Cu)^2$	
LDB:	4.541 "	+0.014(N)	"	"	"	"	+0.132(P)
LU:	4.562 "	"	"		"	"	
D:	4.563 "	+0.075(N)	"	"	"	"	−0.299(PC)
K:	4.631 "	+0.038(N)	"	"	"	"	
DT:	4.637 "	"	"	"	"	"	
CD:	4.654 "	"	"	"	"	"	
NH:	4.665 "	"	"	"	"	"	
BC:	4.748−0.089(M:O)	"	"	+0.045(D)	"	"	
BG:	4.760 "	"	"	"	"	"	−0.143(PC)
CR:	4.762 "	"	"	"	"	"	
A:	4.791 "	"	"	"	"	"	−0.061(PC)
RI:	4.917 "	"	"	"	"	"	
PR:	4.930 "	+0.054(N)	"	"	"	"	
GR:	4.931 "	"	"	"	"	"	+0.204(P)
RR:	5.038 "	+0.012(N)	"	+0.016(D)	"	"	−0.050(PC)
WD:	5.184 "	"	"	"	"	"	+0.173(P)

Leaf Width

V:	6.387	$-0.346(P)$	$-0.062(P)^2$	$-0.063(pH:Zn)$	$-0.198(pH:Zn)^2$	$+0.155(N)^2$	$-0.214(PC)$	$+0.013(Cu)$	
GR:	5.885	"	"	"	"	"	"	"	
DT:	6.154	"	"	"	"	"	"	"	
NH:	6.559	"	"	"	"	"	"	"	
A:	6.865	"	"	"	"	"	"	"	
RI:	8.140	$+1.805(P)$	"	"	"	"	"	"	
D:	8.662	"	"	"	"	"	"	"	
BG:	9.125	$-1.293(P)$	"	"	"	"	"	"	
CD:	9.146	"	"	"	"	"	"	"	
PR:	9.317	$+1.613(P)$	"	"	"	"	"	"	
BC:	9.659	"	"	"	"	"	$+0.889(PC)$	"	
CR:	9.889	"	"	"	"	"	"	"	$-0.806(D)$
LU:	9.937	"	"	"	"	"	"	"	
K:	12.001	"	"	"	"	"	"	"	
RR:	12.013	"	"	"	"	"	"	"	$-0.819(M:O)$
LDB:	12.033	"	"	"	"	"	"	"	$+1.239(N)-0.813(D)$
WD:	12.298	"	"	"	"	"	"	"	

ln Pistillate Florets per Tiller

V:	1.994	$+0.104(M:O)$	$-0.016(P)^2$	$+0.040(N)^2$	$-0.037(D)$	$-0.035(PC)$	$+0.007(Cu)^2$	
DT:	2.282	"	"	"	"	"	"	
GR:	2.322	"	"	"	$+0.361(D)$	"	"	$-0.618(N)$
NH:	2.693	"	"	"	"	"	"	
D:	2.778	"	"	"	"	"	"	
RI:	2.785	"	"	"	"	"	"	
A:	2.870	"	"	"	"	"	"	
R:	2.910	"	"	"	$-0.367(D)$	$-0.300(PC)$	"	
BG:	3.113	"	"	"	"	"	"	$-0.210(P)$
K:	3.238	"	"	"	"	"	"	
CD:	3.320	"	"	"	"	"	"	
LU:	3.320	$-0.379(M:O)$	"	"	"	"	"	
PR:	3.377	"	"	"	"	"	"	
LDB:	3.658	"	"	"	"	"	"	
RR:	3.668	$-0.118(M:O)$	"	"	"	"	"	
WD:	4.498	$-0.346(M:O)$	"	"	"	"	"	
BC:	5.429	"	"	"	"	"	"	$+0.485(P)$

ln Stem Weight per Tiller

V:	-0.396	-0.009(P)^2	+0.003(pH:Zn)	-0.022(N)	-0.008(N)^2	-0.016(D)	+0.017(D)^2	-0.078(PC)	+0.48(Cu)	
DT:	-0.732	"	"	"	"	"	"	"	"	
A:	-0.431	"	"	"	"	"	"	"	"	-0.200(P)
LDB:	-0.430	"	"	"	"	"	"	"	"	
NH:	-0.405	"	"	"	"	"	"	"	"	
CR:	-0.269	"	"	"	"	"	"	"	"	+0.210(M:O)
GR:	-0.257	"	"	"	"	+0.329(D)	"	"	"	
LU:	-0.149	"	"	"	"	+0.348(D)	"	"	"	
D:	-0.113	"	"	"	"	+0.332(D)	"	"	"	
K:	-0.103	"	"	"	"	"	"	"	"	
CD:	0.018	"	"	"	"	"	"	"	"	
WD:	0.314	"	"	"	"	"	"	+0.214(PC)	"	
BG:	0.536	"	"	"	"	"	"	"	"	
BC:	0.634	"	"	+1.212(N)	"	"	"	+0.126(PC)	"	
PR:	0.684	"	"	"	"	"	"	"	"	
RR:	0.844	"	"	"	"	"	"	"	"	-0.181(M:O)
RI:	0.854	"	"	"	"	"	"	"	"	

ln Root Weight per Tiller

V:	-2.653	-0.136(M:O)	-0.025(P)^2	+0.015(pH:Zn)	-0.022(N)^2	-0.076(D)^2	-0.020(PC)	-0.037(PC)^2	+0.039(Cu)	
NH:	-3.096	"	"	"	"	"	"	"	"	
DT:	-2.894	"	"	"	"	"	"	"	"	
GR:	-2.588	"	"	"	"	+0.284(D)	"	"	"	
A:	-2.468	"	"	"	"	"	-0.256(PC)	"	"	
CR:	-2.421	"	"	"	"	"	"	"	"	
D:	-2.315	"	"	"	"	"	"	"	"	
LDB:	-2.102	"	"	"	"	"	"	"	"	
LU:	-1.825	"	"	"	"	"	"	"	"	
RI:	-1.813	"	"	"	"	"	"	"	"	
CD:	-1.799	"	"	"	"	"	"	"	"	
RR:	-1.712	"	"	"	"	"	+0.176(PC)	"	"	
BG:	-1.648	"	"	"	"	"	"	"	"	
PR:	-1.488	"	"	"	"	-0.464(D)	"	"	"	
K:	-1.375	"	"	"	"	"	"	"	"	
WD:	-0.933	"	"	"	"	"	+0.374(PC)	"	"	
BC:	-0.685	"	"	"	"	"	"	"	"	+1.470(N)

ln Seed Length

V:	2.750	−0.030(M:O)	$-0.006(P)^2$	+0.003(PC)
GR:	2.327	"	"	"
BG:	2.439	"	"	"
RR:	2.443	"	"	"
BC:	2.510	"	"	"
A:	2.546	"	"	−0.071(PC)
PR:	2.563	"	"	"
NH:	2.701	+0.046(M:O)	"	"
RI:	2.938	"	"	"

ln Seed Weight

V:	1.014	$-0.021(P)^2$	$+0.008(pH:Zn)^2$	+0.005(D)	+0.033(PC)
BC:	−0.062	"	"	"	"
GR:	0.086	"	"	"	"
RR:	0.533	"	"	"	"
A:	0.601	"	"	"	−0.169(PC)
PR:	0.746	"	"	"	"
BG:	0.807	"	"	"	"
NH:	0.950	"	"	"	"
RI:	1.710	"	"	"	"

APPENDIX 6. Means (± SD) for wild rice variables measured in field populations in 1983 and 1984. N=number of quadrats sampled; number with plants with mature seed in brackets.

	Yr	N	Tillers per Plant	Height	Leaf Width (mm)	Stem Weight (g/tiller)	Root Weight (g/tiller)	Pistillate Florets per Tiller	Seed Length (mm)	Seed Weight (g/100)	Seed Weight (g/plant)
Velos Lake	83	26(13)	1.1±0.2	111±27	6.4±1.3	0.77±0.36	0.08±0.02	7.5±2.4	15.9±1.8	2.33±0.67	0.17±0.09
	84	32(0)	1.9±0.6	110±42	7.2±1.3	1.06±0.33	0.15±0.09	10.4±3.6			
Arm Lake	83	25(20)	1.2±0.4	101±20	7.3±1.0	1.04±0.41	0.16±0.01	21.4±7.6	12.8±0.8	1.94±0.32	0.62±0.43
	84	28(28)	1.2±0.5	137±24	8.2±1.0	1.31±0.38	0.15±0.08	24.5±6.2	12.7±0.9	2.88±0.49	0.93±0.66
Lake #10	84	10(0)	6.0±5.1	98±23	7.4±1.8	2.56±3.67	0.19±0.10	26.4±15.9			
Lake #8	84	11(0)	7.6±4.8	143±21	9.6±2.1	2.31±0.95	0.21±0.09	31.8±12.4			
Lake #6	84	10(0)	8.6±7.2	74±19	7.3±2.3	1.08±0.75	0.32±0.24	20.1±12.9			
Prairie Lake	83	30(18)	2.9±1.1	127±21	10.3±2.0	2.03±0.74	0.28±0.17	29.7±11.2	13.2±1.1	2.12±0.39	1.78±0.94
Cedar River	83	30(0)	1.2±0.2	163±41	9.2±1.2	1.04±0.31	0.08±0.05	18.8±8.7			
	84	35(0)	1.4±0.4	147±40	10.0±1.2	1.10±0.39	0.07±0.05	27.9±13.0			
Philip Lake	84	10(0)	4.3±4.8	85±30	9.2±2.6	1.50±0.94	0.49±0.23	29.1±14.6			
Lac du Bois	84	30(0)	2.4±0.8	86±14	12.1±1.5	0.73±0.38	0.16±0.08	42.1±12.3			
Kaiashkomin Lake	83	28(0)	3.1±1.2	98±18	12.0±1.8	0.87±0.22	0.30±0.15	32.6±11.0			
Rice Lake	84	15(8)	2.6±0.7	172±15	9.4±1.2	2.42±0.39	0.15±0.03	17.5±3.8	18.7±0.5	5.43±0.67	2.59±0.99
Dollar Lake	83	34(0)	5.1±2.4	119±25	8.9±1.0	0.92±0.36	0.11±0.08	18.3±4.7			
	84	14(0)	4.4±2.0	125±19	8.9±1.5	1.43±0.49	0.20±0.08	16.6±5.4			
Beaveroo Lake	84	21(0)	2.5±2.1	118±26	9.8±1.9	1.30±0.53	0.16±0.10	28.2±14.6			
Whitedog Lake	83	32(0)	2.8±1.6	120±20	12.7±1.1	1.31±0.50	0.36±0.23	65.7±22.7			
	84	35(0)	2.1±0.8	132±14	11.4±1.5	1.26±0.36	0.15±0.05	54.2±19.6			
Lulu Lake	83	10(0)	1.9±1.6	108±23	10.5±2.0	0.97±0.38	0.15±0.06	26.3±10.2			
Crowduck Lake	84	20(0)	2.1±0.6	118±12	9.5±0.7	1.06±0.21	0.21±0.05	21.3±6.5			
Big Grassy River	83	15(15)	1.4±0.3	182±24	10.3±1.4	1.71±0.62	0.14±0.06	31.3±8.1	11.0±0.8	2.21±0.42	1.02±0.50
Rat River Bay	83	35(32)	1.7±0.5	146±24	11.4±1.9	2.07±0.84	0.20±0.09	39.4±14.9	11.5±1.0	1.84±0.39	1.31±0.80
Nighthawk Lake	84	30(22)	1.8±0.4	114±11	6.3±0.5	0.72±0.18	0.04±0.01	17.7±4.3	15.7±0.8	2.63±0.31	0.84±0.33
Denton Lake	84	10(0)	1.1±0.1	88±21	5.6±1.1	0.53±0.24	0.08±0.03	9.5±2.9			
Grassy Lake	84	20(8)	1.1±0.2	132±22	5.6±0.9	0.83±0.45	0.08±0.05	16.2±7.0	10.2±0.6	1.08±0.10	0.27±0.14
Big Creek	83	10(10)	5.8±5.3	118±13	10.7±2.8	1.70±0.88	0.43±0.19	97.7±41.0	12.1±0.8	0.97±0.25	5.31±6.88

APPENDIX 7. Method used to estimate standard errors associated with means of values predicted from multiple regression equations.

According to Sokal and Rohlf (1981, p. 641), the standard error of the predicted mean $\bar{y}$ of m items for given values of predictor variables $x_1 \ldots x_k$ may be calculated as follows:

$$\hat{S}\bar{y} = Sy(1/m + 1/n + \sum_{i=1}^{k} c_{ii}x_i^2 + 2 \sum_{ij} c_{ij}x_i x_j)^{1/2}$$

$$= Sy(1/m + a + b + c)^{1/2}$$

The gaussian multipliers (c_{ii} and c_{ij}) are not provided in the output from the SPSS regression subprogramme that was used in this analysis. However, the output does provide a "typical" standard error for a predicted value of y ($\hat{S}y$). In fact, $\hat{S}\bar{y}$ depends on the values of $x_1 \ldots x_k$; there is greater uncertainty associated with a predicted y as the distance of x_i from $\bar{x}_i$ increases.

The equations for $\hat{S}y$ and $\hat{S}\bar{y}$ take similar forms:

$$\hat{S}y = Sy(1 + a + b + c)^{1/2} \qquad \hat{S}\bar{y} = Sy(1/m + a + b + c)^{1/2}$$

$$(\hat{S}y)^2 = (Sy)^2(1 + a + b + c) \qquad (\hat{S}\bar{y})^2 = (Sy)^2(1/m + a + b + c)$$

$$\frac{(\hat{S}y)^2}{(Sy)^2} = 1 + a + b + c \qquad \frac{(\hat{S}\bar{y})^2}{(Sy)^2} = 1/m + a + b + c$$

$$\frac{(\hat{S}y)^2}{(Sy)^2} - 1 = \frac{(\hat{S}\bar{y})^2}{(Sy)^2} - 1/m$$

$$(\hat{S}\bar{y})^2 = (\hat{S}y)^2 - (Sy)^2(1 - 1/m)$$

$$\hat{S}\bar{y} = [(\hat{S}y)^2 - (Sy)^2(1 - 1/m)]^{1/2}$$

where $\hat{S}y$ is taken as the "typical" standard error of a predicted y (given by SPSS), $(Sy)^2$ is the unexplained variance from the ANOVA for the overall regression (the residual mean square), and m is the sample size on which the predicted mean is based. The standard error of the predicted mean ($\hat{S}\bar{y}$) calculated in this way is inexact, since the means of the predictors $\bar{x}_i$ associated with the predicted $\bar{y}$ are not necessarily the same as the values of predictors x_i giving a "typical" $\hat{y}$. However, it will serve as an adequate approximation for the purposes of visual presentation in Figures 4.3 and 4.4.

APPENDIX 8. Means and ranges of principal component (PC) scores for field populations sampled over two years and for source/introduced population pairs. A different suffix for means of pair members indicates that they were significantly ($p \leq 0.01$) different in a Kruskal-Wallis test. The nonparametric procedure was used due to extreme heteroscedasticity in the data set.

PC		Arm Lake		Cedar River		Dollar Lake		Whitedog Lake	
		1983	1984	1983	1984	1983	1984	1983	1984
M:O	mean	0.69a	0.18b	1.27	1.00	0.27a	-1.21b	0.98a	0.46b
	minimum	-0.99	-0.80	-0.22	-0.42	-1.24	-1.78	0.20	0.02
	maximum	1.68	1.16	2.58	1.95	1.06	-0.80	1.76	1.03
P	mean	-1.37a	0.66b	0.09a	0.55b	0.30	0.66	-1.61a	0.14b
	minimum	-2.55	-2.50	-1.18	1.31	-1.46	-0.98	-3.41	-0.73
	maximum	0.08	1.65	1.29	1.73	1.86	1.23	-0.44	0.76
pH:Zn	mean	-0.32a	1.28b	0.50	0.25	-0.27	-0.16	-1.32a	-0.17b
	minimum	-1.44	0.67	-0.73	-0.43	-1.89	-1.24	-2.89	-0.48
	maximum	2.05	3.18	3.20	0.76	1.95	1.90	2.44	0.60
N	mean	-0.19a	-0.69b	-0.56	-0.67	1.65a	-0.57b	1.20a	0.07b
	minimum	-1.33	-1.55	-1.25	-1.47	0.17	-1.38	-0.14	-1.09
	maximum	1.29	0.75	1.30	1.08	2.77	0.12	2.55	1.47
D	mean	-1.44a	0.10b	0.74	0.39	-0.07a	0.71b	1.20a	0.07b
	minimum	-3.05	-1.51	-0.52	-0.76	-2.00	0.20	-1.19	-0.39
	maximum	0.66	1.44	2.10	1.83	1.06	1.86	0.84	1.73
PC	mean	-0.56a	-0.28b	-0.14	0.20	-0.38	-0.24	-0.05a	0.34b
	minimum	-1.26	-0.76	-0.77	-0.63	-1.20	-0.80	-1.18	-0.24
	maximum	2.07	2.75	3.11	4.16	0.11	0.07	3.34	2.29
Cu	mean	0.46	-0.15	-0.48	0.12	0.38	-0.06	-0.52	-0.22
	minimum	-3.18	-1.81	-3.10	-1.02	-1.68	-2.13	-2.67	-1.37
	maximum	2.74	1.58	0.83	1.58	2.60	0.66	1.92	1.14

		Velos Lake		#8	Lake			Lake		
		1983	1984		Crowduck	#6	du Bois	Beaveroo	#10	Philip
M:O	mean	-0.58a	-1.64b	-0.21a	-2.49a	-1.40b	0.06a	-0.25a	0.07a	-0.44b
	minimum	-1.06	-2.34	-1.54	-2.86	-2.09	-0.58	-0.83	-0.22	-0.84
	maximum	1.00	-0.89	0.21	-2.01	-0.47	1.19	0.59	0.69	0.66
P	mean	0.14	0.02	-0.46	-1.19a	-0.18b	0.80a	-0.12b	0.60a	0.26c
	minimum	-0.63	-1.25	-1.67	-1.97	-1.04	-1.50	-0.91	-0.03	-0.30
	maximum	0.94	1.02	1.04	-0.46	0.80	1.38	0.92	1.07	1.20
pH:Zn	mean	-0.72a	0.01b	-1.45c	0.06a	-0.55b	-0.80a	0.19b	-1.02a	1.31c
	minimum	-2.01	-0.65	-2.23	-0.36	-1.00	-1.84	-0.55	-1.64	0.62
	maximum	0.71	0.60	-0.84	0.43	-0.01	0.89	1.06	-0.62	2.16
N	mean	0.06a	-0.50b	0.00	-0.41	0.00	-0.34a	-0.89b	-0.08a	0.88c
	minimum	-1.07	-1.20	-1.12	-1.12	-0.97	-0.98	-1.71	-0.18	0.14
	maximum	1.14	0.06	1.20	0.12	0.68	0.72	-0.26	0.34	1.32
D	mean	0.30	0.13	0.41	0.75a	-0.83b	-1.00a	-0.46b	-1.13a	-0.67a
	minimum	-0.70	-0.99	-0.68	0.14	-1.45	-2.40	-2.19	-1.96	-1.48
	maximum	1.56	2.28	1.24	1.29	-0.26	0.15	0.36	-0.57	-0.10
PC	mean	-0.38	-0.50	-0.41	-0.21	-0.20	-0.12a	-0.34a	-0.18a	0.52b
	minimum	-1.41	-0.82	-1.19	-0.40	-0.74	-0.74	-0.70	-1.07	-0.35
	maximum	1.37	-0.10	0.54	0.00	0.70	5.47	0.17	0.15	2.05
Cu	mean	-0.28a	0.18b	0.82c	0.37	0.12	-0.02a	0.23a	1.00b	0.27a
	minimum	-0.90	-0.84	-0.02	-0.55	-0.68	-1.11	-0.56	0.70	-1.00
	maximum	0.55	3.16	2.68	0.77	0.83	1.22	1.86	1.60	1.25

APPENDIX 9. Raw data obtained in three experiments comparing various wild rice populations under greenhouse cultivation. Analyses and interpretations are presented in Chapter 1. Abbreviations used in the tables are as follows:

Population codes: A, Arm Lake; S, Mercer River, Sask.; V, Velos Lake; RL, Rice Lake (Red Lake District); D, Dollar Lake; PRE, Press Lake; B, Beaveroo Lake; CH, Charnock Lake; RR, Rat River Bay; WD, Whitedog Lake; BC, Big Creek.

Region codes: P, Pickle; N, Nakina; I, Ignace; K, Kenora; E, Lake Erie.

Variable names: SEQ, sequence number; REG, Region (climatic grouping); POPN, Seed source population; SOI, Soil type (1=Organic; 2=Clay); GHS, Greenhouse Number; DFO, Days to first pistillate floret opening; PTI, Tillers per plant; HT, Height; LEAFW, Leaf width; PSWT, Shoot weight per plant; TSWT, Shoot weight per tiller; PRWT, Root weight per plant; TRWT, Root weight per tiller; PFEM, Pistillate florets per plant; TFEM, pistillate florets per tiller; PSDWT, Seed weight (potential) per plant; HSDWT, weight per 100 seeds; SEEDL, Seed length.

Experiment 1

SEQ	REG	POPN	DFO	PTI	HT	LEAFW	PSWT	TSWT
1	P	V	59	8	96	7.30	10.02	1.252
2	P	V	68	10	106	6.00	9.93	0.993
3	P	V	98	2	66	4.70	0.69	0.345
4	P	V	86	2	77	6.40	0.75	0.375
5	P	V	61	9	115	7.50	13.87	1.541
6	P	V	59	8	130	5.90	13.28	1.660
7	P	V	69	7	126	6.30	8.99	1.284
8	P	V	59	11	121	6.80	17.49	1.590
9	P	V	76	7	110	6.70	4.77	0.681
10	P	V	91	7	120	6.60	6.92	0.989
11	K	WD	88	6	122	9.40	9.62	1.603
12	K	WD	65	4	150	9.40	17.80	4.450
13	K	WD	92	5	123	10.60	17.37	3.474
14	K	WD	75	5	148	11.40	14.90	2.980
15	K	WD	77	6	135	8.20	10.62	1.770
16	K	WD	88	7	120	7.90	17.33	2.476
17	K	WD	88	10	130	10.60	19.30	1.930
18	K	WD	96	8	133	9.60	16.36	2.045
19	K	WD	96	6	143	9.60	13.03	2.172
20	K	WD	70	9	187	12.50	35.78	3.976
21	K	WD	78	8	155	10.00	25.49	3.186
22	I	CH	62	13	121	8.00	18.88	1.452
23	I	CH	95	4	104	7.50	5.88	1.470
24	I	CH	67	6	146	8.00	12.86	2.143
25	I	CH	88	10	119	8.60	13.38	1.338
26	I	CH	80	13	113	7.00	11.07	0.852
27	I	CH	65	8	122	9.00	17.52	2.190
28	I	CH	92	8	132	8.60	12.50	1.562
29	I	CH	66	8	146	8.50	17.16	2.145
30	I	CH	92	9	89	7.60	10.39	1.154
31	I	CH	80	11	145	7.80	19.92	1.811
32	I	CH	65	9	136	7.50	20.22	2.247
33	I	CH	71	8	167	8.70	26.43	3.304
34	E	BC	73	11	136	6.80	11.55	1.050
35	E	BC	101	10	172	8.00	17.74	1.774
36	E	BC	99	9	212	6.80	24.28	2.698
37	E	BC	98	10	160	7.30	21.02	2.102
38	E	BC	128	6	171	15.00	25.68	4.280
39	E	BC	83	17	186	8.00	25.12	1.478
40	E	BC	97	12	171	10.70	30.54	2.545
41	E	BC	110	4	161	10.70	15.51	3.878
42	E	BC	88	8	210	10.20	26.44	3.305
43	E	BC	104	5	205	13.90	19.51	3.902
44	E	BC	100	8	202	11.80	30.60	3.825
45	E	BC	112	8	222	17.60	25.55	3.194
46	E	BC	98	14	225	8.60	36.92	2.637
47	E	BC	100	9	214	12.60	27.01	3.001
48	E	BC	119	10	173	12.40	27.62	2.762

SEQ	PRWT	TRWT	PFEM	TFEM	PSDWT	HSDWT	SEEDL
1	2.240	0.280	104	13.00	5.30	5.1	15.7
2	2.250	0.225	96	9.60	5.86	6.1	17.2
3	0.130	0.065	27	13.50	1.46	5.4	16.4
4	0.160	0.080	30	15.00	1.74	5.8	16.8
5	3.930	0.437	184	20.44	9.57	5.2	17.5
6	3.000	0.375	112	14.00	5.12	4.6	14.2
7	2.800	0.400	74	10.57	3.03	4.1	15.7
8	5.410	0.492	202	18.36	8.89	4.4	16.0
9	0.600	0.086	63	9.00	2.71	4.3	15.8
10	2.460	0.351	91	13.00	2.73	3.0	15.5
11	1.950	0.325	172	28.67	9.12	5.3	16.1
12	4.290	1.072	179	44.75	9.31	5.2	13.9
13	1.820	0.364	154	30.80	6.93	4.5	11.6
14	3.310	0.662	199	39.80	9.35	4.7	11.5
15	1.740	0.290	321	53.50	16.05	5.0	13.6
16	13.240	1.891	238	34.00	13.33	5.6	15.7
17	2.220	0.222	140	14.00	10.08	7.2	17.6
18	5.660	0.707	100	12.50	6.00	6.0	16.1
19	3.630	0.605	198	33.00	10.30	5.2	15.2
20	7.450	0.828	351	39.00	21.06	6.0	13.9
21	4.440	0.555	336	42.00	21.17	6.3	15.6
22	3.630	0.279	170	13.08	6.12	3.6	14.0
23	1.530	0.382	120	30.00	6.00	5.0	15.4
24	5.670	0.945	305	50.83	12.81	4.2	14.8
25	4.130	0.413	217	21.70	10.85	5.0	14.4
26	3.290	0.253	198	15.23	12.28	6.2	17.5
27	10.410	1.301	185	23.12	10.36	5.6	15.4
28	3.660	0.458	179	22.37	12.89	7.2	18.7
29	4.820	0.602	435	54.38	21.75	5.0	16.7
30	2.690	0.299	134	14.89	6.97	5.2	13.2
31	8.010	0.728	383	34.82	12.26	3.2	12.2
32	6.080	0.676	394	43.78	16.55	4.2	12.9
33	12.730	1.591	323	40.38	14.21	4.4	13.1
34	1.400	0.127	293	26.64	12.01	4.1	16.3
35	25.400	2.540	975	97.50	15.60	1.6	13.1
36	37.200	4.133	1340	148.89	18.76	1.4	12.2
37	39.460	3.946	1530	153.00	16.83	1.1	10.2
38	16.580	2.763	1979	329.83	23.75	1.2	9.6
39	60.370	3.551	1579	92.88	13.42	0.9	9.8
40	32.860	2.738	1863	155.25	26.08	1.4	10.8
41	8.540	2.135	1228	307.00	19.65	1.6	10.8
42	65.130	8.141	1501	187.62	28.52	1.9	11.9
43	28.710	5.742	1048	209.60	15.72	1.5	111.3
44	41.480	5.185	1239	154.87	21.06	1.7	11.4
45	25.280	3.160	1733	216.62	24.26	1.4	10.7
46	19.470	1.391	2169	154.93	26.03	1.2	10.1
47	22.940	2.549	1142	126.89	11.42	1.0	10.1
48	35.150	3.515	2847	284.70	51.25	1.8	13.4

Experiment 2

SEQ	REG	POP	SOI	DFO	PTI	HT	PSWT	TSWT
1	P	V	1	45	13	60	3.60	0.277
2	P	V	1	31	23	92	7.80	0.339
3	P	V	2	43	3	80	1.50	0.500
4	P	V	2	37	2	93	1.10	0.550
5	P	V	2	39	40	77	9.40	0.235
6	K	WD	1	77	19	134	28.00	1.474
7	K	WD	1	51	24	125	20.10	0.837
8	K	WD	1	64	20	140	50.00	2.500
9	K	WD	1	47	21	125	54.40	2.590
10	K	WD	1	27	18	122	23.60	1.311
11	K	WD	1	52	10	119	18.90	1.890
12	K	WD	1	54	21	100	10.50	0.500
13	K	WD	2	42	31	144	73.90	2.384
14	K	WD	2	56	25	133	34.40	1.376
15	K	WD	2	61	30	143	54.20	1.807
16	K	WD	2	49	18	159	67.80	3.767
17	K	WD	2	48	28	156	87.10	3.111
18	I	D	1	69	38	115	36.40	0.958
19	I	D	1	70	50	108	47.30	0.946
20	I	D	1	44	40	131	63.40	1.585
21	I	D	1	52	60	128	51.30	0.855
22	I	D	1	60	55	112	34.80	0.633
23	I	D	1	50	37	119	38.10	1.030
24	I	D	1	62	55	116	57.50	1.045
25	I	D	1	70	26	90	15.10	0.581
26	I	D	1	101	24	55	14.00	0.583
27	I	D	2	50	2	70	1.10	0.550
28	I	D	2	37	43	142	63.60	1.479
29	I	D	2	39	39	95	11.90	0.305
30	I	D	2	44	33	126	34.60	1.048
31	I	D	2	46	73	129	101.60	1.392
32	I	D	2	56	49	115	32.50	0.663
33	I	D	2	48	65	138	79.60	1.225
34	I	D	2	46	47	126	79.80	1.698
35	I	D	2	55	65	140	82.30	1.266
36	I	D	2	52	92	114	102.80	1.117
37	I	CH	1	71	3	90	0.90	0.300
38	I	CH	1	56	36	140	56.60	1.572
39	I	CH	1	51	21	130	24.20	1.152
40	I	CH	1	42	20	123	24.80	1.240
41	I	CH	1	48	19	146	24.80	1.305
42	I	CH	1	60	21	98	28.90	1.376
43	I	CH	2	63	5	78	2.00	0.400
44	I	CH	2	41	9	136	15.40	1.711
45	I	CH	2	53	45	176	104.80	2.329
46	I	CH	2	68	5	90	1.70	0.340
47	I	CH	2	47	30	133	42.00	1.400
48	I	CH	2	43	31	117	41.60	1.342
49	I	CH	2	36	50	123	43.00	0.860
50	I	CH	2	43	21	80	6.60	0.314

SEQ	PRWT	TRWT	PFEM	TFEM	PSDWT	HSDW	SEEDL
1	0.400	0.031	85	6.00	0.00	0.0	0.0
2	1.000	0.043	274	12.00	0.00	0.0	0.0
3	0.500	0.167	30	10.00	0.00	0.0	0.0
4	0.300	0.150	24	12.00	0.00	0.0	0.0
5	4.300	0.108	298	7.00	7.69	2.6	13.2
6	9.200	0.484	1121	59.00	24.30	2.2	10.2
7	5.100	0.212	825	34.00	0.00	0.0	0.0
8	25.000	1.250	1280	64.00	38.00	3.0	10.5
9	16.100	0.767	553	26.00	9.07	1.6	10.9
10	5.800	0.322	540	30.00	0.00	0.0	0.0
11	10.200	1.020	547	55.00	16.60	3.0	9.7
12	2.700	0.129	577	27.00	0.00	0.0	0.0
13	10.800	0.348	569	18.00	20.20	3.5	13.4
14	8.900	0.356	789	32.00	22.80	2.9	11.7
15	23.500	0.783	1232	41.00	25.90	2.1	9.8
16	18.400	1.022	727	40.00	20.00	2.7	13.0
17	20.000	0.714	922	33.00	28.10	3.0	13.5
18	17.100	0.450	1162	30.00	18.00	1.6	12.1
19	47.000	0.940	1181	24.00	28.00	2.4	12.4
20	21.600	0.540	1108	28.00	22.20	2.0	12.6
21	32.500	0.542	1313	22.00	22.00	1.7	11.3
22	9.300	0.169	948	17.00	24.00	2.5	14.2
23	9.800	0.265	890	24.00	24.50	2.8	14.2
24	16.500	0.300	1013	18.00	16.80	1.7	13.1
25	5.900	0.227	824	32.00	0.00	0.0	0.0
26	2.100	0.087	376	16.00	0.00	0.0	0.0
27	2.300	1.150	35	18.00	0.00	0.0	0.0
28	29.800	0.693	574	13.00	17.40	3.4	14.0
29	5.100	0.131	506	13.00	16.00	3.2	14.2
30	8.300	0.252	703	21.00	17.50	2.5	13.2
31	23.300	0.319	1352	18.00	23.90	1.8	10.8
32	3.100	0.063	586	12.00	12.70	2.1	11.1
33	24.400	0.375	1687	26.00	45.50	2.7	13.7
34	24.600	0.523	846	18.00	21.50	2.5	13.2
35	51.200	0.788	1827	28.00	40.20	2.2	11.5
36	45.900	0.499	1143	12.00	29.90	2.6	13.7
37	1.100	0.367	44	15.00	0.00	0.0	0.0
38	13.200	0.367	1652	46.00	56.17	3.4	14.4
39	7.700	0.367	819	39.00	19.40	2.3	11.0
40	7.000	0.350	603	30.00	17.60	2.9	12.4
41	6.200	0.326	966	51.00	29.00	3.0	12.3
42	34.400	1.638	1973	94.00	44.50	2.2	9.4
43	0.320	0.064	65	13.00	0.00	0.0	0.0
44	2.400	0.267	181	20.00	4.15	2.3	12.4
45	35.600	0.791	2578	57.00	50.70	2.0	11.2
46	0.200	0.040	102	20.00	0.00	0.0	0.0
47	20.900	0.697	931	31.00	15.20	1.6	8.7
48	11.900	0.384	1358	44.00	40.80	3.0	10.8
49	17.200	0.344	1097	22.00	33.10	3.0	13.2
50	1.100	0.052	493	23.00	0.00	0.0	0.0

Experiment 3

SEQ	REG	POP	DFO	PTI	HT	LEAFW	PSWT	TSWT
1	P	V	47	30	174	11.00	68.99	2.300
2	P	V	57	0	0	11.80	0.00	0.000
3	P	V	51	10	152	10.40	21.76	2.176
4	P	V	45	28	156	8.40	31.09	1.110
5	P	V	45	0	0	7.40	0.00	0.000
6	P	V	46	10	133	7.80	7.89	0.789
7	P	V	54	3	0	6.40	1.78	0.593
8	P	V	46	13	120	14.70	18.01	1.385
9	P	V	45	17	94	7.40	9.37	0.551
10	P	V	41	0	0	5.60	0.00	0.000
11	P	V	37	14	65	5.50	3.41	0.244
12	P	V	37	14	101	6.40	8.42	0.601
13	P	V	45	7	89	8.50	3.59	0.513
14	P	V	76	12	78	6.50	5.97	0.498
15	P	V	32	25	115	6.40	15.85	0.634
16	P	V	36	18	81	6.10	6.43	0.357
17	K	WD	35	35	145	6.70	58.63	1.675
18	K	WD	41	24	150	10.30	45.23	1.885
19	K	WD	52	14	150	10.10	43.71	3.122
20	K	WD	59	9	141	10.20	17.92	1.991
21	K	WD	49	17	117	7.70	39.77	2.339
22	K	WD	44	18	156	10.40	45.46	2.526
23	K	WD	41	49	127	7.80	48.27	0.985
24	K	WD	42	20	124	9.00	70.27	3.513
25	K	WD	56	32	135	9.40	39.09	1.222
26	K	WD	70	17	163	13.60	58.51	3.442
27	K	WD	71	8	157	13.20	37.36	4.670
28	K	WD	51	6	156	13.40	33.99	5.665
29	K	WD	77	8	177	17.20	49.50	6.187
30	K	WD	56	11	181	12.80	46.93	4.266
31	K	WD	0	10	170	13.50	46.38	4.638
32	K	WD	63	11	175	10.00	42.63	3.875
33	K	WD	67	9	184	16.60	41.12	4.569
34	K	WD	61	9	183	13.60	55.61	6.179
35	K	WD	66	8	168	19.20	42.05	5.256
36	K	WD	83	9	140	13.80	46.44	5.160
37	I	D	44	38	143	8.90	61.22	1.611
38	I	D	37	30	113	5.50	15.54	0.518
39	I	D	37	48	128	6.30	43.33	0.903
40	I	D	38	34	108	6.70	23.82	0.701
41	I	D	58	19	158	9.20	32.42	1.706
42	I	D	49	41	126	7.70	49.98	1.219
43	I	D	40	11	104	6.90	8.38	0.762
44	I	D	57	67	110	7.90	63.70	0.951
45	I	D	58	0	0	7.00	0.00	0.000
46	I	D	77	51	148	7.60	60.58	1.188
47	I	D	75	37	168	9.70	68.55	1.853
48	I	D	58	42	120	8.90	43.69	1.040
49	I	D	56	8	105	8.20	4.62	0.577

SEQ	REG	POP	DFO	PTI	HT	LEAFW	PSWT	TSWT
50	I	D	62	0	0	0.00	0.00	0.000
51	I	D	58	0	0	8.80	0.00	0.000
52	I	B	43	58	137	8.40	34.02	0.587
53	I	B	40	48	115	7.40	46.20	0.962
54	I	B	66	39	99	5.60	22.79	0.584
55	I	B	55	18	107	8.00	25.82	1.434
56	I	B	48	32	155	9.00	44.58	1.393
57	I	B	45	38	155	7.40	75.69	1.992
58	I	B	46	11	125	8.90	18.93	1.721
59	I	B	74	15	129	9.50	31.67	2.111
60	I	B	65	18	159	11.60	40.19	2.233
61	I	B	61	34	134	11.40	63.58	1.870
62	I	B	66	52	160	8.60	78.86	1.517
63	I	B	64	24	157	10.60	58.27	2.428
64	I	B	57	9	130	10.20	12.08	1.342
65	I	B	69	26	170	13.60	67.76	2.606
66	I	B	0	6	66	6.10	4.53	0.755
67	I	B	63	27	153	12.20	61.41	2.274
68	N	A	43	19	137	8.20	25.97	1.367
69	N	A	56	12	178	7.50	36.67	3.056
70	N	A	46	17	149	9.20	43.46	2.556
71	N	A	42	27	119	6.70	22.60	0.837
72	N	A	47	12	144	9.20	24.99	2.082
73	N	A	68	20	142	9.70	25.43	1.271
74	N	A	48	21	133	8.10	27.28	1.299
75	N	A	59	13	177	11.30	31.69	2.438
76	N	A	45	17	124	9.00	35.06	2.062
77	N	A	57	15	166	8.30	30.04	2.003
78	N	A	60	10	157	12.60	27.29	2.729
79	N	A	43	10	174	11.20	42.49	4.249
80	I	PRE	48	59	149	7.60	65.22	1.105
81	I	PRE	86	19	94	9.20	20.45	1.076
82	I	PRE	44	48	172	9.00	107.17	2.233
83	I	PRE	58	34	133	10.40	43.03	1.266
84	I	PRE	64	20	106	13.10	24.31	1.215
85	I	PRE	59	57	114	9.40	56.65	0.994
86	I	PRE	54	0	0	7.90	0.00	0.000
87	I	PRE	54	0	0	10.60	0.00	0.000
88	I	PRE	62	30	159	11.40	66.06	2.202
89	I	PRE	66	32	110	11.10	44.41	1.388
90	K	RR	61	18	102	12.40	20.17	1.121
91	K	RR	53	17	171	10.00	47.35	2.785
92	K	RR	59	13	113	9.70	18.01	1.385
93	K	RR	59	22	150	8.00	47.68	2.167
94	K	RR	71	19	168	11.70	52.23	2.749
95	K	RR	103	14	175	18.00	38.43	2.745
96	K	RR	90	11	210	15.30	41.29	3.754
97	K	RR	71	8	153	17.20	37.42	4.677
98	K	RR	69	11	184	14.20	58.98	5.362
99	K	RR	85	12	156	13.40	47.11	3.926
100	K	RR	62	17	161	12.50	33.65	1.979

SEQ	REG	POP	DFO	PTI	HT	LEAFW	PSWT	TSWT
101	K	RR	63	20	163	14.10	48.71	2.435
102	I	RL	38	12	109	8.20	11.86	0.988
103	I	RL	37	32	151	10.80	54.67	1.708
104	I	RL	56	34	127	9.30	28.53	0.839
105	I	RL	49	45	119	10.00	46.82	1.040
106	I	RL	48	32	137	10.00	55.52	1.735
107	I	RL	45	15	141	9.20	16.45	1.097
108	I	RL	47	22	168	18.00	44.39	2.018
109	I	RL	50	3	74	4.50	1.62	0.540
110	I	RL	61	24	134	13.20	31.22	1.301
111	I	RL	62	12	223	16.40	44.23	3.686
112	I	RL	58	4	89	7.20	2.13	0.532
113	I	RL	55	2	105	6.00	2.44	1.220
114	P	S	70	16	139	11.40	32.67	2.042
115	P	S	49	20	120	9.00	30.46	1.523
116	P	S	52	7	121	5.30	11.30	1.614
117	P	S	55	21	131	12.30	63.66	3.031
118	P	S	46	19	148	8.40	50.60	2.663
119	P	S	45	35	144	7.20	37.73	1.078
120	P	S	33	43	134	6.40	51.58	1.200
121	P	S	49	17	114	6.00	18.77	1.104
122	P	S	49	11	144	9.60	38.29	3.481
123	P	S	50	73	98	6.60	26.31	0.360
124	P	S	50	22	105	7.90	35.23	1.601
125	P	S	55	18	96	9.60	11.65	0.647
126	P	S	64	20	141	9.60	37.94	1.897
127	P	S	51	47	145	7.80	51.25	1.090
128	P	S	0	0	0	12.20	0.00	0.000
129	P	S	58	0	0	12.80	0.00	0.000
130	P	S	54	0	0	10.10	0.00	0.000

SEQ	PRWT	TRWT	PFEM	TFEM	PSDWT	HSDW	SEED
1	11.410	0.380	1068	35.60	36.10	3.4	12.0
2	0.000	0.000	0	0.00	0.00	2.5	10.6
3	5.590	0.559	681	68.10	18.11	2.7	10.3
4	3.910	0.140	952	34.00	33.32	3.5	13.2
5	0.000	0.000	0	0.00	0.00	1.6	9.7
6	0.860	0.086	265	26.50	6.89	2.6	11.8
7	0.680	0.227	54	18.00	1.68	3.1	11.2
8	4.220	0.325	1086	83.50	30.50	2.8	11.5
9	0.820	0.048	296	17.40	8.84	3.0	13.4
10	0.000	0.000	0	0.00	0.00	0.0	0.0
11	0.620	0.044	227	16.20	5.44	2.4	12.2
12	1.000	0.071	358	25.60	11.47	3.2	13.4
13	0.610	0.087	132	18.80	3.66	2.8	12.2
14	0.760	0.063	278	23.20	10.25	3.7	15.5
15	1.710	0.068	445	17.80	13.88	3.1	13.3
16	0.790	0.044	223	12.40	7.81	3.5	13.9
17	6.410	0.183	1544	44.10	39.20	2.5	10.2
18	7.180	0.299	1694	70.60	41.85	2.5	11.8
19	5.250	0.375	962	68.70	21.74	2.3	11.3
20	2.850	0.317	495	55.00	13.27	2.7	12.2
21	3.660	0.215	585	34.40	15.67	2.7	12.8
22	5.490	0.305	2106	117.00	46.33	2.2	10.5
23	6.910	0.141	2185	44.60	58.13	2.7	10.9
24	6.080	0.304	808	40.40	25.13	3.1	13.0
25	2.880	0.090	2010	62.80	40.59	2.0	10.2
26	8.200	0.482	2593	152.50	43.04	1.7	8.4
27	5.350	0.669	848	106.00	0.00	0.0	0.0
28	9.030	1.505	1160	193.30	21.57	1.9	8.2
29	10.930	1.366	1563	195.40	34.70	2.2	10.3
30	14.400	1.309	1498	136.20	28.02	1.9	10.5
31	8.980	0.898	1738	173.80	26.07	1.5	9.1
32	10.330	0.939	1320	120.00	19.14	1.5	9.6
33	13.610	1.512	1580	175.60	27.82	1.8	9.7
34	19.820	2.202	1640	182.20	31.81	1.9	10.3
35	13.790	1.724	2114	264.20	40.37	1.9	9.1
36	13.190	1.466	1718	190.90	29.21	1.7	9.8
37	7.990	0.210	1364	35.90	42.97	3.1	11.6
38	1.760	0.059	597	19.90	17.97	3.0	12.8
39	3.380	0.070	941	19.60	42.34	4.5	15.8
40	2.120	0.062	500	14.70	21.89	4.4	16.3
41	9.370	0.493	722	38.00	21.95	3.0	13.9
42	8.330	0.203	816	19.90	29.86	3.7	15.6
43	0.900	0.082	404	36.70	13.56	3.4	13.6
44	13.090	0.195	1119	16.70	0.00	0.0	0.0
45	0.000	0.000	0	0.00	0.00	0.0	0.0
46	9.300	0.182	1698	33.30	38.38	2.3	11.9
47	13.970	0.378	1510	40.80	41.36	2.7	13.2
48	6.110	0.145	1525	36.30	39.64	2.6	11.4
49	1.710	0.214	234	29.20	3.88	1.7	9.0
50	0.000	0.000	0	0.00	0.00	0.0	0.0
51	0.000	0.000	0	0.00	0.00	0.0	0.0

SEQ	PRWT	TRWT	PFEM	TFEM	PSDWT	HSDW	SEED
52	4.910	0.085	1885	32.50	58.43	3.1	12.6
53	12.960	0.270	2122	44.20	57.28	2.7	11.9
54	3.060	0.078	585	15.00	26.27	4.5	17.0
55	4.450	0.247	412	22.90	13.81	3.3	13.6
56	10.250	0.320	1904	59.50	67.21	3.5	13.9
57	10.780	0.284	1075	28.30	41.08	3.8	15.5
58	2.890	0.263	176	16.00	7.62	4.3	15.8
59	5.140	0.343	623	41.50	17.06	2.7	12.5
60	10.390	0.577	1451	80.60	33.66	2.3	10.4
61	11.250	0.331	1703	50.10	36.45	2.1	9.7
62	12.630	0.243	2070	39.80	52.98	2.6	12.0
63	13.210	0.550	2501	104.20	67.27	2.7	11.8
64	2.100	0.233	690	76.70	13.74	2.0	10.8
65	22.870	0.880	2366	91.00	52.05	2.2	10.9
66	0.680	0.113	167	27.80	0.00	0.0	0.0
67	11.860	0.439	1620	60.00	33.05	2.0	9.2
68	5.050	0.266	695	36.60	15.86	2.3	12.1
69	4.750	0.396	674	56.20	11.94	1.8	10.3
70	9.740	0.573	1071	63.00	22.49	2.1	10.8
71	2.900	0.107	586	21.70	11.72	2.0	11.8
72	7.690	0.641	578	48.20	13.01	2.2	11.8
73	8.260	0.413	1282	64.10	20.64	1.6	9.4
74	7.350	0.350	668	31.80	19.23	2.9	12.4
75	6.380	0.491	1516	116.60	26.07	1.7	9.8
76	9.440	0.555	675	39.70	17.55	2.6	11.3
77	6.690	0.446	1128	75.20	22.90	2.0	11.7
78	11.330	1.133	1459	145.90	22.76	1.6	9.7
79	6.950	0.695	946	94.60	18.83	2.0	11.3
80	5.980	0.101	1676	28.40	44.74	2.7	12.3
81	1.600	0.084	665	35.00	11.97	1.8	10.2
82	13.890	0.289	2410	50.20	84.10	3.5	12.7
83	10.140	0.298	2533	74.50	65.35	2.6	12.0
84	1.630	0.081	788	39.40	10.87	1.4	8.2
85	11.150	0.196	2936	51.50	35.23	1.2	8.1
86	0.000	0.000	0	0.00	0.00	0.0	0.0
87	0.000	0.000	0	0.00	0.00	0.0	0.0
88	19.560	0.652	2343	78.10	42.41	1.8	8.9
89	9.630	0.301	2582	80.70	26.08	1.0	7.8
90	5.580	0.310	1375	76.40	28.60	2.1	10.5
91	13.490	0.794	1530	90.00	41.92	2.7	10.2
92	2.600	0.200	632	48.60	14.15	2.2	11.4
93	13.680	0.622	1602	72.80	36.20	2.3	11.8
94	15.730	0.828	2094	110.20	0.00	0.0	0.0
95	23.890	1.706	1917	136.90	48.30	2.5	8.9
96	11.330	1.030	1211	110.10	27.49	2.3	9.6
97	11.200	1.400	1281	160.10	24.85	1.9	9.6
98	12.820	1.165	801	72.80	21.62	2.7	11.0
99	11.200	0.933	1606	133.80	23.76	1.5	8.4
100	5.440	0.320	947	55.70	23.96	2.5	10.6
101	12.740	0.637	1618	80.90	20.55	1.3	7.5
102	1.470	0.122	502	41.80	10.83	2.2	9.8

SEQ	PRWT	TRWT	PFEM	TFEM	PSDWT	HSDW	SEED
103	13.020	0.407	1427	44.60	39.11	2.7	10.7
104	4.020	0.118	1142	33.60	33.82	3.0	11.4
105	7.860	0.175	2277	50.60	73.55	3.2	11.4
106	6.730	0.210	1619	50.60	46.63	2.9	10.8
107	3.120	0.208	438	29.20	11.87	2.7	10.8
108	16.850	0.766	2556	116.20	66.47	2.6	9.5
109	0.350	0.117	20	6.70	0.52	2.6	11.3
110	8.160	0.340	1548	64.50	30.96	2.0	8.4
111	10.000	0.833	2348	195.70	58.48	2.5	10.0
112	0.430	0.108	36	9.00	0.00	0.0	0.0
113	0.540	0.270	14	7.00	0.57	4.0	13.9
114	4.460	0.279	1320	82.50	35.11	2.7	11.0
115	4.360	0.218	628	31.40	11.37	1.8	9.7
116	1.780	0.254	129	18.40	4.89	3.8	13.1
117	12.990	0.619	3148	149.90	74.92	2.4	10.4
118	6.090	0.321	561	29.50	19.00	3.4	12.3
119	3.550	0.101	732	20.90	22.31	3.0	15.4
120	5.490	0.128	1436	33.40	39.06	2.7	11.6
121	2.880	0.169	218	12.80	7.83	3.6	13.9
122	7.700	0.700	371	33.70	13.42	3.6	12.6
123	2.840	0.039	1358	18.60	0.00	0.0	0.0
124	5.260	0.239	1197	54.40	12.81	1.1	8.8
125	0.620	0.034	745	41.40	13.56	1.8	9.1
126	6.700	0.335	1576	78.80	38.77	2.5	9.7
127	7.220	0.154	1673	35.60	38.15	2.3	10.6
128	0.000	0.000	0	0.00	0.00	2.4	11.2
129	0.000	0.000	0	0.00	0.00	0.0	0.0
130	0.000	0.000	0	0.00	0.00	0.0	0.0