Characterization of White Floury Corn (*Zea mays* L.) Landraces of Ontario

Christian Azar

Department of Plant Science

McGill University, Montréal

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DEDICATION

To my life companion Sasithorn Tajchakavit

THESIS FORMAT DESCRIPTION

This thesis consists of papers submitted or to be submitted for journal publications. The format is consistent with all requirements outlined in the Guidelines for Thesis Preparation of the Faculty of Graduate Studies and Research of McGill University. These requirements for a manuscript-based thesis are listed below:

"Candidates have the option of including, as part of the thesis, the text of a paper(s) submitted or to be submitted for publication, or the clearly-duplicated text of a published paper(s). These texts must be bound as an integral part of the thesis.

If this option is chosen, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.

The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: A Table of Contents, an abstract in English and French, and introduction which clearly states the rationale and objectives of the study, a comprehensive review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Supervisors must attest to the accuracy of such statements at the oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers. Under no circumstances can a co-author of any component of such a thesis serve as an examiner for that thesis."

GENERAL ABSTRACT

Characterization of White Floury Corn (*Zea mays* L.) Landraces of Ontario

M.Sc. **Christian Azar** **Plant Science**

Data were collected on 24 traits to characterize and classify 35 white floury corn (*Zea mays* L.) landraces collected on native reserves in Ontario. Several landrace x landrace and landrace x inbred crosses were evaluated. Test crosses were made to determine whether the landraces carry the *floury-1* (fl_1) allele. Most traits examined exhibited considerable variation among the landraces. Variation was also observed within many of the landraces for ear and cob colour, for endosperm texture and row number. The landraces were grouped into 10 clusters by centroid clustering analysis. Significant heterosis over the mid-parent value was observed in the crosses among landraces. Some crosses between landraces and inbreds yielded more than either parent. Crossing the landraces with the inbreds improved some agronomic characteristics, but disrupted some of the ear characteristics of the landraces. The floury factor responsible for the characteristic endosperm texture of the IAPO landraces was identified as being the dosage dependent fl_1.

RÉSUMÉ

Caractérisation d'Écotypes de Maïs (*Zea mays* L.) Blanc Farineux de l'Ontario

Maîtrise **Christian Azar** **Phytotechnie**

Vingt-quatre traits ont été observés pour caractériser et classifier 35 écotypes de maïs (*Zea mays* L.) blanc farineux obtenus de réserves indiennes en Ontario. Quelques croisements écotype x écotype et écotype x lignée-fixée ont été évalués. Des croisements ont aussi été effectués pour déterminer si les écotypes sont porteurs du gène fl_1. La plupart des traits examinés ont montré une variation parmi les écotypes. La couleur des grains et des rafles, la texture de l'endosperme et le nombre de rang sur l'épi étaient variables à l'intérieur des écotypes. Les écotypes ont été classifiés en 10 groupes en utilisant la méthode de groupement centroïde. Une quantité significative d'hétérosis, au delà de la moyenne parentale, a été observée dans les croisements entre écotypes. Certain croisements impliquant des écotypes et des lignées fixées, ont produit plus de grains que chaque parent considéré individuellement. Le croisement d'écotypes et de lignés fixées a amélioré certains traits agronomiques, mais a modifié certains traits caractéristiques des épis des écotypes. Le facteur responsable de la texture farineuse caractéristique de l'endosperme des écotypes, a été identifié comme étant le gène fl_1.

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TABLE OF CONTENTS

DEDICATION ii

THESIS FORMAT DESCRIPTION iii

GENERAL ABSTRACT v

RÉSUMÉ vi

ACKNOWLEDGEMENTS vii

TABLE OF CONTENT ix

LIST OF TABLES xii

LIST OF FIGURES xiii

LIST OF APPENDIX FIGURES AND TABLES xiv

CHAPTER 1 1

CONTRIBUTION OF CO-AUTHORS 1

CHAPTER 2 2

GENERAL INTRODUCTION 2

CHAPTER 3 3

LITERATURE REVIEW 3
Corn 3
Corn today 6
Alkali-cooking 7
Corn landraces of Ontario 9
Endosperm texture 9
Cob and kernel colour 11
Kernel shape 13
Stalk lodging 14
Tillering 15
Ear-row number 17

CHAPTER 4 19

PREFACE 19

CORN (*Zea mays* L.) LANDRACES OF THE ST. LAWRENCE-GREAT LAKES REGION OF NORTH AMERICA 20
Abstract 20
Introduction 21
Materials and Methods 22
Results and Discussion 25
Kernel characters 25
Ear characters 26
Grain yield 27
Other characters 28
Cluster analysis 29
Conclusions 29

CHAPTER 5 43

PREFACE 43

HETEROSIS AND ENDOSPERM TEXTURE IN CROSSES INVOLVING CORN (*Zea mays* L.) LANDRACES OF THE ST.LAWRENCE-GREAT LAKES REGION OF NORTH AMERICA . . 44
Abstract 44
Introduction 45
Materials and Methods 46
Experiment 1 47
Experiment 2 48
Experiment 3 49
Results and Discussion 49
Experiment 1 49
Experiment 2 51
Experiment 3 52
Conclusions 53

CHAPTER 6 59

GENERAL DISCUSSION 59
Variation among landraces 59
Landraces vs commercial hybrids 60
Genetic improvement of the landraces 62

CHAPTER 7 65

SUGGESTED RESEARCH 65

CHAPTER 8 67

REFERENCES 67

APPENDIX A 75

APPENDIX B 79

LIST OF TABLES

Table no. **Page no.**

Table 4.1. Origin of collection, original collection size, kernel colour, cob colour, ear row number, and endosperm texture of 36 entries . . 31

Table 4.2. Means and standard errors of six traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1994 34

Table 4.3. Means and standard errors of six traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994 36

Table 4.4. Means and standard errors of six traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994 38

Table 4.5. Ten clusters grouping the 35 white floury landraces and the experimental cultivar I-37 based on seven traits observed in Ste-Anne de-Bellevue and Ottawa in 1994 40

Table 5.1. Origin of ten landraces and two inbreds 54

Table 5.2. Means of four white floury landraces and crosses among them in Ste-Anne-de-Bellevue and Ottawa for grain yield in 1994, and for grain moisture content, lodging and kernel area, in 1993 and 1994 55

Table 5.3. Means of two white floury landraces, two white inbreds, and their crosses in Ste-Anne-de-Bellevue and Ottawa for grain yield in 1994, and for grain moisture content, lodging and kernel area in 1993 and 1994 57

LIST OF FIGURES

Figure no. **Page no.**

Figure 4.1 Location of Akwesasne, Moravian, Oneida, Six Nations, and Tyendinaga reserves in southern Ontario, and of the Sandborn reserve in New York State, where corn landraces were collected between 1986 and 1989 41

Figure 4.2 Dendrogram of the centroid clustering of 35 white floury landraces and one experimental population (I-37) based on seven traits observed in Ste-Anne-de-Bellevue and Ottawa in 1994 42

LIST OF APPENDIX FIGURES AND TABLES

Figures no. **Page no.**

Figure A.1. (a) Cross section of an eight-row ear showing the wide, crescent-shaped kernels of the landraces; (b) field view showing clear height differences among two landraces and their profusive tillering growth habit; (c) example of the long husk leaf blades typical of Northern Flints; (d) cob colour segregation within landraces, ranging from white, pink, red to brown 76

Figure A.2. (a,b) Ears of the two best yielding landraces I-20 and I-17; (b,c) ears of the two lowest yielding landraces I-12 and I-8 (See Chapter 4). 77

Figure A.3. (a,b) Pairs of ears of landrace parents (left and right) and their F_1 progeny (the centre pair of ears) (See Chapter 5, experiment 1); (c,d) one ear of the control hybrid (left), the landrace (second pair of ears form the right) and inbred (right) parents, and their crosses (third pair of ears form the right) (See Chapter 5, experiment 2) . 78

Table no.

Table B.1. Means of six traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1994 80

Table B.2. Means of three traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994 82

Table B.3. Means of three traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994 84

Table B.4. Means of three traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994 86

Table B.5. Means of three traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994 88

CHAPTER 1

CONTRIBUTION OF CO-AUTHORS

The two manuscripts are co-authored by C. Azar, D.E. Mather and R.I. Hamilton. Dr. Mather has been my research supervisor during my M.Sc. studies. She assisted me in the design of experiments, the analysis of data and for manuscript preparation and presentation. Dr. Hamilton provided the germplasm necessary to the four experiments constituting this study. He also provided me with technical information and assisted me with the manuscript preparation.

CHAPTER 2

GENERAL INTRODUCTION

The Indian Agricultural Program of Ontario (IAPO) is a non-profit corporation owned by Status Indian farmers in Ontario. This corporation assists Status Indian farmer to manage their agricultural resources. Among other services, the Native Crop Development program looks for alternative farm income sources using crops native to North America. Their interest focuses on crops that are profitable on small acreage.

From 1986 to 1989, the Native Crop Development program of IAPO collected 35 corn (*Zea mays* L.) landraces from native reserves in Ontario and New York State. Food products like hulled corn soup, corn flour, toasted corn nuts and corn chips were produced and were marketed.

The low grain yield of their landraces did not meet IAPO's main goal of promoting high-value low-acreage cropping. Therefore, IAPO sought help from researchers at the Central Research Farm of Agriculture and Agri-Food Canada, in Ottawa.

Nothing was known about these corn landraces. Basic characterization had to be done and was the main goal of the present study. Furthermore, the need to improve this corn demanded the assessment of experimental crosses involving the IAPO landraces; this was the second objective of this study.

CHAPTER 3

LITERATURE REVIEW

Corn

Corn (*Zea mays* L.) is a member of the family Poaceae. The *Zea* genus is composed of corn (*Z. mays* L. ssp. *mays*) and of teosinte subspecies (*Z. mays* L. ssp. *mexicana*, ssp. *parviglumis* and ssp. *huehuetenagensis*), and of a series of teosinte species (*Z. diploperennis*, *Z. perennis* and *Z. luxurians*) (Doebley, 1990). Corn appears to have its centre of origin in the Tehuacan Valley of Mexico where 80,000 years old pollen similar to that of the *Zea* genus has been found in drill cores taken from old lake beds near Mexico City (Janik *et al.* 1974). The earliest archeological materials date to about 5000 B.C. in the Tehuacan Valley (Goodman 1976). Domestication of the *Zea* genus yielded over 250 different races of corn (Doebley *et al.* 1986).

The prehistoric corn remains encountered in the Great Plains of North America were composed of a mixture of races including eight-row corn (Wagner, 1994). From examination of archaeological corn remains, Brown and Anderson, (1947) concluded that the eight-rowed, slender-eared flint corn was the predominant type of corn grown in the pre-Columbian American northeast. This eastern eight-row corn belongs to the racial complex Northern Flints and Flours (Goodman, 1978). According to Wagner (1994), scholars agree on the southern origin of the eastern eight-row complex, but disagreements arise among them regarding the development and spread of archaeological types or races and their classification.

Jacques Cartier in 1535 and Samuel de Champlain in 1605 saw large corn fields on both sides of the St. Lawrence river as they progressed toward the Great Lakes of North America (Parker, 1910). In fact, the explorers of the Americas found corn growing wherever climate and soil conditions allowed its cultivation, from southern Canada to within 1600 km from Cape Horn, in the Caribbean islands, and at altitudes above 4000 metres in the Andean region (Weatherwax, 1954).

During pre-Columbian times, the Iroquois native tribes were located along the upper shores of the St. Lawrence river and southeast of the North American Great Lakes. They had developed agriculture to a point where hunting had become a hobby (Assiniwi, 1973). Squash, pumpkin, sunflower, Jerusalem artichoke and bean were important crops for these agricultural nations, with corn being their most important and favourite food crop (Parker, 1910; Assiniwi, 1973). Corn probably reached Ontario before A.D. 800 (Cutler and Blake, 1976: cited in Bendremer and Dewar, 1994).

Although the eastern agricultural complex can be traced back to 1000-300 B.C., corn became a significant part of the northeast natives subsistence system from about A.D. 1000 (Wymer, 1994; Bendremer and Dewar, 1994). The importance of corn for the American natives is reflected in their numerous myths, legends and their ceremonialism related to corn and its origin (Witthoft, 1949; Jenness, 1956; Nicolar, 1979). Pre-Columbian Iroquois tribes grew floury, flint, sweet, pop and pod corn of various colours (Harrington, 1908). At the beginning of this century, the Mohawk and the Seneca, both Iroquois tribes, were still growing white floury Tuscarora (also called "squaw") varieties, sweet, hominy, pop and pod corn of various colours (Parker, 1910).

The Iroquois tribes used corn to prepare hulled corn, hulled corn soup, boiled corn bread, leaf bread, baked green corn, pop corn pudding and other foods (Harrington, 1908; Parker, 1910). They used the stalks of the corn plants to make tubes to store medicine. For these, a section of a stalk was cut, its pith removed and plugs were inserted at both ends. The pith of the stalks was used as an absorbent. The juice of the green stalks and roots was used to treat cuts and bruises. Floaters for fish lines were made from dry stalks. Many children's toys were constructed from the stalks (Parker, 1910).

The Iroquois tribes used sifted hardwood ashes in the proportion of about one litre of ashes to five litres of water to cook their corn (Harrington, 1908). The corn was boiled with ashes until the pericarp slipped easily away when rolled between the fingers. The pericarp was removed by rinsing and stirring. The corn was then boiled in clear water until soft.

A study of ethnographic literature (Katz *et al.*, 1974) focusing on more than 50 New World native tribes showed that corn was a major part of their diet only where alkali-cooking techniques were used. It has been suggested that the increase in availability of essential amino acids resulting from alkali cooking made corn nutritious enough to be used as a major component of the native diets (Katz *et al.*, 1974). Where lime was readily available, the Americas natives used it instead of ash to cook their corn. At equal weight, hardwood ashes have the same neutralizing power as ground limestone (Alth, 1977).

Corn today

Grain corn (*Zea mays* L.) was the world's leading grain producer in 1994, with 569,557,000 t harvested. In terms of surface area occupied, it was third after wheat and rice (FAO Yearbook, 1995).

Yellow dent corn is now the prevailing type grown in North America, but some sweet and pop types are cultivated. Wet-corn millers use some *waxy* types and the food industry uses some white dents (Leath and Hill, 1987).

The United States produced 216,000,000 t of grain corn in 1994. The American market for grain corn use is divided as follows: 62 % feed, 5 % high fructose corn syrup, 3 % glucose and fructose, 3 % starch, 6 % fuel alcohol, 1 % beverage alcohol, 1 % food (corn chips, corn bread, cereals, etc.), 17 % export (Baker and Riley, 1994).

Canadian grain corn production area was close to 1,000,000 ha in 1995 and generated 7,013,000 t of grain, ranking fourth after wheat, barley and canola. The surface area occupied by grain corn production in Canada ranked fifth after wheat, barley, oat and canola. Ontario was the province producing the most grain corn (4,902,000 t) followed by Québec (2,000,000 t) (Statistics Canada, 1995).

Annually, 1,400,000 t of grain corn are used for human food and industrial use in Canada (Statistics Canada, 1995). Ontario uses 27% of its corn for industrial purposes, 0.3 % for seed and the balance as animal feed. Corn transformation industries include wet mills, dry mills, ethanol plants, distilleries, breweries and alkali-cooking plants. Ontario's processing industry is diversified and uses corn in a variety of food and industrial products including corn flour, snack food, breakfast cereals, semolina, alcoholic beverages, starch, dextrose, dextrine and ethanol (Chartrand and Bolduc, 1995).

Alkali-cooking

Alkali-cooking plants produce a dough called masa, which is used for production of food products including tortillas, taco shells, tortilla chips, corn chips and tamales. The technology used by the modern alkali-cooking processing plants is basically the same as the one used by the natives, except for the sophistication of the equipment and the purity of the ingredients (Rooney and Serna-Saldivar, 1987). Alkali-cooking plants use hydrated lime or quicklime, which is obtained from the calcination of limestone. The concentration of the lime used to cook corn depends on the end product desired. For tortilla chips, alkali-cooking requires a lime concentration of 0.8-1.25 % of the corn weight (Serna-Saldivar *et al.*, 1990).

The basic industrial alkali cooking process of corn is as follows (Serna-Saldivar *et al.*, 1991; Frenette, 1994):

1. The corn is rinsed with clear water,
2. is put to steep with lime until swollen,
3. is boiled for approximately one hour,
4. is rinsed free of lime,
5. is left to steep in clear water for 8-10 hours.
6. The pericarp and lime residues are removed by stirring and rinsing.
7. The corn is ground to produce a dough called masa.

Alkali-cooking disrupts the protein matrix in the kernels endosperm by degrading disulphide bonds and also by causing starch granules to swell (Wall and Paulis, 1978).

Quality criteria for alkali processing include white kernel and cob colour, ease of pericarp removal, intermediate to hard endosperm, shallow perfect kernel indentations, rounded crowns, absence of cracks in the pericarp, uniformity of kernel size and high specific density.

The purpose of these criteria is to obtain homogeneity in the cooking process with minimal losses and a predictable end product. The cob colour is important because coloured cobs tissues remaining attached to the kernels can alter the colour of the end product (Watson, 1988; Serna-Saldivar *et al.*, 1990). White corn alone or only a small proportion of yellow corn is generally preferred because 100 % yellow corn results in an off-flavour during frying of the tortilla due to the carotenoid destruction (Serna-Saldivar *et al.*, 1990). Consumers also prefer a lighter-coloured food product (Hallowell, 1993). Hard starch must be present in the kernels because soft starch gelatinizes too fast and produces a dough that is too sticky (Johnson, 1991).

Despite the specific kernel quality requirements of the alkali-cooking industry, the genotype, environment, field management and storage conditions of corn can alter kernel physical characteristics, making the alkali-cooking process variable (Shumway *et al.*, 1992).

In Canada, the white corn destined for alkali cooking is grown in southern Ontario only, where the long maturation season favours good quality. Canadian white corn is used for domestic and export food corn markets. A total of 12,500 t were produced in Ontario in 1994, representing 0.3 % of the production (Johnson, 1995).

Corn landraces of Ontario

Between 1986 and 1989, the Indian Agricultural Project of Ontario (IAPO) collected landraces on six native reserves in Ontario and New York State. These greatly resemble one of the Tuscarora varieties described by Sturtevent (1899); they have short (20 cm) white cobs with eight rows of dull white floury larger than deep kernels. The Tuscarora varieties belong the Northern Flints and Flours complex.

After collecting germplasm, IAPO developed food products including corn chips derived from alkali-cooking, and designed a marketing strategy that emphasized the use of traditional landraces. Native farmers began to produce the landraces on a field scale, but encountered difficulties due to poor standability, high tillering, and low yields. Furthermore, both kernel size and cob colour were more variable than desired for alkali-cooking.

The main objective of the research described in this thesis is to characterize the IAPO landraces, with considerations for endosperm texture, cob and kernel colour, kernel shape, stalk lodging, tillering and ear-row number.

Endosperm texture

Corn kernels show a diversity of endosperm textures. The endosperm often contains both vitreous (or hard or translucent or horny or corneous) and floury (or soft or opaque) starch, with the vitreous portion on the periphery of the kernel (Dombrink-Kurtzan and

Bietz, 1993).

In normal dent kernels, the vitreous endosperm is composed of tightly compact polygonal starch granules (Robutti *et al.*, 1974) held together by matrix protein. The vitreous starch contains numerous protein bodies composed of the alcohol-soluble zein (prolamine) fraction of the endosperm protein (Duvick, 1961). In the floury endosperm portion of dent kernels, the starch granules are spherical and are covered with matrix protein that does not contain protein bodies (Duvick, 1961; Hoseney, 1986).

As kernels dry, the vitreous endosperm protein matrix loses water and shrinks. The starch granules become tightly packed, expelling air and resulting in the vitreous appearance typical of the hard endosperm (Hoseney, 1986).

In the floury portion of dent kernels, the protein matrix of the floury starch shrinks and ruptures without having tightly compacted the starch granules. This leaves numerous air spaces between the starch granules producing the characteristic opacity of floury kernels (Hoseney, 1986). The expression of the floury endosperm texture resulting from a change in the balance and composition of zein bodies is controlled by several genetic factors (Tsai, 1983; Coe *et al.*, 1988). The following factors can determine the floury texture of the kernels endosperm: cfl_2, fl_1, fl_2, fl_3, h, Mc, o_1, o_2, o_4 o_5, o_7, o_9, o_{10}, o_{11}, o_{12} o_{13}, *pro*, sen_1 through sen_6, sh_4, and Sup_1 (Coe *et al.*, 1988).

Some of the genetic factors (fl_2, fl_3, o_2, o_6 and o_7) responsible for the floury endosperm texture of corn kernels affect their lysine content (Wall, 1978). Other factors (fl_1, o_1 and h) cause floury kernel texture without affecting the amino acid composition (Nelson *et al.*, 1965). The fl_2 factor does not modify starch synthesis (Mertz *et al.*, 1964; Creech, 1968), but affects starch deposition, resulting in smaller starch granules (Brown *et al.*, 1971). The fl_2 and o_2 factors result in zein protein bodies that are distorted, smaller and less uniform than normal ones (Christianson *et al.*, 1974). The cfl_2 factor is complementary to fl_2 (Coe *et al.*, 1988). Homozygous o_6o_6 plants die at the seedling stage. Homozygous fl_3fl_3 plants produce very light kernels, which may not germinate in some genetic backgrounds (Ma and Nelson, 1975).

The *fl* series is dosage dependant. The *h* and *pro* factors and the *o* series are recessive. The *Mc* allele is dominant. The o_4 factor is allelic to fl_1 but truly recessive. The *sen* series is a group of duplicate factors with a 15:1 interaction (Coe *et al.*, 1988). Neuffer *et al.* (1968), described fl_2 as being phenotypically dominant rather than dosage dependent, so that one dose of fl_2 will result in a floury endosperm.

The *h* and the dosage dependent fl_1 and fl_2 factors are difficult to classify in segregating material (Weijer, 1952; Coe *et al.*, 1988). The weak relationship of *fl* and *h* dosages with endosperm texture phenotype may be due to effects of soil fertility on the relative content of floury and vitreous starch (Hamilton *et al.*, 1951). There is considerable variation in endosperm texture among and within hybrids due to micro-environmental variation on the ear and variation within and between fields due to moisture, temperature, and soil nitrogen supply and uptake fluctuations (Watson, 1987)

Cob and kernel colour

Anthocyanins and related flavonoid pigments may colour plant tissues. Among other functions, the plant pigments provide a light screen against ultraviolet radiation, and act as feeding deterrents against insects (Jayaram and Peterson, 1990).

In corn, two classes of flavonoid pigments are found, the anthocyanins and the phlobaphenes. The anthocyanins can be found in almost any tissue, whereas the phlobaphenes are predominantly located in the cob and pericarp (Jayaram and Peterson, 1990). There are 20 different genes known to affect flavonoid synthesis in corn tissues, producing a diversity of colours and shades in practically all plant parts (Coe *et al.*, 1988).

The *P* locus controls the synthesis of the red pigment observed in the cob and pericarp (Styles and Ceska, 1977). The *P* locus, in association with other gene combinations, will produce colourless, light red to purple, orange or brown cobs (Styles and Ceska, 1977; Coe *et al.*, 1988). The pericarp, endosperm and embryo can exhibit various colours since a large number of genetic factors act and interact on their pigment synthesis and content (Neuffer *et al.*, 1968; Styles and Ceska, 1977; Coe *et al.*, 1988).

The effect of the pollen on the endosperm colour and quality characteristics is called xenia. The pericarp and aleurone must be colourless for the true colour of the endosperm to be seen from outside. The triploid nature of the endosperm results in a dosage effect on the phenotypic expression of pigmentation related genes (Rhoades, 1936). The dosage effect of the Y_1 (yellow) gene on the kernel vitamin A content and yellow endosperm colour of corn was demonstrated by Mangelsdorf and Fraps (1931). In addition to the dosage effect of the Y_1 locus the endosperm colour can shift to white, or to pale yellow or orange-pink because of the effects of other factors (Coe *et al.*, 1988).

Kernel shape

There are six major types of corn kernel: dent, flint, flour, sweet, pop, and pod. The quality, quantity, and pattern of endosperm composition are responsible for the differentiation among kernel types (Johnson, 1991).

Flint corn has a rounded crown and the hardest kernels due to the presence of a large and continuous volume of vitreous endosperm. Flour corn generally also has a rounded or flat crown but contains mostly soft endosperm. Dent corn has a rigid cylinder of vitreous endosperm surrounding soft starch at the centre of the kernels. As these kernels dry, a depression (dent) forms because the cylinder of vitreous endosperm prevents the soft starch from shrinking uniformly (Watson, 1987).

The inheritance of the dent and flint forms is complex and has been difficult to study (1977; Coe *et al.*, 1988). Anderson and Cutler (1942), state that the large number of genes involved in the determination of the indentation presence and depth, make this trait an important criterion in classification of cultivars and races, even though the rating may be subjective. Coe *et al.* (1988) warned that the genetic descriptions for visible kernel characteristics are so specific to the genetic background in which they are studied that over-generalizations are risky.

Johnson and Russell (1982), found that the more deeply dented kernels tended to break more and to have a lower specific gravity than the flint types. Also, the flinty, breakage-resistant, dense-kernel type inbreds tended to produce smaller kernels.

Stalk lodging

In open-pollinated varieties, stalks were often weak, leading to lodging because of the weight of the ear or the force of the wind. Once on the ground, a corn ear may rot or get eaten by rodents. The kernels in contact with the moist soil often lose their dormancy and initiate germination. The bent stalks increase the difficulty of mechanical harvesting (Burtt-Davy, 1914; Baker, 1984).

Stalk strength has been reported to be inherited as an additive quantitative trait (Hayes and McClelland, 1928; Horner *et al.*, 1976).

Shorter basal internodes are associated with reduced stalk lodging (Wilson, 1930). Also, crushing strength and rind thickness of the second internode are related to stalk strength and can be used for selection (Singh, 1970; Esechie, 1985). Various other methods are used to select stronger stalks. According to Twumasi-Afriyie and Hunter, (1981), the rind puncture method is suitable as a selection criterion, because of its simplicity, consistency and high correlation with stalk strength. Anderson and White (1994) also considered rind puncture at anthesis to be the best method for selection of strong stalks. The rind puncture method also offers the advantage of being nondestructive.

Selection for erect plants within synthetics to reduce stalk lodging is often associated with reduction in yield (Thompson, 1972; Thompson, 1982). On the other hand, Colbert *et al.* (1984), successfully reduced stalk lodging without yield reduction by using a stalk crushing strength selection method. The authors hypothesized that to only select for erect plants results in a reallocation of the photosynthates at the expense of yield. Selection for stalk crushing strength probably focuses on a mode of stalk strength enhancement which requires less diversion of the photosynthate destined to the ear.

Selection for higher yield, high rates of fertilizer application, and high plant stands, may result in ears being placed higher on the stalks. Therefore, selection efforts have been made to lower ear height (Horner *et al.*, 1976). During 10 cycles of selection for low ear placement in a synthetic, Josephson and Kinder (1977) did not find a significant correlation between lower ear position and reduced stalk lodging. No correlation was found between either ear height or ear weight and stalk lodging in S_1 families and F_1 variety crosses (Helms and Compton, 1984). On the other hand, Thompson (1972), selected solely for erect plants in two synthetics for six cycles and obtained a significant negative correlation between increases in the number of erect plants and reduction of ear height.

Because some stalk disease organisms spread only on dead cells, there is greater stalk strength in plants having higher pith moisture and stalks that senesce later (Pappelis and Smith, 1963). This has been recognized by corn breeding companies and the "stay-green" ability of stalks is now exploited in commercial hybrids to obtain better stalk strength.

Tillering

The number of tillers produced depends on the genotype, the soil fertility and the planting density. Higher moisture and soil fertility will increase tiller production.

Higher planting density will reduce the number of tillers (Wallace and Bressman, 1937; Downey, 1972).

Tillers produce ears with irregular shapes and they cause problems in combine adjustment at harvesting. Also, the tiller ears mature later than main-stalk ears leading to mixtures of kernels of uneven size and moisture content (Rood, 1985). Dungan (1931) showed that profusive tillering may be detrimental to the main stalk grain yield in dry weather. Jones *et al.* (1935) found tiller presence to be beneficial to sweet corn yield. Rosenquist (1941) found that tiller removal reduces the main stalk dry matter by 10 %, and that ear-bearing tillers were dry matter and grain yield detrimental to the main stalk. Earley *et al.* (1971) found that tiller removal did not result in a grain yield increase and that ear-bearing tillers of single cross hybrids did not translocate significant amount of photosynthates to the main-stalk ear. Alofe and Schrader (1975), demonstrated that during grain filling, the main-stalk ears of corn hybrids acted as sinks for photosynthates from tillers when the tillers bore no ears. Russelle *et al.* (1984), demonstrated that a significant amount of nutrient is translocated from small barren tillers to the main stalk.

Rood and Major (1981) studied early maturing inbreds and found that early maturity and profusive tillering were associated. This is in agreement with the general characteristics of the Northern Flints corn which have a tendency to tiller and mature early (Brown and Anderson 1947; Goodman and Brown 1988).

Teosintes (Zea mays L ssp) can be crossed with corn and produce fertile hybrids (Reeves, 1950). It has been hypothesized that the tendency to tiller of the Northern Flints probably comes from teosintes (Reeves, 1950). In crosses involving corn and teosintes, the mean number of tillers increases with the proportion of teosinte germplasm (Rogers, 1950).

Among other impacts on inflorescence and plant morphology, the *Cgl, Tlr,* Tp_1 and *tb* factors increase tillering and are said to have teosintoid effects, to underline the teosinte like appearance of plants possessing these factors (Coe *et al.*, 1988).

Ear-row number

The ear of corn has kernels that are usually set in 8 to 30 longitudinal rows. In open-pollinated varieties, some ears may have only 4 rows. When row numbers are much above 30, the kernels are crowded and the rows are obscured. Modification and concealment of the row pattern may result from various irregularities. In most varieties, the paired spikelets produce an even row number (Anderson and Brown, 1948). Each spikelet normally contains one fertile and one sterile ovule. In certain varieties, the second ovule may develop and produce crowded and irregular rows of kernels (Poehlman, 1987).

It has long been apparent that the genetic basis for differences in row number is complex. Anderson and Brown (1948) reported that extensive and careful studies had been carried on for several decades, but the results were contradictory and were not published. Emerson and Smith (1950) mentioned that several genes are involved in row number determination and that non-genetic effects play an important role. The authors also observed that the factors present in a specific line may be different from those present in another line having equal row number, as proven by the row number segregation observed in the progeny resulting from crossing the lines.

Although the pistillate spikelets on corn cobs are usually paired, Hepperly (1949) detected the presence of a recessive gene (*pd*) which results in the production of single spikelets. Lindstrom (1931) and Galinat (1971) found *tr* mutants, which produce four row ears instead of eight row ears when homozygous. The four row condition is considered reversion to a primitive teosinte (Galinat, 1971). In both South America and the southwestern United States, archaeological investigation has demonstrated that the earliest corn varieties had 12 or 14 rows, and eight- and ten-rowed varieties appeared later (Carter and Anderson, 1945). Galinat and Gunnerson (1963), suggested that the eight-rowed condition is probably a result of introgression of teosinte genes into the Chapalote corn race. This introgression may have taken place around 500 B.C..

The number of rows of kernels is related to tassel condensation (Anderson, 1944). Anderson and Brown (1948) found that eight-rowed varieties, without exception, had no tassel condensation, and had central tassel spikes with pairs of spikelets in whorls of 2 at each node. They maintained that if properly understood, tassel condensation could often permit an estimate of the row number by glancing at a tassel in the field. Although statistically the correlation is good between the two characters, a breeder would have difficulty making accurate estimates of the row number from the condensation of the tassel, because a specific condensation index number can correspond to a range of possible row number (Wellhausen *et al.*, 1954).

CHAPTER 4

PREFACE

This experiment was carried out to characterize the IAPO landraces by observing various quantitative and qualitative characters and secondly to detect the presence of variation among the landraces. The third goal of this experiment was to classify the landraces to further understand the composition of the IAPO landrace collection. This work constitutes the first published description of the IAPO landrace collection. This manuscript was co-authored by C. Azar, D.E. Mather and R.I. Hamilton.

CORN (*Zea mays* L.) LANDRACES OF THE ST. LAWRENCE-GREAT LAKES REGION OF NORTH AMERICA

Abstract

Thirty-five white corn (*Zea mays* L.) landraces were obtained by the Indian Agricultural Program of Ontario (IAPO) from native farmers in Ontario and New York State between 1986 and 1989. These landraces belong to the racial complex Northern Flints and Flours. The 35 landraces, one experimental population and one control hybrid were evaluated in a three-replicate randomized complete block design at two sites in 1993 and 1994. Data were collected on 24 traits in order to characterize and classify the IAPO landraces. Most quantitative traits examined exhibited considerable variation among the IAPO landraces. Variation was also observed within many of the landraces for ear and cob colour, and for endosperm texture. The number of rows of kernels per ear varied among and within landraces. Based on seven traits from the two sites in 1994, the IAPO population was grouped into 10 clusters by centroid clustering analysis.

Introduction

The native people of the Great Lakes region of North America grew their own corn (*Zea mays* L.) for centuries before the arrival of Europeans (Parker, 1910), and they still do. The corn was grown in isolated garden plots where it was hand harvested and later husk braided and left to dry. Hulled-corn soup and boiled corn bread were particularly appreciated preparations (Harrington, 1908).

The Indian Agricultural Program of Ontario (IAPO) is a non-profit corporation owned by status native farmers of the province of Ontario. Between 1986 and 1989, IAPO obtained a series of 35 white corn landraces (Figure 4.1) from native farmers/horticulturists on six reserves in Ontario and New York State. Corn has been grown along the St. Lawrence river and near Lake Ontario, Lake Erie and Lake St. Clair for more than 1000 years. Corn probably reached Ontario before A.D. 800 (Cutler and Blake, 1976). It became a significant part of the natives subsistence system in northeastern North America from about A.D. 1000 (Wymer, 1994; Bendremer and Dewar, 1994).

The IAPO landraces belong to the racial complex Northern Flints and Flours. The IAPO landraces mainly have flint shape (non-dented) kernels possessing floury endosperm texture. Galinat and Gunnerson (1963) suggested that this racial complex originated from an intercrossing of the Chapalote corn race and the eight-row floury Harinoso de Ocho, with teosinte (*Zea mays* L. ssp.), which is a wild relative of corn. The Northern Flints and Flours were for centuries the most widely grown type of corn in eastern North America, where no other kind of corn has been reported by archaeologists (Brown and Anderson, 1947). This racial complex now consists of early maturing corns adapted to very short and relatively cool growing seasons of this region (Doebley *et al.*, 1986).

The Northern Flints and Flours are characterized by relatively short, highly tillered, frequently two-eared plants with narrow leaves, well developed husk-leaf blades, slender culms, long thick shanks, and ears that are frequently enlarged at the base and that have 8 to 10 rows of crescent-shaped kernels (Brown and Anderson, 1947; Goodman and Brown, 1988).

Today very little flint corn is grown in North America. It is more widely grown in South America and Africa where it is used mainly for human consumption, and in northern Europe, where it is used as livestock feed.

The objectives of this experiment were 1) to characterize the IAPO landraces, primarily by assessing variation of vegetative and reproductive characters; 2) and to classify the IAPO landraces.

Materials and Methods

Thirty-six open-pollinated corn populations and one control hybrid were evaluated in a three-replicate randomized complete block design at Ste-Anne-de-Bellevue, Québec (45°26' N latitude) and at Ottawa, Ontario, (45°31' N latitude) in 1993 and 1994. The entries (Table 4.1) included: 35 open-pollinated landraces collected from First Nations reserves in southern Ontario, Canada and northern New York State, USA; an open-pollinated experimental population (designated I-37) from the King Agro, Ltd. seed company; and a commercial single cross hybrid, Pioneer 3902 (Pioneer Hi-Bred) requiring about 2700 Corn Heat Units to reach maturity (Ontario Ministry of Agriculture, Food and Rural Affairs, 1995).

At Ste-Anne-de-Bellevue, the experiment was grown on a Saint-Amable sandy loam in 1993 and on a Dalhousie clay loam in 1994. At Ottawa, the experiment was grown on a Manotick sandy loam in both years. Fertilizer was broadcast and incorporated before planting, to adjust to 90-90-90 kg ha^{-1} of N-P_2O_5-K_2O, taking into account soil fertility and residues from previous crops. Trials were seeded in mid-May at both sites in both years. Due to extensive bird damage to young seedlings in Ste-Anne-de-Bellevue in 1993, that site was re-seeded in the first week of June, 1993.

Each experimental plot consisted of three 5-m rows. Plots were seeded at a high density and thinned to a final density of 45 000 plants ha^{-1}. Metolachlor and triazine formulations were applied to control weeds. Escaped weeds were controlled by cultivation. Because most of the First Nations landraces were expected to have white floury kernels, the entries that were not (Pioneer 3902, I-37, and the flinty landrace I-15) were detasselled to avoid xenia effects.

Data were gathered from the centre row of each plot, excluding three plants at each end of the row. Eight traits were assessed on a plot basis: days to 50% tasselling of the main culm tassels (50% of plants shedding pollen), days to 50% silking of the apical ears (50% of primary ears having 1 cm of exposed silk), stalk lodging (plants whose main stalks were tilted below the apical ear at 45° or more were considered lodged), grain yield (calculated on a 15.5 % grain moisture basis), grain moisture at harvest, grain test weight, and 100-kernel weight.

In addition, seven traits were assessed on 10 consecutive individual plants in each experimental plot: number of leaves above the apical ear on the main culm, number of ears on the main culm, ear height (from soil level to the apical ear node on the main culm), number of tillers per plant, plant height (from soil level to the tip of the extended tassel of the main culm), main culm diameter (at the centre of the internode above the node of the apical ear), and shank length of the apical ear on the main culm.

After harvest, seven traits were assessed on 10 randomly chosen apical ears from each experimental plot: ear length, ear diameter, kernel row number on the ear, kernel colour, cob colour, a visual estimate of endosperm texture (vitreous or floury), and a visual estimate of the degree of indentation on the kernels, rated on a scale from 1 (no indentation) to 5 (deep indentation).

Two traits were assessed on a sample of 60 kernels per plot using Leco 2001 digital image analysis software (Leco Corporation, St-Joseph, Michigan): kernel size (area) and F-shape. The F-shape is the ratio of the kernel's minimum diameter over its maximum diameter.

Due to late re-seeding of the Ste-Anne-de-Bellevue site in 1993, and due to further damage from birds feeding on the maturing kernels at both sites in that year, the traits grain yield, ear number, grain specific weight, 100-kernel weight, days to 50% tasselling and days to 50% silking will be reported for 1994 only.

Data from seven traits with no significant heterogeneity of variance or entry-by-site interaction over the two sites in 1994 were used to cluster the IAPO landraces.

Discriminant canonical analysis was used to visualize the cluster formation by plotting the canonical variables. The data were then standardized to remove block and site effects. Cluster analysis was done using the centroid method (SAS Institute Inc., 1989).

Results and Discussion

The landraces differed significantly ($P<0.05$) for grain yield, ear number, grain test weight, 100 kernel weight, days to tasselling and days to silking at both sites in 1994 and for kernel moisture at harvest, ear length, ear diameter, kernel size, kernel F-shape, kernel indentation, lodging, plant height, ear height, leaf number, culm diameter and shank length at both sites in 1993 and 1994. The landraces differed significantly ($P<0.05$) for total tiller number per plant at both sites in 1993.

Kernel characters

All landraces had cream-white kernel colour (Table 4.1). The kernels of all landraces had a tendency to develop red pigments when the husks were peeled, exposing the kernels to sunlight during the growing season. Within landraces I-6, I-29, I-36, and the experimental population I-37 there were also ears with some kernels of other colours.

All landraces had floury endosperm texture. On some ears of landraces I-4, I-15, and I-20, all kernels had floury endosperm texture, while on other ears there were both floury and vitreous kernels. On some ears of landrace I-35, all kernels had floury endosperm texture, while on other ears there were both floury and sweet kernels.

The floury endosperm texture resulted in low kernel test weight relative to the dent control (Table 4.2). The mean kernel test weight was 62.3 kg hL^{-1} for the landraces and 78.0 kg hL^{-1} for the control. The experimental population I-37 had a higher kernel test weight than the landraces because of its rounder and denser kernels.

The round shape of the kernels of the experimental population I-37 was reflected in its F-shape value of 0.84, which was the highest of all the entries (Table 4.3). The control hybrid had elongated kernels, and a F-shape of 0.71. The kernels of the landraces tended to be almost as wide as deep, giving F-shape values between 0.78 (I-33) and 0.83 (I-2).

Most of the entries had somewhat higher 100-kernel weight and larger kernel size (area) than the control hybrid (Table 4.2, Table 4.3). The exceptions were I-15, I-37 and I-29. The I-37 experimental population is not IAPO germplasm, and the landrace I-15 is known to have outcrossed with non-IAPO corn. The same may be true for landrace I-29, since some of its ears had some pale yellow kernels probably reflecting a previous outcross with commercial hybrids.

As expected, the control hybrid always had deeply dented kernels. Kernels from the landraces usually had no indentation or only a very shallow indentation on some ears toward the butt (data not shown). Landraces I-27, I-30, I-3, I-6 and I-31 had deeper indentations than others. Deep indentation was observed on the ears of these five landraces mainly in 1994 and particularly at the Ottawa site.

Ear characters

All landraces had white cobs but only 16 landraces had only white cobs (Table 4.1). The others also had some plants with pink, red, or brown cobs.

The range of the numbers of rows of kernels on apical ears differed among landraces (Table 4.1). In all landraces, most ears had eight rows of kernels, whereas the experimental population I-37 usually had a higher row number.

Considerable variation was also observed in ear length among landraces, ranging from 14.8 to 20.7 cm (Table 4.3). The experimental population I-37 had shorter ears than all the landraces, while among the landraces, I-18 had the shortest ears. The control mean ear length was almost equal to that of the landraces.

The landraces all had slender ears, averaging 35 mm in diameter compared to 43.5 mm for the control hybrid, which had the thickest ears of all entries (Table 4.3). The experimental population I-37 had thicker ears than the landraces with a mean of 38 mm. There was little variation among the landraces, ranging from 32.3 to 37.4 mm.

Grain yield

For grain yield, there was significant variation among the landraces, ranging from 1.87 to 5.54 t ha^{-1} (Table 4.2). All landraces produced much less grain than the control hybrid, which yielded 8.57 t ha^{-1}. The landraces were not identical in their responses to environmental differences among sites. Some landraces were stable across sites (I-28, I-27, I-7, I-23, I-30, I-4, I-14, I-11), while others varied considerably (I-22, I-24, I-19, I-3, I-33, I-40) (see Appendix B).

There was a general trend for high yielding landraces to be more prolific ($r=0.57$; $P<0.004$). The average number of main-culm ears per plant ranged from 0.9 to 1.5 (Table 4.2). The control hybrid had an average of 1.1 ears per plant. Landrace I-22 was the most prolific, with 1.5 main-culm ears per plant.

Other characters

The control hybrid rarely tillered, while the landraces had an average of 2.27 tillers per plant (Table 4.4). Of these, 27.3 % formed tassels. A few tillers initiated an ear, but always too late in the season to produce grain.

The control and the experimental population (I-37) showed little lodging, 1.4 and 6.8 %, respectively. There was extensive stalk lodging in most of the landraces with a mean of 30.6 % (Table 4.3). The best standing landraces were I-13 and I-32; the worst were I-8 and I-26. Among the best yielding landraces, I-20 and I-40 lodged the least.

The landraces silked later and had higher kernel moisture at harvest than the control hybrid, which needs 2700 corn heat units to reach maturity (Table 4.2). This is consistent with the fact that all landraces were collected from locations that normally accumulate 2700 to 3300 corn heat units. There was a seven-day period between the silking of the earliest and the latest landraces and considerable variation in grain moisture among landraces, ranging from 27.9 to 41.3 %. Silking and grain moisture were significantly correlated ($r=0.63$; $P<0.0001$).

There was less variation among the landraces for tasselling time than for silking time. A differentiation among landraces must have taken place during the flowering interval, making silking time more closely correlated to grain moisture than tasselling time.

Plant height, ear height and shank length varied considerably among landraces, whereas leaf number above the apical ear and culm diameter varied little (Table 4.4). Landrace I-40 had significantly taller plants and higher ears than the other landraces.

Cluster analysis

Based on plots of canonical variables and the hierarchical dendrogram, the IAPO landraces were grouped into 10 clusters (Fig. 4.2, Table 4.5). The mean characteristics of each cluster are presented in Table 4.5. Clusters 1 to 9 are each composed of one or two landraces. Cluster 10 contains 26 of the 36 landraces. Cluster 1 contains only the experimental population I-37; it is the most distant from the other clusters. Cluster 2 classified the landrace I-8 as the second furthest entry from the bulk of landraces. It had the lowest grain yield and test weight. Clusters 3 (I-18) and 4 (I-12) are quite similar and could be grouped together. Cluster 6 (I-22) had the highest grain yield.

The centroid method successfully separated the experimental population I-37 and landraces I-8, which were both known to be distinctive from the bulk of the IAPO population. In an adjacent experiment (see Chapter 5) there was high mid-parent heterosis in crosses involving I-8 and three members of cluster 10 (I-3, I-13 and I-40). Further crosses could be made to test the heterotic pattern among members of different clusters and within clusters to improve the knowledge of the divergence and similarity among landraces.

Conclusions

Considerable variation was found among the IAPO landraces for grain yield, grain moisture at harvest, ear number, ear length, ear diameter, ear height, kernel size, kernel F-shape, kernel indentation, grain test weight, 100-kernel weight, days to tasselling, days to silking, plant height, shank length, leaf number, culm diameter, total tiller number and stalk lodging.

The landraces had only white kernel colour except for I-6, I-29, I-36 and the experimental population I-37 where kernel colour variation was observed. Only 16 landraces had only white cobs. The others also had some plants with pink, red, or brown cobs. All landraces had floury endosperm texture. On some ears of landraces I-4, I-15, and I-20, all kernels had floury endosperm texture, while on other ears there were both floury and vitreous kernels. On some ears of landrace I-35, all kernels had floury endosperm texture, while on other ears there were both floury and sweet kernels. The number of rows of kernels varied among and within landraces.

Centroid clustering analysis based on grain yield, test weight, 100-kernel weight, shank length, culm diameter, ear number and days to silking grouped the IAPO population into 10 clusters.

Table 4.1. Origin of collection, original collection size, kernel colour, cob colour, ear row number, and endosperm texture of 36 entries.

Entry	Collection origin	Collection size (ear)	Kernel colour	Cob colour	Row number	Endosperm texture
I-1	Akwesasne	many	white	white	8-12	floury
I-2	Oneida	one	white	white	6-12	floury
I-3	Six Nations	one	white	white	4-10	floury
I-4	Tyendinaga	one	white	white	4-10	floury,[a] fl.+ vitreous
I-5	Six Nations	one	white	white, pink, red	4-12	floury
I-6	Six Nations	one	white, light brown	white, pink, red	6-10	floury
I-7	Six Nations	one	white	white, pink, red, brown	8-12	floury
I-8	Oneida	one	white	white	4-8	floury
I-10	Akwesasne	one	white	white, pink, red	4-10	floury
I-11	Tyendinaga	one	white	white, pink, red	4-8	floury
I-12	Akwesasne	one	white	white	6-12	floury
I-13	Six Nations	one	white	white, pink	4-8	floury
I-14	Unknown	one	white	white	6-12	floury

Table 4.1 (cont.)

Entry	Collection origin	Collection size (ear)	Kernel colour	Cob colour	Row number	Endosperm texture
I-15	Tyendinaga	many	white	white	4-12	floury, fl. + vitreous
I-17	Unknown	one	white	white, pink	4-10	floury
I-18	From I-10	one	white	white	6-12	floury
I-19	Six Nations	one	white	white	4-12	floury
I-20	Akwesasne-NY[b]	one	white	white	4-12	floury, fl. + vitreous
I-21	Unknown	one	white	white, pink, red	6-12	floury
I-22	Tyendinaga	one	white	white, pink, red	4-8	floury
I-23	Moravian	one	white	white, pink, brown	4-12	floury
I-24	Unknown	one	white	white, pink	4-12	floury
I-25	Unknown	many	white	white, pink, red	6-10	floury
I-26	Oneida	one	white	white	6-12	floury
I-27	Akwesasne	many	white	white	4-8	floury
I-28	Akwesasne-NY	one	white	white, red	4-10	floury

Table 4.1 (Cont.)

Entry	Collection origin	Collection size (ear)	Kernel colour	Cob colour	Row number	Endosperm texture
I-29	Tyendinaga	one	white, white + light yellow	white, pink, red	8-12	floury
I-30	Six Nations	one	white	white, pink, red, brown	8-12	floury
I-31	Six Nations	one	white	white	4-12	floury
I-32	Akwesasne	one	white	white	6-12	floury
I-33	Unknown	one	white	white	4-10	floury
I-35	Six Nations	one	white	white, pink	4-12	floury, fl.+ vitreous, fl.+ sweet
I-36	Sandborne-NY	many	white, white + purple or brown	white, pink, red	4-10	floury
I-37	From KA 8-22[c]	one	multi-coloured	white, pink, red	8-14	floury
I-40	Six Nations	many	white	white	4-10	floury
I-42	Six Nations	many	white	white, pink	4-12	floury

[a] (,): among ears; (+): among kernels on the same ear.

[b] NY: New York State (USA).

[c] KA: King Agro seed company.

Table 4.2. Means and standard errors of six traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1994.

Entry	Grain yield ($t\ ha^{-1}$)	Test weight ($kg\ hL^{-1}$)	100-kernel weight (g)	Days to tasselling	Days to silking	Ear number
1-1	4.04 ±0.31	68.5 ±0.6	43.1 ±1.0	67.3 ±0.9	72.2 ±0.8	0.9 ±0.04
1-2	4.04 ±0.14	70.2 ±0.3	37.2 ±0.8	64.3 ±0.6	67.7 ±0.8	1.2 ±0.05
1-3	4.05 ±0.51	67.1 ±0.5	40.8 ±0.8	64.7 ±0.8	68.2 ±0.9	1.2 ±0.07
1-4	4.37 ±0.29	67.9 ±0.3	36.5 ±0.5	65.5 ±0.8	70.7 ±1.0	1.3 ±0.05
1-5	4.19 ±0.43	67.7 ±0.6	44.6 ±0.9	64.7 ±0.7	67.5 ±0.8	1.0 ±0.05
1-6	3.48 ±0.28	68.8 ±0.4	36.9 ±1.0	67.3 ±1.1	72.0 ±0.9	1.2 ±0.05
1-7	4.81 ±0.23	68.3 ±0.4	44.4 ±1.0	65.8 ±0.8	69.8 ±0.7	1.1 ±0.05
1-8	1.87 ±0.23	66.3 ±0.5	41.7 ±1.2	67.0 ±1.0	71.8 ±1.2	0.9 ±0.10
1-10	3.14 ±0.31	68.4 ±0.5	40.0 ±0.8	65.8 ±0.7	72.2 ±0.6	0.9 ±0.05
1-11	4.04 ±0.32	69.4 ±0.6	40.7 ±1.3	68.7 ±1.2	71.8 ±0.9	1.0 ±0.02
1-12	2.76 ±0.23	68.2 ±0.5	40.8 ±1.2	62.2 ±1.1	69.0 ±1.0	1.0 ±0.06
1-13	4.32 ±0.41	69.7 ±0.5	45.7 ±0.7	65.2 ±0.8	69.7 ±0.7	1.0 ±0.04
1-14	4.09 ±0.38	71.5 ±0.4	42.7 ±0.6	64.7 ±0.8	68.7 ±0.7	1.1 ±0.06
1-15	4.56 ±0.42	70.3 ±0.4	35.6 ±0.5	- -	70.2 ±0.3	1.2 ±0.07
1-17	5.42 ±0.34	67.8 ±0.5	42.0 ±0.6	66.8 ±0.8	70.7 ±0.8	1.2 ±0.07
1-18	2.99 ±0.33	67.1 ±0.5	36.9 ±1.0	63.0 ±0.8	66.8 ±1.1	0.9 ±0.07
1-19	4.09 ±0.53	68.2 ±0.6	39.9 ±0.7	63.7 ±1.2	68.0 ±1.0	1.3 ±0.07
1-20	5.54 ±0.17	67.5 ±0.6	43.5 ±1.2	66.3 ±0.8	71.5 ±0.6	1.2 ±0.05

Table 4.2 (Cont.)

Entry	Grain yield (t ha⁻¹)	Test weight (kg hL⁻¹)	100-kernel weight (g)	Days to tasselling	Days to silking	Ear number
I-21	4.77 ±0.32	69.9 ±0.4	37.8 ±1.0	64.5 ±0.9	67.7 ±0.7	1.3 ±0.07
I-22	5.21 ±0.41	67.1 ±0.2	39.1 ±0.7	64.5 ±0.5	66.8 ±0.4	1.5 ±0.07
I-23	4.48 ±0.37	67.7 ±0.7	43.5 ±0.7	64.5 ±0.7	69.5 ±0.8	1.1 ±0.05
I-24	4.82 ±0.48	66.6 ±0.8	39.4 ±1.0	61.7 ±0.6	65.5 ±0.7	1.0 ±0.06
I-25	5.13 ±0.24	68.7 ±0.7	42.1 ±1.1	65.7 ±1.5	68.0 ±1.1	1.2 ±0.09
I-26	4.56 ±0.36	67.6 ±0.6	41.2 ±0.7	63.7 ±0.5	67.0 ±0.5	1.2 ±0.07
I-27	5.03 ±0.20	68.1 ±0.7	46.4 ±1.1	64.2 ±0.4	69.2 ±0.5	1.0 ±0.04
I-28	5.12 ±0.24	67.8 ±0.3	41.0 ±1.0.	62.7 ±0.5	65.2 ±0.6	1.2 ±0.06
I-29	4.52 ±0.44	70.3 ±0.5	34.4 ±0.6	65.5 ±1.0	69.7 ±0.8	1.2 ±0.08
I-30	4.46 ±0.20	64.6 ±0.5	43.7 ±0.9	64.6 ±0.8	68.1 ±1.0	1.1 ±0.03
I-31	3.19 ±0.27	67.0 ±0.4	41.8 ±0.8	65.7 ±0.8	69.5 ±0.5	0.9 ±0.04
I-32	4.33 ±0.21	69.3 ±0.8	44.9 ±1.0	65.7 ±1.6	68.5 ±1.0	1.1 ±0.04
I-33	3.87 ±0.41	67.4 ±0.6	43.8 ±2.0	66.2 ±0.8	71.8 ±0.9	1.1 ±0.07
I-35	4.71 ±0.20	69.4 ±0.8	42.2 ±0.7	65.0 ±1.0	69.8 ±1.0	1.1 ±0.06
I-36	4.70 ±0.36	67.1 ±0.3	45.0 ±0.9	63.7 ±1.3	67.8 ±0.7	1.1 ±0.05
I-37	4.16 ±0.67	75.5 ±0.5	33.8 ±0.6	- -	73.2 ±0.3	1.1 ±0.04
I-40	5.20 ±0.48	67.4 ±0.5	44.0 ±0.8	67.2 ±0.7	71.7 ±0.4	1.1 ±0.05
I-42	4.63 ±0.22	69.1 ±0.4	42.9 ±0.9	65.5 ±1.1	71.7 ±0.4	1.0 ±0.06
P3902	8.57 ±0.31	78.0 ±0.2	37.0 ±0.3	- -	63.3 ±0.5	1.2 ±0.03

Table 4.3. Means and standard errors of six traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994.

Entry	Ear Length (cm)	Ear Diameter (mm)	Kernel area (mm^2)	F-Shape D.min/D.max	Kernel moisture (%)	Lodging (%)
I-1	18.5 ±0.4	35.8 ±0.3	76.3 ±0.6	0.80 ±0.003	32.1 ±1.1	23.7±2.5
I-2	17.5 ±0.3	33.1 ±0.3	71.3 ±0.5	0.83 ±0.003	27.9 ±1.5	33.5±7.0
I-3	16.5 ±0.3	33.1 ±0.3	71.5 ±0.6	0.81 ±0.003	31.5 ±0.7	36.6±6.8
I-4	17.3 ±0.3	33.2 ±0.3	73.8 ±0.5	0.82 ±0.003	33.3 ±1.9	34.4±5.8
I-5	17.6 ±0.3	36.1 ±0.3	81.2 ±0.6	0.81 ±0.003	31.2 ±1.8	39.5±6.7
I-6	17.6 ±0.3	34.5 ±0.2	68.8 ±0.5	0.81 ±0.003	41.3 ±2.1	44.8±5.2
I-7	16.9 ±0.3	37.4 ±0.3	78.2 ±0.6	0.79 ±0.003	35.4 ±1.6	22.4±3.3
I-8	17.2 ±0.4	33.3 ±0.3	70.6 ±0.5	0.79 ±0.003	31.4 ±1.8	56.9±5.3
I-10	16.3 ±0.3	36.0 ±0.3	76.6 ±0.6	0.82 ±0.003	37.0 ±1.9	23.3±4.4
I-11	16.2 ±0.3	33.0 ±0.3	75.1 ±0.6	0.82 ±0.003	36.9 ±1.7	33.0±3.6
I-12	15.9 ±0.3	36.1 ±0.3	73.6 ±0.5	0.81 ±0.003	34.0 ±2.3	27.2±6.1
I-13	18.2 ±0.3	35.2 ±0.2	81.1 ±0.5	0.82 ±0.003	35.8 ±1.7	18.1±4.7
I-14	16.2 ±0.3	36.3 ±0.2	78.2 ±0.6	0.80 ±0.003	29.9 ±1.1	25.9±5.3
I-15	16.5 ±0.3	34.0 ±0.3	67.4 ±0.5	0.82 ±0.003	35.0 ±1.9	24.2±4.1
I-17	19.2 ±0.3	34.1 ±0.3	77.2 ±0.5	0.79 ±0.003	34.7 ±1.5	27.8±5.9
I-18	14.8 ±0.3	34.3 ±0.3	69.8 ±0.5	0.82 ±0.003	33.3 ±1.5	33.6±6.0
I-19	18.9 ±0.3	35.0 ±0.3	70.5 ±0.6	0.79 ±0.003	30.3 ±1.8	36.6±6.4
I-20	20.7 ±0.3	33.4 ±0.3	78.0 ±0.6	0.82 ±0.003	35.9 ±2.1	30.1±5.5

Table 4.3.(Cont.)

Entry	Ear Length (cm)	Ear Diameter (mm)	Kernel area (mm^2)	F-Shape D.min/D.max	Kernel moisture (%)	Lodging (%)
I-21	17.8 ±0.3	34.9 ±0.3	71.7 ±0.5	0.81 ±0.003	29.3 ±1.5	33.6±4.2
I-22	16.7 ±0.3	34.3 ±0.3	80.1 ±0.7	0.82 ±0.003	31.6 ±1.8	30.0±4.7
I-23	18.9 ±0.4	35.9 ±0.3	78.0 ±0.6	0.81 ±0.003	31.9 ±1.3	33.4±4.5
I-24	17.0 ±0.3	35.5 ±0.3	78.1 ±0.6	0.83 ±0.003	31.5 ±2.0	22.9±5.7
I-25	17 9 ±0.3	35.8 ±0.2	78.6 ±0.6	0.81 ±0.003	33.3 ±1.8	40.2±5.6
I-26	17.8 ±0.3	34.6 ±0.3	73.6 ±0.6	0.82 ±0.003	31.1 ±1.5	54.3±4.9
I-27	18.8 ±0.2	35.8 ±0.3	80.7 ±0.6	0.81 ±0.003	34.6 ±1.7	27.9±7.0
I-28	16.5 ±0.3	34.2 ±0.3	76.0 ±0.6	0.82 ±0.003	28.9 ±1.5	22.7±5.9
I-29	19.0 ±0.2	32.3 ±0.2	63.1 ±0.4	0.82 ±0.003	28.8 ±1.4	29.9±4.4
I-30	18.9 ±0.3	36.6 ±0.3	81.3 ±0.7	0.81 ±0.003	36.7 ±1.9	27.3±4.8
I-31	18.7 ±0.3	35.4 ±0.2	75.8 ±0.6	0.81 ±0.003	36.9 ±2.4	33.8±6.0
I-32	16.9 ±0.4	37.1 ±0.3	80.0 ±0.6	0.81 ±0.003	32.1 ±1.6	19.9±5.6
I-33	18.1 ±0.3	36.6 ±0.3	80.7 ±0.7	0.78 ±0.003	35.7 ±2.8	37.3±5.2
I-35	16.3 ±0.3	35.5 ±0.3	77.5 ±0.6	0.83 ±0.003	35.7 ±1.8	43.7±8.2
I-36	20.0 ±0.3	35.7 ±0.3	82.9 ±0.7	0.79 ±0.003	32.4 ±2.3	29.6±3.5
I-37	14.7 ±0.2	38.0 ±0.4	55.2 ±0.4	0.84 ±0.003	36.1 ±1.7	6.8 ±1.9
I-40	19.2 ±0.4	35.1 ±0.3	79.0 ±0.6	0.81 ±0.003	37.7 ±1.8	23.2±4.1
I-42	19.3 ±0.4	35.1 ±0.3	80.1 ±0.7	0.81 ±0.003	37.5 ±2.2	23.0±5.4
P3902	17.0 ±0.1	43.5 ±0.1	67.3 ±0.2	0.71 ±0.002	27.0 ±0.7	1.4 ±1.1

Table 4.4. Means and standard errors of six traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994.

Entry	Plant Height (cm)	Ear Height (cm)	Leaf number	Tiller number	Culm diameter (mm)	Shank length (cm)
I-1	260.3 ±2.4	89.0 ±1.7	6.1 ±0.1	2.4 ±0.1	18.0 ±0.2	14.1±0.6
I-2	237.0 ±1.9	66.5 ±1.8	5.3 ±0.1	2.8 ±0.1	17.8 ±0.2	14.7±0.6
I-3	228.8 ±2.4	79.3 ±1.4	5.2 ±0.1	2.4 ±0.1	17.7 ±0.3	10.0±0.5
I-4	225.3 ±2.3	69.5 ±1.8	4.7 ±0.1	2.2 ±0.1	17.2 ±0.2	13.7±0.6
I-5	248.8 ±2.0	81.0 ±2.2	5.7 ±0.1	2.1 ±0.1	17.5 ±0.2	11.7±0.5
I-6	261.3 ±2.5	85.3 ±1.9	5.4 ±0.1	2.2 ±0.1	19.1 ±0.2	11.9±0.5
I-7	255.8 ±2.5	89.0 ±2.0	5.0 ±0.1	2.3 ±0.1	17.8 ±0.2	13.2±0.6
I-8	237.3 ±2.7	91.8 ±2.0	5.1 ±0.1	2.1 ±0.1	18.4 ±0.3	17.4±0.9
I-10	255.3 ±3.5	85.8 ±1.9	5.1 ±0.1	2.3 ±0.1	18.7 ±0.3	15.9±0.7
I-11	267.0 ±2.1	90.0 ±1.7	5.7 ±0.1	2.1 ±0.1	16.9 ±0.2	13.5±0.6
I-12	215.8 ±2.2	69.5 ±1.5	5.6 ±0.1	1.6 ±0.1	20.8 ±0.3	8.0 ±0.4
I-13	249.3 ±2.5	81.3 ±2.1	5.4 ±0.1	2.2 ±0.1	18.9 ±0.3	13.7±0.7
I-14	242.0 ±2.6	83.5 ±1.9	4.8 ±0.1	2.2 ±0.1	17.1 ±0.2	11.2±0.5
I-15	- -	76.5 ±2.0	- -	2.0 ±0.1	17.3 ±0.2	17.3±0.9
I-17	258.3 ±3.0	92.3 ±2.4	5.6 ±0.1	1.9 ±0.1	18.4 ±0.3	10.6±0.5
I-18	225.8 ±2.5	70.5 ±1.8	5.7 ±0.1	2.2 ±0.1	16.3 ±0.2	8.9 ±0.4
I-19	230.0 ±2.4	73.8 ±1.7	5.4 ±0.1	2.3 ±0.1	18.6 ±0.2	15.1±0.8
I-20	271.5 ±2.3	98.8 ±1.8	5.4 ±0.1	2.6 ±0.1	17.7 ±0.2	11.5±0.6

Table 4.4. (Cont.)

Entry	Plant Height (cm)	Ear Height (cm)	Leaf number	Tiller number	Culm diameter (mm)	Shank length (cm)
I-21	258.3 ±2.8	82.8 ±2.0	5.5 ±0.1	2.6 ±0.1	17.8 ±0.2	12.1±0.5
I-22	225.0 ±2.5	74.5 ±1.9	5.2 ±0.1	2.1 ±0.1	16.7 ±0.2	9.5 ±0.4
I-23	251.8 ±2.7	81.5 ±1.7	5.7 ±0.1	2.4 ±0.1	19.4 ±0.3	12.6±0.9
I-24	238.5 ±2.2	73.0 ±1.7	5.6 ±0.1	2.2 ±0.1	17.0 ±0.2	11.8±0.6
I-25	252.5 ±2.8	82.3 ±2.0	5.4 ±0.1	2.3 ±0.1	18.5 ±0.3	14.5±0.7
I-26	241.8 ±2.1	85.8 ±2.0	5.3 ±0.1	2.7 ±0.1	17.0 ±0.3	14.2±0.6
I-27	264.0 2.6	87.0 ±2.2	5.5 ±0.1	2.5 ±0.1	18.8 ±0.3	13.7±0.6
I-28	236.5 ±2.1	76.3 ±2.0	5.7 ±0.1	2.5 ±0.1	17.4 ±0.2	16.1±0.7
I-29	258.5 ±2.8	92.0 ±2.0	5.5 ±0.1	2.5 ±0.1	17.3 ±0.2	18.5±0.9
I-30	240.5 ±2.4	81.5 ±2.1	4.6 ±0.1	2.3 ±0.1	17.5 ±0.2	12.2±0.6
I-31	243.0 ±2.9	81.0 ±2.0	6.0 ±0.1	2.5 ±0.1	19.0 ±0.3	9.9 ±0.5
I-32	215.5 ±3.3	74.0 ±1.9	5.2 ±0.1	1.9 ±0.1	18.7 ±0.3	10.3±0.6
I-33	243.3 ±2.6	79.8 ±1.7	5.7 ±0.1	2.0 ±0.1	19.0 ±0.3	15.6±0.8
I-35	247.3 ±2.5	83.3 ±1.9	5.4 ±0.1	2.3 ±0.1	18.8 ±0.3	11.8±0.6
I-36	265.5 ±2.4	87.3 ±2.1	5.7 ±0.1	2.1 ±0.1	17.6 ±0.2	17.1±1.0
I-37	- -	78.0 ±1.2	- -	2.2 ±0.1	18.4 ±0.2	13.7±0.5
I-40	274.8 ±2.5	103.3 ±2.4	5.7 ±0.1	2.3 ±0.1	18.6 ±0.3	11.8±0.6
I-42	273.8 ±2.6	95.8 ±2.1	5.8 ±0.1	2.6 ±0.1	19.4 ±0.3	13.4±0.7
P3902	- -	105.0 ±0	- -	0.3 ±0.03	18.0 ±0.1	19.8±0.4

Table 4.5. Clusters grouping the 35 white floury landraces and the experimental population 1-37 based on seven traits observed in Ste-Anne-de-Bellevue and Ottawa in 1994.

Cluster Number	Entries	Grain yield (t ha^{-1})	Test weight (kg hL^{-1})	100-kernel weight (g)	Shank length (cm)	Culm diameter (mm)	Ear number	Days to silking
1	1-37	4.1570	75.5	33.8	15.0	18.0	1.1	73.2
2	1-8	1.8648	66.3	41.7	18.8	18.3	0.9	71.8
3	1-18	2.9952	67.1	36.9	9.1	17.1	0.9	66.8
4	1-12	2.7618	68.2	40.8	9.1	22.3	1.0	69.0
5	1-31	3.1848	66.7	41.8	10.3	19.7	0.9	69.5
6	1-22	5.2142	67.1	39.1	10.3	17.3	1.4	66.8
7	1-15, 1-29	4.5403	70.3	35.0	19.4	17.2	1.2	69.9
8	1-6	3.4802	68.8	36.9	13.2	19.1	1.2	72.0
9	1-14	4.0858	71.5	42.7	11.2	17.0	1.1	68.7
10	1-1, 1-10, 1-11, 1-13, 1-36, 1-30 1-17, 1-19, 1-2, 1-20, 1-4, 1-32, 1-5 1-21, 1-23, 1-24, 1-25, 1-40, 1-33 1-26, 1-27, 1-28, 1-3, 1-42, 1-35, 1-7	4.5320	68.1	42.2	14.4	18.3	1.1	69.3

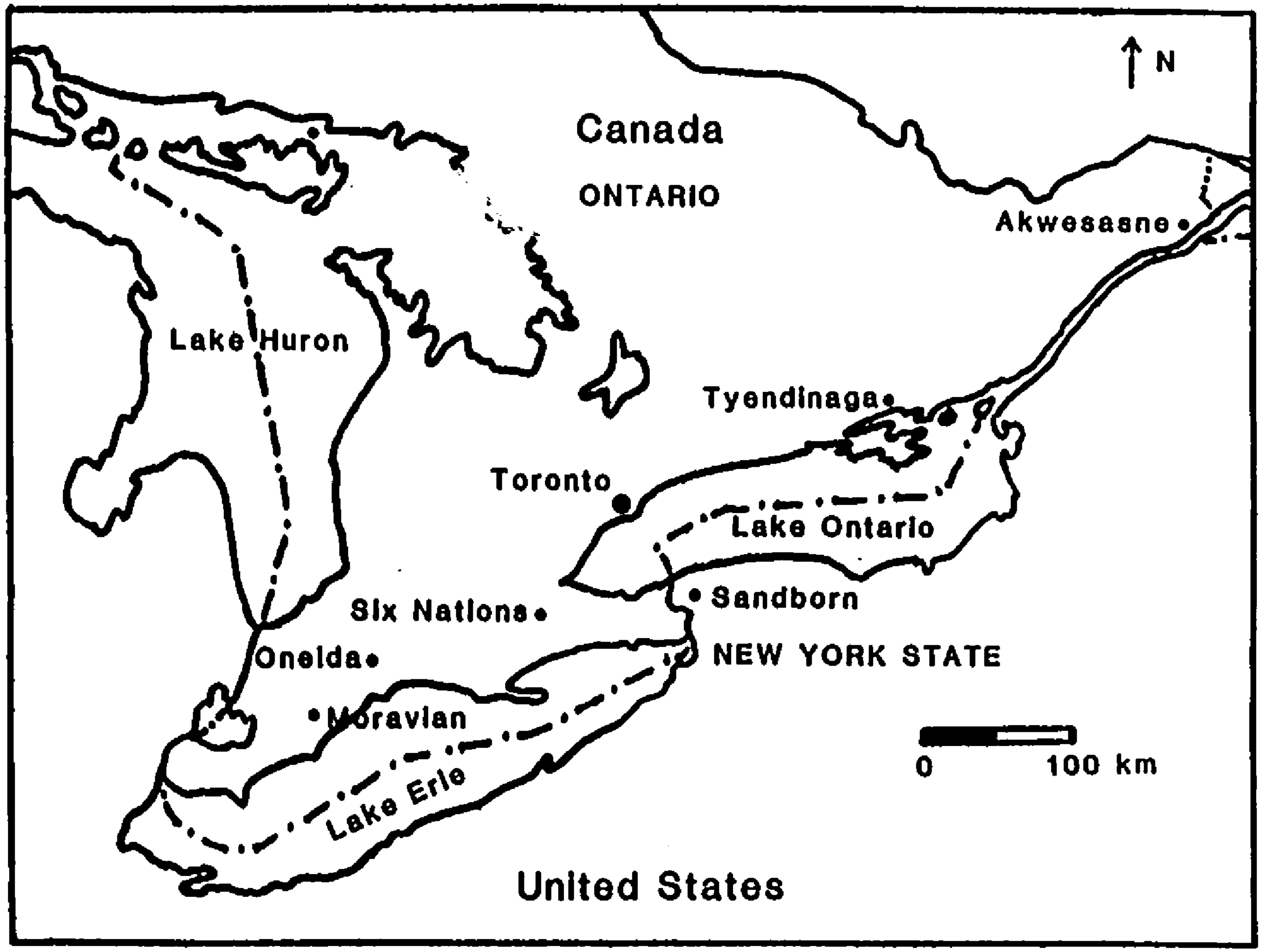

Figure 4.1. Location of Akwesasne, Moravian, Oneida, Six Nations, and Tyendinaga reserves in southern Ontario, and of the Sandborn reserve in New York State, where corn landraces were collected between 1986 and 1989.

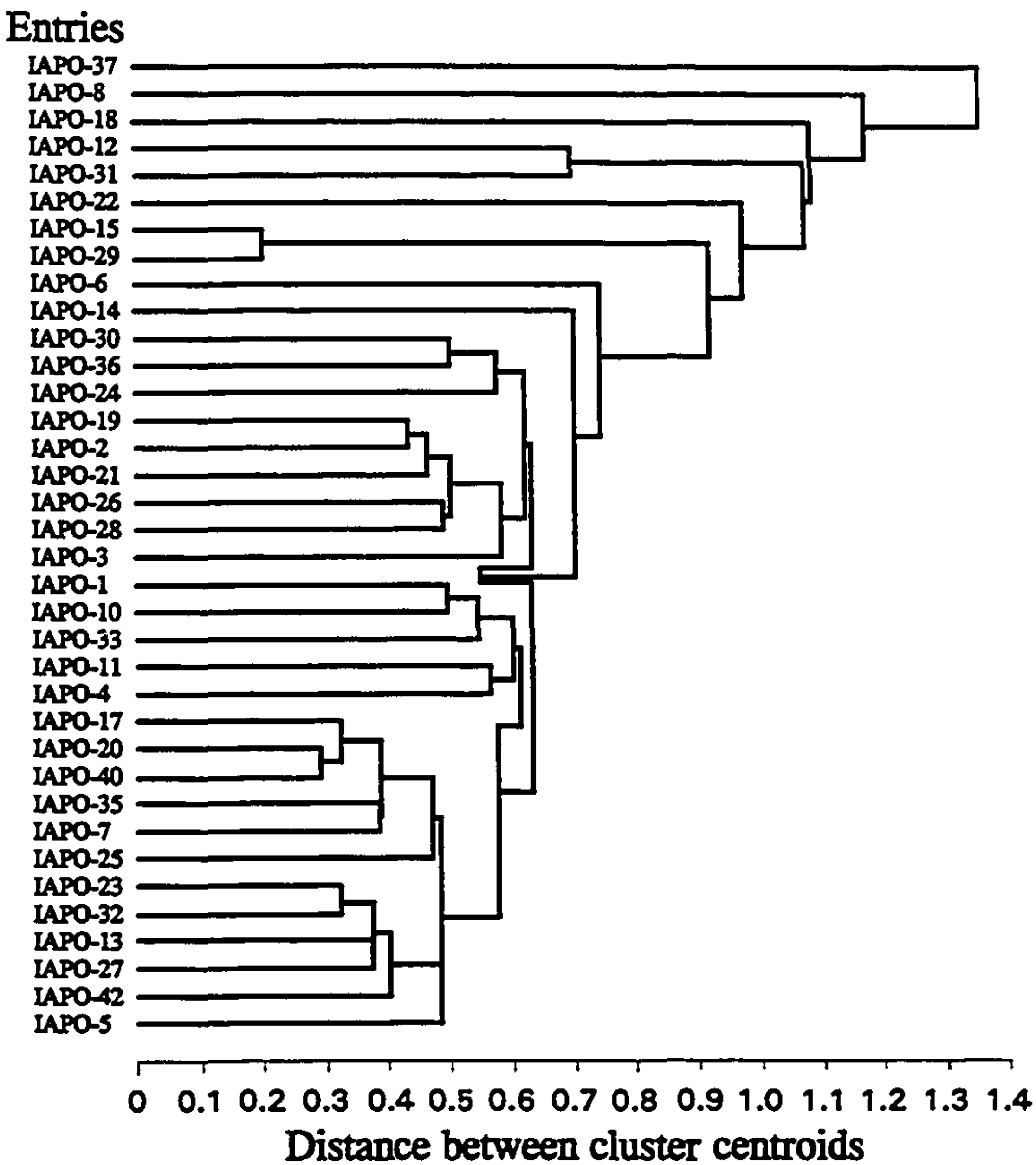

Fig. 4.2 Dendrogram of the centroid clustering of 35 white floury landraces and one experimental population (IAPO-37) based on seven traits observed in Ste-Anne-de-Bellevue and Ottawa in 1994.

CHAPTER 5

PREFACE

This chapter describes experiments that were carried out to investigate the heterotic patterns of IAPO x IAPO and IAPO x inbred crosses. These crosses were made as part of genetic improvement efforts undertaken with the IAPO landraces at the Central Research Farm in Ottawa. A test cross experiment was also studied, where tester inbreds were used to identify the gene imparting the floury endosperm texture of the IAPO landraces. The floury endosperm texture of the landraces is one of their distinctive characteristics and is a factor to consider in their genetic improvement and the industrial processing of their grain. This manuscript was co-authored by C. Azar, D.E. Mather and R.I. Hamilton.

HETEROSIS AND ENDOSPERM TEXTURE IN CROSSES INVOLVING FLOURY CORN (*Zea mays* L.) LANDRACES OF THE ST.LAWRENCE-GREAT LAKES REGION OF NORTH AMERICA

Abstract

The native peoples of the St. Lawrence-Great Lakes region of North America grow and protect their own landrace varieties of corn (*Zea mays*, L.) and use the grain as food. Between 1986 and 1989, 35 white corn landraces were obtained by the Indian Agricultural Program of Ontario (IAPO) from native farmers in Ontario and New York State. The IAPO landraces have poor standability, and yield poorly, when compared to currently used hybrids. The objectives of this research were: to evaluate several IAPO x IAPO crosses, to evaluate several crosses between IAPO landraces and white flint inbreds, and to determine whether the IAPO material carries the fl_1 allele. The crosses were evaluated in three-replicate randomized complete block designs at two sites, in 1993 and 1994. Significant heterosis over the mid-parent value was observed in crosses involving a low yielding landrace from one reserve of origin with higher yielding landraces from another reserve. However, these variety crosses did not yield significantly more than the best yielding landrace. Crosses between landraces and white flint inbreds yielded more than either parent. At one evaluation site, they yielded significantly more than the best yielding landrace. Crossing of the landraces with the inbreds improved some agronomic characteristics, but disrupted some of the ear characteristics of the landraces. The factor responsible for the floury endosperm texture of the IAPO landraces was identified as being the dosage dependent fl_1.

Introduction

First Nations (native) peoples of the St. Lawrence-Great Lakes region of North America still grow their own landrace varieties of corn (*Zea mays*, L.) in garden plots, and use the grain as food. Some of these landraces have white floury kernels, with little or no vitreous endosperm. They probably belong to the racial complex Northern Flints and Flours, which is characterized by ears that are frequently enlarged at the base, with 8 to 10 rows of crescent-shaped kernels (Brown and Anderson, 1947; Goodman and Brown, 1988).

Between 1986 and 1989, the Indian Agricultural Program of Ontario (IAPO) collected a series of 35 of these landraces from native farmers/horticulturists in Ontario and New York State. Subsequently, IAPO developed food products using the white floury corn, and designed a marketing strategy that emphasizes the traditional characteristics of the landraces.

Compared to commercial corn hybrids, the IAPO landraces have poor standability, and yield poorly. Both kernel size and cob colour are more variable than desired for processing. In plant breeding to overcome these limitations, the challenge is to improve the agronomic characters without losing the ear, kernel and endosperm characters typical of the IAPO germplasm. One approach would be to make crosses among landraces, to exploit heterosis for agronomic traits. It is not known whether the genetic divergence among the landraces is sufficient to cause enough heterosis for this. Another approach would be to cross one or more landraces with outside germplasm. For this, the choices of outside germplasm are limited, because there are few, if any, sources of improved early-maturing white floury flint corn. Therefore, most crosses between IAPO x non-IAPO germplasm would result in hybrids lacking some or all of the typical IAPO characteristics. One of the most important of these characteristics is the floury endosperm texture.

According to Coe *et al.* (1988), the floury endosperm texture can be regulated by many different alleles (cfl_2, fl_1, fl_2, fl_3, h, Mc, o_1, o_2, o_5, o_7, o_9, o_{10}, o_{11}, o_{12}, o_{13}, pro, sen_1 through sen_6, sh_4 and Sup_1). The floury corn used by the natives of the Americas carries the fl_1 and (or) one or more of the other floury alleles listed above (Coe *et al.*, 1988).

Prior to the experiment reported here, nothing was known about the potential for heterosis among IAPO landraces or between IAPO landraces and other germplasm, nor about the genetic factor(s) causing the floury endosperm texture of the IAPO landraces. Therefore, the objectives of this research were: to evaluate several IAPO x IAPO crosses, to evaluate several crosses between IAPO landraces and white flint inbreds, and to determine whether the IAPO material carries the fl_1 allele.

Materials and Methods

Two experiments (Experiment 1 and 2) were evaluated in three-replicate randomized complete block designs at Ste-Anne-de-Bellevue, Québec (45°26' N latitude) and at Ottawa, Ontario, (45°31' N latitude) in 1993 and 1994. At Ste-Anne-de-Bellevue, the experiment was grown on a Saint-Amable sandy loam in 1993 and on a Dalhousie clay loam in 1994. At Ottawa, the experiments were grown on a Manotick sandy loam in both years. Fertilizer was broadcast and incorporated before planting, to adjust to 90-90-

90 kg ha^{-1} of N-P_2O_5-K_2O, taking into account soil fertility and residues from previous crops. Trials were seeded in mid-May at both sites in both years. Due to extensive bird damage to young seedlings at Ste-Anne-de-Bellevue in 1993, that site was re-seeded in the first week of June, 1993. Each experimental plot consisted of three 5-m rows. Plots were seeded at a high density and thinned to a final density of 45 000 plants ha^{-1}. Metolachlor and triazine formulations were applied to control weeds. Escaped weeds were controlled by cultivation. Data were gathered from the centre row of each plot, excluding three plants at each end of the row.

Experiment 1

The entries of this experiment were four white floury open-pollinated landraces from the IAPO collection (I-3, I-8, I-13 and I-40) (Table 5.1) and the six possible crosses among them, with no reciprocals.

Four traits were assessed on a plot basis: grain yield (calculated on a 15.5 % grain moisture basis), grain moisture at harvest, stalk lodging (with plants whose main stalks were tilted below the apical ear at 45° or more were considered lodged) and kernel area. Kernel area was assessed on a sample of 60 kernels per plot using Leco 2001 digital image analysis software (Leco Corporation, St-Joseph, Michigan). In addition, cob colour, row number and endosperm texture were recorded on 10 apical ears.

Due to late re-seeding of the Ste-Anne-de-Bellevue site in 1993, and due to further damage from birds feeding on the maturing kernels at both sites in that year, grain yield will be reported for 1994 only.

Error variances were heterogeneous across site-years for grain moisture and there were significant genotype-by-environment interactions for grain moisture, kernel area, and stalk lodging. Therefore, data were analyzed on a site-year basis, except for grain yield which met the assumptions for analysis of variance. The Griffing diallel analysis method II, model-1 (Griffing, 1956) was used to estimate general (GCA) and specific (SCA) combining ability for grain yield.

Experiment 2

The entries of this experiment were two white floury open-pollinated landraces from the IAPO collection (I-13 and I-40); two white flinty inbreds (F477 and 433-1-2); the crosses I-13 x F477, I-40 x F477, I-13 x 443-1-2, I-40 x 443-1-2; and a commercial single cross hybrid control, Pioneer 3902 (Pioneer Hi-Bred), requiring about 2700 Corn Heat Units to reach maturity (Ontario Ministry of Agriculture, Food and Rural Affairs, 1995) (Table 5.1).

Using the same methods as in Experiment 1, the following traits were assessed: grain yield, grain moisture, stalk lodging, kernel area, cob colour, row number, and endosperm texture. Grain yield is reported for 1994 only, for the reasons mentioned for Experiment 1.

Error variances were heterogeneous across site-years for the four quantitative traits and there were significant genotype by environment interactions for grain moisture and lodging, therefore data were analyzed on a site-year basis.

Experiment 3

In 1993, landraces I-23, I-26, I-27, I-29, I-36 and I-42 were chosen to represent each of the six native reserves of origin (Table 5.1). Each of these was crossed with two inbreds homozygous for the dosage dependant *floury-1* (*fl_1*) allele (88-3209 and 88-3207-1 from the Maize Genetic Cooperation Stock Centre, University of Missouri, Columbia, Missouri) in 1993. In 1994, the 12 crosses were grown and selfed in a three-replicate randomized complete block design at Ste-Anne-de-Bellevue, with the parents included as controls. Four ears per plot were harvested. From each of these, four kernels per ear were cut transversally at the top of the embryo to visually score the thickness of the vitreous endosperm layer, rated on a scale from 1 (floury) to 10 (vitreous).

Results and Discussion

Experiment 1

In the combined analysis of variance for grain yield, entry and site main effects were significant ($P<0.01$). The data for grain yield met all the conditions and restrictions for Griffing's method II, model-1 diallel analysis (Griffing, 1956). General (GCA) and specific (SCA) combining ability mean squares were significant ($P<0.01$). Landraces I-8 and I-3 had relatively low yields and significant negative GCA effects, whereas landraces I-13 and I-40 had relatively high yields and significant positive GCA effects (Table 5.2).

Despite the positive significant ($P < 0.01$) heterosis over mid-parent values and the SCA effects observed in four of the crosses, none of these yielded significantly more than the I-40 landrace (Table 5.2). Furthermore, the crosses were not significantly different from their parents for grain moisture, stalk lodging and kernel area, except in the I-13 x I-40 cross at Ottawa in 1994 for kernel area, and in the I-8 x I-13 cross at Ste-Anne-de-Bellevue in 1994 for grain moisture (Table 5.2). The standard deviations for kernel area ranged from 11.6 to 16.4 mm^2 in the landraces and from 11.8 to 17.9 mm^2 in the crosses among them.

The variety cross hybrids had the general ear characteristics of the landraces, as seen in the kernel colour, the endosperm texture and row number which remained true to the parental type, but they lacked sufficient grain yield advantage to justify their use as cultivars.

In the experiment reported here, too few crosses were done to draw any conclusions on heterotic patterns in crosses among landraces from different reserves. However, high and significant mid-parent heterosis and SCA effects were observed in the crosses involving I-8 (Table 5.2), which is from the Oneida reserve and I-3, I-13, and I-40, all of which come from the Six Nations Reserve (Table 5.1). It might be worthwhile to intercross the best yielding landraces from the different reserves of origin. Experimental crosses could involve the landraces I-20, I-27 and I-28 from the Akwesasne reserve, I-26 from the Oneida reserve, I-40 and I-42 from the Six Nations reserve, I-22 from the Tyendinaga reserve, I-23 from the Moravian reserve, and I-36 from the Sandborn reserve (see Chapter 4).

Experiment 2

Entry main effects for grain yield were significant ($P<0.01$) at both sites, with the landrace I-40 and the crosses between landraces and inbreds yielding more than the inbreds and the I-13 landrace (Table 5.3). Heterosis over the mid-parent value was significant for all crosses at both sites (Table 5.3). The crosses yielded significantly more than I-40 at Ste-Anne-de-Bellevue. The control hybrid Pioneer 3902 yielded more than any of the crosses at Ste-Anne-de-Bellevue and at Ottawa: 8.99 and 7.75 t ha^{-1}, respectively.

Yield differences between Ste-Anne-de-Bellevue and Ottawa were 1.24 t ha^{-1} for the control hybrid and 1.26 and 2.03 t ha^{-1} for the inbreds, ranged from 0.37 to 0.73 t ha^{-1} for the crosses, and were only 0.10 and 0.16 t ha^{-1} for the landraces. Based on these differences, it seems that the landraces had more yield stability than the crosses which were in turn more stable than the control and inbreds. The genetic heterogeneity of the landraces and crosses may have buffered them against environmental stress.

The landraces had greater variability in kernel size, as seen in their standard deviation for kernel area, which ranged from 11.7 to 18.8 mm^2, compared to a range of 4.4 to 7.9 mm^2 for the inbreds. The crosses were intermediate, with standard deviations between 8.2 and 14.6 mm^2.

The inbreds had smaller kernels, earlier maturity and less lodging than the landraces (Table 5.3). The crosses frequently had significantly smaller kernels and lower grain moisture than their parents. The I-40 x 443-1-2 cross lodged significantly less than its IAPO parent in Ottawa 1993 and Ste-Anne-de-Bellevue 1994.

The inbreds had vitreous kernels and more rows of kernels than the landraces. The F_1 plants had ears bearing both floury and vitreous kernels and with more rows of kernels than the landraces (Table 5.3). The crosses occasionally had pink cobs, at about the same frequency (0.2%) as observed in the landraces.

Experiment 3

The objective of this experiment was to determine if the dosage-dependent fl_1 allele is responsible for the floury endosperm texture of the landraces. The endosperm genotype of the floury inbred testers was known to be $fl_1\,fl_1\,fl_1$ (Stock Centre, University of Missouri). Following a cross of one of those testers with a plant homozygous for Fl_1, the genotype of the F_1 plants would be $Fl_1\,fl_1$. The endosperm genotypes of selfed kernels on those F_1 plants would be: $fl_1fl_1fl_1$, $Fl_1fl_1fl_1$, $Fl_1\,Fl_1fl_1$ and $Fl_1\,Fl_1\,Fl_1$. These genotypes correspond to a range of phenotypes from floury (rated as 1 in this study) to vitreous (rated as 10).

The ratings of the endosperm texture of the six landraces, the two inbred testers, and their 12 crosses ranged from 1.5 to 2.6, 1.5 to 1.8 and 1.4 to 2.5, respectively. Because the crosses did not show endosperm texture ratings higher than observed in the floury landraces, we concluded that the gene responsible for the floury endosperm texture of the landraces must be allelic to the one present in the testers. Thus, each of the six landraces tested must carry either the fl_1 or o_4 allele.

Based on the range of vitreous starch layer thickness observed in the F_2 kernels of crosses between IAPO landraces and nonfloury inbreds (Experiment 2), it seems likely that the landraces carry the dosage dependant fl_1 allele, not the fully recessive o_4 allele.

The range of variation from 1.4 to 2.6 observed in the floury endosperm ratings can be explained by experimental error or local variation in soil fertility (Hamilton *et al.*, 1951). Also, the fl_1 factor is known to be sensitive to background effects, making its expression difficult to classify (Weijer, 1952; Coe *et al.* 1988).

Conclusions

Significant heterosis over the mid-parent value was observed in crosses involving a low yielding landrace from one reserve of origin with higher yielding landraces from another reserve. However, these variety crosses did not yield significantly more than the best yielding landrace I-40. Crosses among the best yielding landraces from each of the six reserves of origin may be more promising and should be made and evaluated.

Crosses between landraces and white flint inbreds yielded more than either parent. At one evaluation site, they yielded significantly more than the best yielding landrace. Crossing of the landraces with the inbreds improved some agronomic characteristics, but disrupted some of the ear characteristics of the landraces. Better heterotic patterns involving the IAPO landraces should be found or developed. The identification of a promising IAPO x inbred cross would require the backcrossing of the floury gene in an appropriate inbred. The floury factor responsible for the characteristic endosperm texture of the IAPO landraces was identified as being the dosage dependent *floury-1* gene.

Table 5.1. Origin of ten landraces and two inbreds.

Entry	Origin
IAPO white floury landraces	
I-3, I-13, I-40, I-42	Six Nations reserve, southern Ontario, Canada
I-8, I-26	Oneida reserve, southern Ontario, Canada
I-27	Akwesasne reserve, southern Ontario, Canada
I-23	Moravian reserve, southern Ontario, Canada
I-29	Tyendinaga reserve, southern Ontario, Canada
I-36	Sandborn reserve, New York State, United States
White inbreds	
F477	F49 (Blanc Chalosse X HD United BL) X F47 (Pouyastruc), (INRA-France)
443-1-2	Central Experimental Farm (Agriculture and Agri-Food Canada, Ottawa)

Table 5.2. Means of four white floury landraces and crosses among them in Ste-Anne-de-Bellevue and Ottawa for grain yield in 1994, and for grain moisture content, lodging and kernel area, in 1993 and 1994.

		Landraces (GCA effects for grain yield)				Crosses (SCA effects for grain yield) (*% heterosis over the mid-parent*)					
Site-years	$LSD_{(0.05)}$	I-3	I-8	I-13	I-40	I-3 X I-8	I-3 X I-13	I-3 X I-40	I-8 X I-13	I-8 X I-40	I-13 X I-40
Grain yield ($t\ ha^{-1}$)											
Ottawa and Ste-Anne-de-Bellevue 94	0.94	3.86 (-0.14**)	2.43 (-0.49**)	4.63 (0.15**)	5.11 (0.47**)	5.07 (0.85**) (*61.1***)	4.96 (0.10) (*16.9*)	5.63 (0.45**) (*25.4***)	5.53 (1.02**) (*56.7***)	5.81 (0.99**) (*54.2***)	5.38 (-0.08) (*10.6*)
Grain moisture (%)											
Ste-Anne-de-Bellevue 93	5.7	43.5	45.3	46.2	51.0	41.8	42.1	48.1	48.1	-	50.9
Ottawa 93	-[a]	41.9	34.7	34.4	38.3	33.1	32.2	35.0	33.7	-	38.7
Ste-Anne-de-Bellevue 94	3.5	32.7	36.2	32.5	34.9	35.4	32.8	34.5	27.5	-	32.7
Ottawa 94	-	33.4	31.6	32.7	32.5	32.3	27.8	29.1	30.0	-	32.4
Stalk lodging (%)											
Ste-Anne-de-Bellevue 93	15.5	45.0	51.0	22.0	11.7	32.0	36.0	8.0	21.7	-	9.0
Ottawa 93	18.6	22.3	52.1	37.3	24.3	40.3	32.3	20.0	48.3	-	27.3
Ste-Anne-de-Bellevue 94	-	23.6	21.1	11.1	11.1	13.5	14.8	11.1	9.3	-	9.3
Ottawa 94	19.9	17.4	41.6	10.6	5.0	12.3	7.2	8.2	3.9	-	2.0

Table 5.2. (Cont.)

Site-years	$LSD_{(0.05)}$	Landraces				Crosses					
		I-3	I-8	I-13	I-40	I-3 X I-8	I-3 X I-13	I-3 X I-40	I-8 X I-13	I-8 X I-40	I-13 X I-40
<u>Kernel area (mm²)</u>											
Ste-Anne-de-Bellevue 93	-	76.3	73.0	76.9	70.4	78.9	75.0	82.3	80.6	80.9	78.7
Ottawa 93	-	68.8	73.1	77.1	82.5	78.7	78.9	81.0	73.1	76.7	80.8
Ste-Anne-de-Bellevue 94	5.5	73.9	68.1	74.6	77.8	78.0	72.0	76.2	69.0	79.3	78.6
Ottawa 94	6.1	72.9	71.4	78.5	75.9	77.8	78.1	80.1	71.4	78.4	85.3
<u>Kernel row number</u>		4-12	4-12	4-10	4-12	4-12	6-8	4-10	8-14	6-10	4-10

*, ** significantly different from the mid-parent at the 0.05 and 0.01 level, respectively.

[a] The site-years without LSD values showed no statistically significant differences among entries.

Table 5.3. Means of two white floury landraces, two white inbreds, and their crosses in Ste-Anne-de-Bellevue and Ottawa for grain yield in 1994, and for grain moisture content, lodging and kernel area in 1993 and 1994.

		Landraces		Inbreds		Landraces X inbreds (% heterosis over the mid-parent)			
Site-years	$LSD_{(0.05)}$	I-13	I-40	F477	443-1-2	I-13 X F477	I-40 X F477	I-13 X 433-1-2	I-40 X 433-1-2
Grain yield ($t\ ha^{-1}$)									
Ste-Anne-de-Bellevue 94	0.85	4.37	6.12	4.04	4.09	7.46 (77.4**)	7.07 (39.2**)	7.12 (68.3**)	7.16 (40.3**)
Ottawa 94	1.84	4.47	5.96	2.78	2.06	6.73 (85.7**)	6.42 (46.9*)	7.73 (136.8**)	6.79 (69.3**)
Grain moisture (%)									
Ste-Anne-de-Bellevue 93	4.8	48.7	53.5	-	33.0	33.2	48.7	36.2	38.5
Ottawa 93	4.2	36.9	37.9	-	33.4	32.2	32.2	29.7	34.1
Ste-Anne-de-Bellevue 94	3.3	34.0	33.6	-	29.5	27.8	31.0	32.5	34.2
Ottawa 94	5.1	32.9	38.3	-	30.6	27.1	33.3	32.6	32.3
Stalk lodging (%)									
Ste-Anne-de-Bellevue 93	-[a]	19.7	6.7	4.0	11.7	9.3	11.0	10.3	6.7
Ottawa 93	15.3	32.3	31.3	0	3.7	26.7	19.0	24.7	8.7
Ste-Anne-de-Bellevue 94	10.8	2.2	23.1	0	2.0	6.0	14.2	1.9	3.6
Ottawa 94	-	0	12.0	0	0	3.5	3.3	1.9	2.6

Table 5.3. (Cont.)

		Landraces		Inbreds		Landraces X inbreds			
Site-years	$LSD_{(0.05)}$	I-13	I-40	F477	443-1-2	I-13 X F477	I-40 X F477	I-13 X 433-1-2	I-40 X 433-1-2
<u>Kernel area (mm²)</u>									
Ste-Anne-de-Bellevue 93	5.7	79.0	72.1	46.7	28.3	70.9	77.8	57.8	57.3
Ottawa 93	5.6	77.0	79.5	57.0	31.4	76.5	76.7	69.9	63.9
Ste-Anne-de-Bellevue 94	2.9	72.7	76.4	42.5	28.0	66.4	66.6	57.3	55.4
Ottawa 94	10.5	65.8	76.8	42.5	28.5	70.3	68.4	58.4	58.3
<u>Kernel row number</u>	-	4-10	6-10	8-14	10-20	8-12	6-16	10-14	8-14

*, ** significantly different from the mid-parent at the 0.05 and 0.01 level, respectively.

[a] The site-years without LSD values showed no statistically significant differences among the entries.

CHAPTER 6

GENERAL DISCUSSION

Variation among landraces

Significant variation was observed among the landraces for the 23 quantitative and qualitative traits studied (Chapter 4). The characters that allowed variation among landrace to be observed visually were plant height, time to tasselling and silking, tillering, lodging, endosperm texture, kernel size and colour, and cob colour. For example, landraces I-6, I-15, I-29, and I-31 had kernel characteristics visually distinct from the bulk of the landraces. The landrace classification in clusters was based on seven quantitative traits which did not readily permit visual classification but nonetheless grouped the above landraces apart from the bulk of the landraces. The centroid clustering grouped together 26 of the 35 landraces in cluster 10. The grouping of more than 70 % of the population in one cluster brings up the question of the ancestry of these landraces. Cluster 10 is composed of members collected from all six reserves of origin suggesting a certain homogeneity of the landraces among the Iroquois reserves. To compare genetic markers among and within reservations could provide us with some answers concerning the pedigree relationships among the landraces.

Are the cultivars collected by IAPO really the landraces that the natives have been using for centuries or are they simply remnants from improved populations used by farmers at the beginning of the century? The IAPO landraces fit the general description of landraces used by the natives at the beginning of this century (Harrington, 1908; Parker, 1910) but they also closely match the descriptions of some improved cultivars used by non-native farmers at the same time in history (Sturtevant, 1899; Dimmock, 1926). The eight-row ears of the landraces and their typical Northern Flint and Flour appearance (Brown and Anderson, 1947) rules out a recent introduction in the region. In favour of the original landrace hypothesis, there is the spiritual link of the natives with their corns and their historical reluctance to adopt the non-native way of living. To grow some of the old cultivars along with the IAPO landraces could provide us with part of the answer.

Although it has been hypothesized that open-pollinated corn populations never really reach genetic equilibrium (Sprague, 1955; Adams and Shank, 1959), one event may have disrupted this equilibrium even more. In the early 1980's, competitions took place on some of the reserves, with prizes awarded for the largest ear of corn. Many of the IAPO accessions trace back to one or few prize-winning ears. This simple event may have affected the population genetic make-up in different ways. The competition may have stopped seed exchange within and among reserves. The narrowing down of the selection criteria may have resulted in losses of germplasm within landraces or even to abandonment of some landraces altogether. The small selection sample size may have led to inbreeding. This event may explain the impractical growth habit of a landrace like I-8 (Chapter 4).

Landraces vs commercial hybrids

The most obvious descriptive feature of the IAPO landraces is their high tillering capacity relative to commercial hybrids. Corn planting patterns used by natives and farmers earlier this century differed from the precision planting now used by farmers (Parker, 1910; Weatherwax, 1954). One planting pattern commonly used was to plant three kernels per hills, which were spaced about one meter apart in all directions (Wallace and Bressman, 1937). The plants often tillered profusely. The tillers played an important role in light interception. In the IAPO landraces, tillering of the border plants was profusive up to the fourth plant within the row. In contrast, only the end plants tillered in rows of the control hybrid. The control hybrid also tillered profusely when space planted. It seems that the tillering behaviour of the landraces is more sensitive to shade than the commercial hybrid used as a control.

The second main characteristic differentiating the IAPO landraces from today's commercial hybrids is their severe tendency to lodge in early fall. The space planting that was practiced at the beginning of the century reduced the etiolation of the corn plants (Horner *et al.*, 1976), making the stalks stronger. In the experiment described in Chapter 4, some landraces grew in a space-planted condition for a few weeks because of bird damage. These plants were shorter and resisted lodging better than the more densely planted ones.

Furthermore, we can hypothesize that native people did not directly or indirectly select plants with strong stalks mainly because the ears were harvested early in the fall (before lodging) to be put to dry in husk braids. Whereas modern corn producers may try to reduce their energy costs by field drying their corn, the native people reduced losses by harvesting early enough to avoid bird damage, ear disease and animal predation.

Landrace I-8, assessed in Chapter 4, behaved in a non-domesticated way, lodging before or during pollination. Either it completely relies on space planting to strengthen its stalk or it has specific environment requirements, or the accession tested here was genetically altered by narrow selection and limited seed supply.

When the IAPO landraces were left to dry until the end of October in the field, very severe ear rot problems occurred. Few ears had intact kernels, and many had their kernels covered with mycelium. The numerous and thick husk leaves and erect position of the ears, even after dry down, reduced moisture loses and favoured penetration of the rain within the husks. The ears in contact with the soil rotted very rapidly.

Genetic improvement of the landraces

The assessment of crosses among the IAPO landraces failed to provide the yield advantage that would justify the use of such variety crosses. Only a few crosses were tested here. The classification information obtained in Chapter 4 could be used to choose specific crosses involving relatively high yielding landraces from distant clusters.

Crossing the landraces with non-IAPO cultivars or inbreds may lead to significant agronomic improvements of the IAPO population, as seen in Chapter 5. But Chapter 5 also demonstrated that the use of germplasm possessing the ear characteristics of the IAPO population is important in order to retain the general characteristics of the IAPO populations.

The biggest limiting factor to the genetic improvement of the IAPO landraces population are the native peoples' requirements themselves. Their requirements to maintain the ear characteristics while improving the agronomic characteristics narrows the breeder's options. To understand such demands we must remember how corn was considered by the natives. Corn was not a plant to be exploited to make a profit. The natives lived close to nature and its cycles. Their precarious life gave a sacred dimension to a plant that could save their lives during the cold, long winter months when hunting was difficult. The row number also had a meaning because of its correspondence to the four cardinal directions which are important in the natives cosmology (Andrews, 1981). An ear with rows in a multiple of four like the eight-row flints was considered more in equilibrium with the laws underlying the mysteries of life (Waters, 1963; Andrews, 1981). Also, it was reported that tribes used the shape and colour of their corn ears to identify and distinguish their respective community or tribe (Weatherwax, 1954).

The floury and white characters are also appreciated for practical reasons. Floury corn is easier to grind, to cook and to eat. White corn tastes better and may be less bitter than yellow, especially after cooking.

If the natives maintain their requirements concerning the general ear appearance of the landraces, the genetic improvement may be slow because of the limited availability of improved germplasm possessing the general IAPO characteristics. If the natives decide to accept a modification of their original landraces, it might be unnecessary to improve these landraces, because high yielding commercial food quality hybrids are already available. However, these may lack some of the special quality characteristics present in the IAPO corn that make the alkali-cooked product (corn chips) derived from it particularly attractive to the consumer. These characteristics may be sufficient to justify efforts towards genetic improvement of the landraces.

CHAPTER 7

SUGGESTED RESEARCH

To know more about the variation among these landraces and their classification, the following experiments are suggested:

a. Compare molecular markers among the landraces.

b. Compare molecular markers between the landraces and old cultivars present at the beginning of the century.

c. Space plant the landraces and characterize them based on their morphological and reproductive characters.

d. Further investigate the variation among the IAPO landraces by characterizing their root systems.

To improve the landraces with a minimum disruption of their characteristics, the following experiments are suggested:

a. Search for improved germplasm possessing most of the IAPO landraces desired characteristics.

b. Make crosses among the best yielding IAPO landraces from each reserve.

c. Make crosses of the best yielding IAPO landraces of cluster 10 (see Chapter 4) with the landraces from the other clusters.

d. Make crosses among the best yielding most distant members of cluster 10.

e. Start a recurrent selection program using the best IAPO landraces as the source population.

f. Start a reciprocal recurrent selection program with two groups of IAPO landraces that show a good heterotic pattern.

To know more about the potential of the IAPO germplasm, the following experiments are suggested:

a. Study the heterotic patterns of the IAPO landraces with other more genetically distant corns.

b. Study the amino acid composition and protein content of the IAPO landraces.

c. Screen the IAPO landraces for sources of resistance to known corn diseases and insects.

d. Investigate kernel quality characteristics of the IAPO landraces that could be exploited in commercial food and industrial corn hybrids.

e. Screen the IAPO landraces to detect the presence of stable mutants.

CHAPTER 8

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APPENDIX A

Photographs shown in Appendix A are related to the three experiments discussed in Chapters 4 and 5. The series of 35 corn landraces belonging to the Northern Flints and Flours racial complex were assessed for variation for a number of traits (see Chapter 4). Figure A.1 shows some of the characteristic plant, ear, kernel and cob attributes associated to the germplasm studied in this research.

Figure A.2 shows that the open-pollinated condition of the landraces results in a visible ear size variation among plants within the landraces. The split between pairs of kernel rows and the swelling at the base of the ear are typical of Northern Flints. Swollen shanks are also associated with this racial complex.

Chapter 5 focused on landrace x landrace and landrace x inbred cross evaluations. Figure A.3.a and A.3.b show landrace parents and their F_1 progeny, which expressed a certain degree of heterosis over the mid-parent in some of the landrace x landrace crosses (See Chapter 5, experiment 1). Figure A.3.c and A.3.d refer to the landrace x inbred experiment (See Chapter 5, experiment 2), where the F_1 hybrids showed disruption of the landrace ear characteristics by having higher row number and a mixture of floury and vitreous endosperm texture kernels on the same ear.

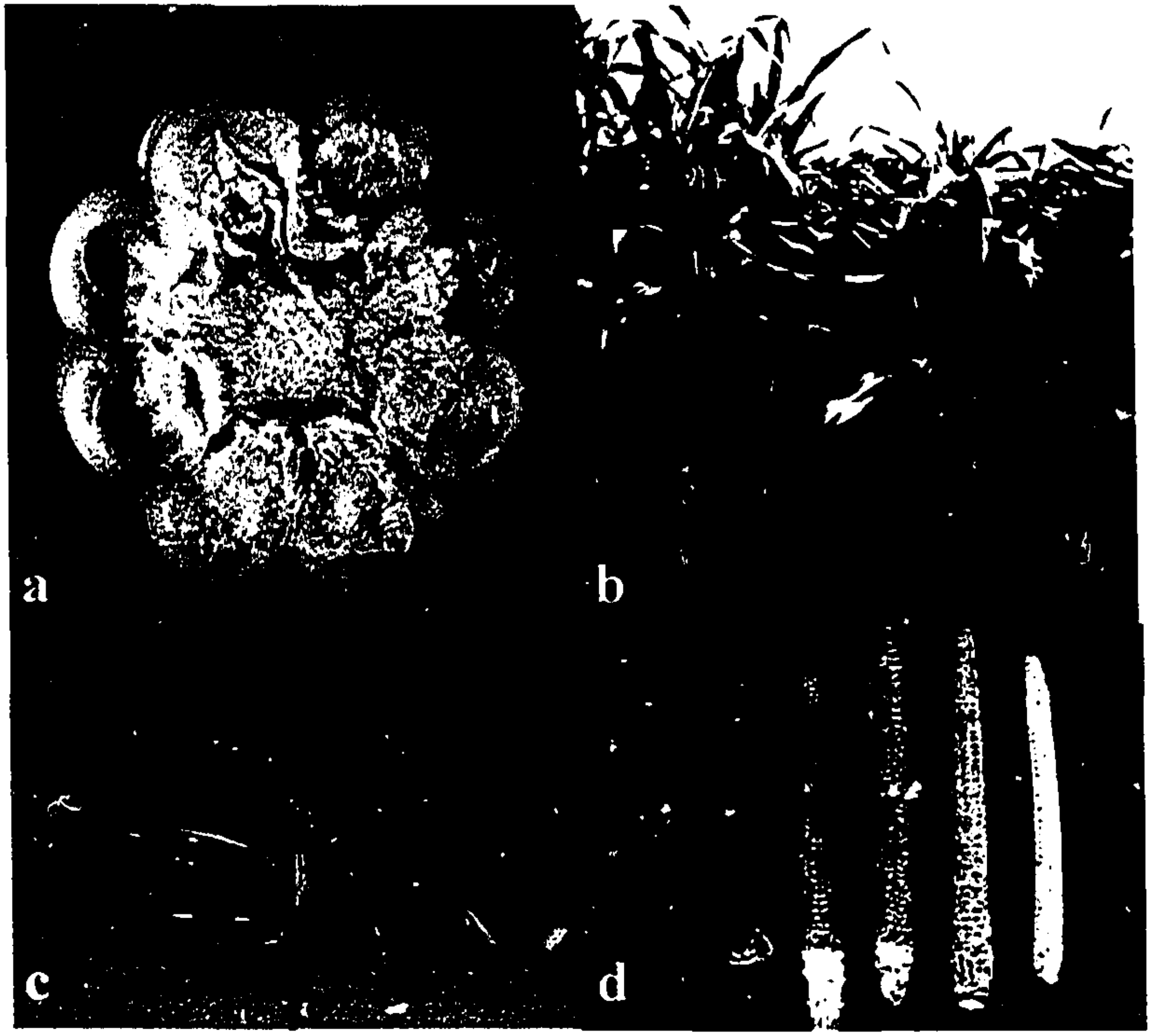

Figure A.1. (a) Cross section of an eight-row ear showing the wide, crescent-shaped kernels of the landraces; (b) field view showing clear height differences among two landraces and their profusive tillering growth habit; (c) example of the long husk leaf blades typical of Northern Flints; (d) cob colour segregation within landraces, ranging from white, pink, red to brown.

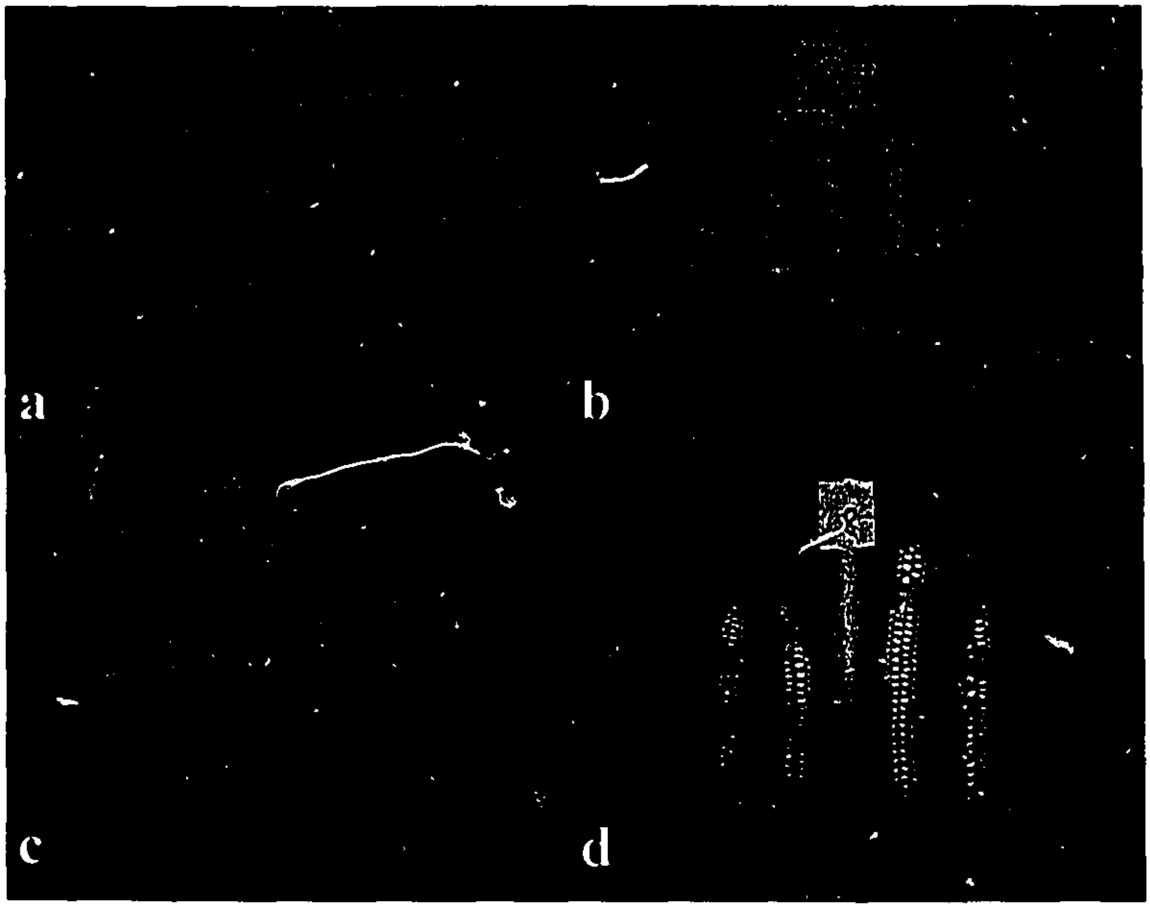

Figure A.2. (a,b) Ears of the two best yielding landraces I-20 and I-17; (b,c) ears of the two lowest yielding landraces I-12 and I-8 (See Chapter 4).

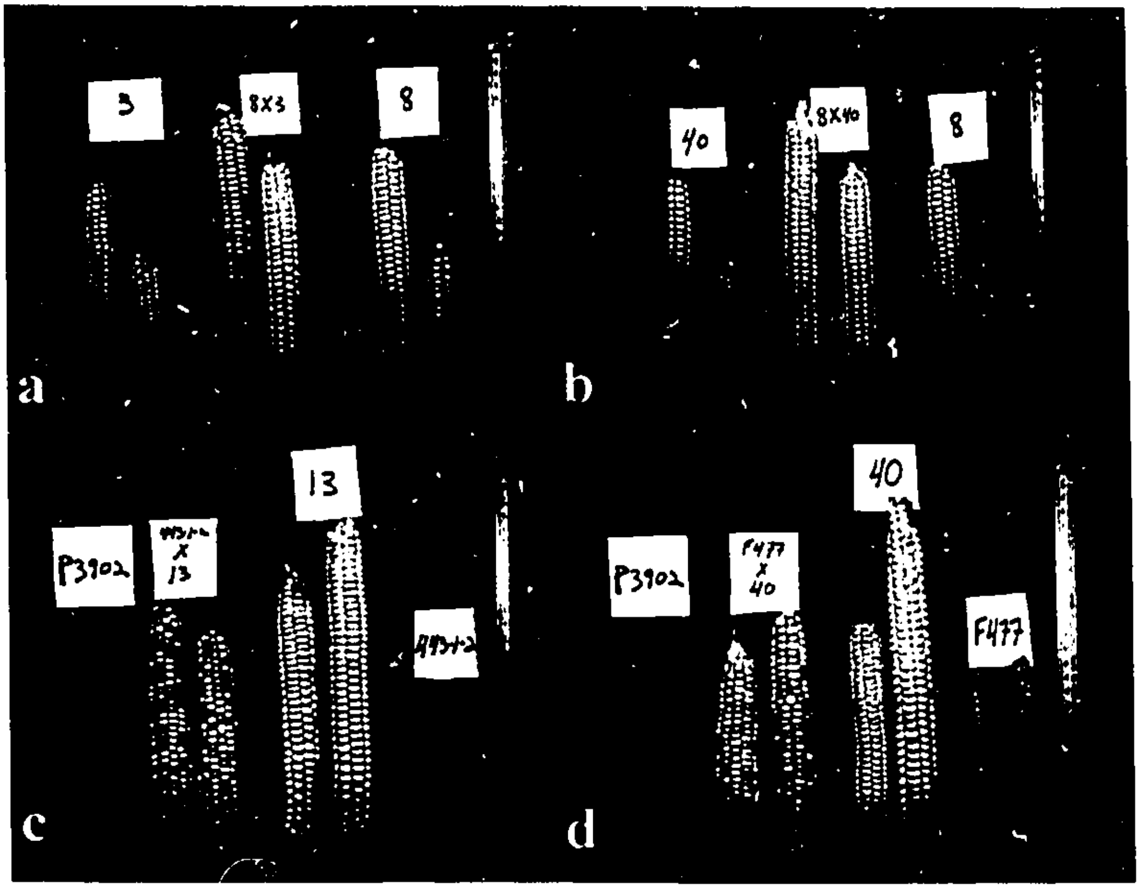

Figure A.3. (a,b) Pairs of ears of landrace parents (left and right) and their progeny (the centre pair of ears) (See Chapter 5, experiment 1); (c,d) one ear of the control hybrid (left), the landrace (second pair of ears from the right) and inbred (rigth) parent, and their crosses (third pair of ears from the right) (See Chapter 5, experiment 2).

APPENDIX B

Assessment of the 35 corn landraces involved recording data on 18 quantitative traits (see Chapter 4). The landraces were grown in a three-replicate randomized complete block design at Ste-Anne-de-Bellevue and at Ottawa, in 1993 and 1994. Appendix B presents the site-year means for 18 quantitative traits. The means across site-years for the same traits are presented in Chapter 4, table 4.2 to table 4.4.

Table B.1. Means of six traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1994.

Entry	Grain yield ($t\ ha^{-1}$)		Test weight ($kg\ hL^{-1}$)		100-kernel weight (g)		Days to tasselling		Days to silking		Ear number	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-1	3.71	4.38	68.7	68.4	43.2	43.0	65.6	69.0	72.3	72.0	0.9	1.0
I-2	3.87	4.21	69.8	70.5	35.8	38.5	63.6	65.0	67.3	68.0	1.1	1.3
I-3	4.91	3.20	67.8	66.3	40.9	40.5	63.6	65.6	67.0	69.3	1.3	1.1
I-4	4.39	4.34	67.5	68.2	37.2	35.6	64.6	66.2	70.3	71.0	1.1	1.2
I-5	4.34	4.04	68.4	67.0	45.0	44.1	64.0	65.3	67.3	67.6	1.1	1.0
I-6	3.83	3.14	68.8	68.6	38.3	35.4	67.0	67.6	73.0	71.0	1.1	1.3
I-7	4.77	4.86	69.1	67.5	46.4	42.3	65.6	66.0	70.0	69.6	1.1	1.1
I-8	2.24	1.49	67.0	65.5	41.5	41.8	68.3	65.6	74.3	69.3	1.2	0.7
I-10	3.68	2.59	69.3	67.5	41.3	38.5	66.3	65.3	72.6	71.6	1.0	0.9
I-11	4.08	4.00	69.8	68.9	40.7	40.5	68.0	69.3	72.0	71.6	1.0	1.0
I-12	2.57	2.95	68.1	68.2	39.3	42.3	64.3	60.0	70.6	67.3	1.1	0.9
I-13	4.72	3.92	70.1	69.2	46.4	44.8	64.6	65.6	69.6	69.6	0.9	1.0
I-14	4.05	4.12	72.2	70.6	43.2	42.2	64.0	65.3	68.0	69.3	1.1	1.1
I-15	4.95	4.17	69.9	70.6	35.1	36.0	-	-	69.6	70.6	1.3	1.2
I-17	5.24	5.60	67.8	67.7	42.0	41.9	66.6	67.0	70.0	71.3	1.1	1.3
I-18	2.85	3.14	67.8	66.4	35.1	38.6	63.3	62.6	67.6	66.0	0.9	0.8
I-19	4.83	3.36	68.3	68.0	39.5	40.2	63.6	63.6	67.6	68.3	1.3	1.3
I-20	5.74	5.34	68.2	66.6	41.6	45.3	65.6	67.0	71.3	71.6	1.2	1.3

Table B.1 (Cont.)

Entry	Grain yield ($t\ ha^{-1}$)		Test weight ($kg\ hL^{-1}$)		100-kernel weight (g)		Days to tasselling		Days to silking		Ear number	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-21	5.19	4.34	70.3	69.4	36.9	38.7	64.3	64.6	68.0	67.3	1.2	1.3
I-22	5.95	4.47	67.4	66.6	38.2	39.9	64.3	64.6	67.3	66.3	1.4	1.7
I-23	4.49	4.48	67.4	67.9	43.6	43.2	65.3	63.6	70.6	68.3	1.1	1.0
I-24	5.81	3.84	67.5	65.5	38.2	40.6	62.6	60.6	66.3	64.6	1.1	0.9
I-25	4.94	5.32*	70.0	67.4	41.9	42.3	65.3	66.0	67.3	68.6	1.2	1.2
I-26	4.84	4.27	68.3	66.9	41.7	40.6	63.3	64.0	67.6	66.3	1.1	1.3
I-27	5.05	5.00	69.3	66.8	45.8	46.9	64.0	64.3	68.3	70.0	1.0	1.0
I-28	5.11	5.12	68.1	67.4	40.2	41.7	62.6	62.6	66.0	64.3	1.3	1.2
I-29	4.67	4.38	70.6	69.9	34.3	34.4	64.6	66.3	69.6	69.6	1.2	1.2
I-30	4.51	4.43	65.5	63.6	43.3	44.0	66.0	63.1	70.0	66.1	1.1	1.1
I-31	3.12	3.26	67.4	66.0	41.6	41.8	64.6	66.6	70.0	69.0	0.9	1.0
I-32	4.57	4.08	70.6	67.9	44.9	44.9	65.3	66.0	68.0	69.0	1.2	1.0
I-33	3.22	4.52	66.7	68.1	41.3	46.1	64.6	67.6	71.0	72.6	1.2	1.1
I-35	4.46	4.95	70.4	68.3	42.1	42.2	65.6	64.3	71.0	68.6	1.0	1.2
I-36	5.10	4.30	67.1	67.0	45.5	44.3	62.6	64.6	67.3	68.3	1.0	1.1
I-37	4.31	4.00	75.3	75.7	34.4	33.1	-	-	72.6	73.7	1.2	1.1
I-40	5.85	4.55	68.2	66.6	44.1	43.8	66.3	68.0	71.0	72.3	1.1	1.1
I-42	5.07	4.19	69.6	68.5	44.0	41.7	65.6	65.3	71.6	71.6	1.1	0.9
P3902	9.31	7.84	78.6	77.2	36.2	37.7	-	-	63.2	63.4	1.1	1.2

Table B.2. Means of three traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994.

Entry	Ear length (cm)				Ear diameter (mm)				Kernel area (mm^2)			
	1993		1994		1993		1994		1993		1994	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-1	17.2	18.7	18.3	19.6	36.2	35.0	35.4	36.4	76.3	74.9	76.9	76.4
I-2	17.0	17.8	17.2	17.8	35.2	33.0	31.8	32.5	80.1	68.8	66.1	70.2
I-3	14.1	17.4	17.3	17.0	34.4	30.6	33.8	33.7	71.3	63.5	74.7	76.5
I-4	15.5	17.6	17.0	18.9	34.2	32.0	34.0	32.3	73.2	74.0	72.8	75.4
I-5	13.8	18.3	19.5	18.4	37.0	35.3	35.4	36.6	83.4	80.5	80.0	80.7
I-6	17.1	18.0	17.3	17.8	34.3	34.3	34.7	34.4	67.9	71.5	69.4	66.4
I-7	15.9	17.7	16.8	16.9	36.6	37.3	38.2	37.4	73.2	83.3	80.6	75.3
I-8	14.8	18.4	18.5	17.0	33.5	33.1	33.7	32.7	71.2	70.8	69.9	70.4
I-10	15.7	17.3	16.2	15.5	36.4	37.9	35.2	34.3	79.2	76.9	76.6	73.4
I-11	14.5	15.5	16.6	17.9	33.5	33.3	32.3	32.9	74.1	77.6	74.1	74.3
I-12	13.6	15.9	16.8	17.2	36.0	34.8	36.7	36.7	74.0	74.7	71.2	74.3
I-13	17.3	18.9	18.6	17.9	35.8	35.0	34.8	35.1	84.1	79.7	80.5	79.7
I-14	14.0	17.4	16.3	17.0	37.5	35.9	35.4	36.2	80.8	78.5	76.0	77.2
I-15	15.9	17.1	16.5	16.4	34.6	33.6	33.6	34.0	64.7	68.7	67.4	67.9
I-17	17.9	18.7	19.7	20.3	34.1	32.4	34.6	35.0	79.6	77.0	74.5	77.7
I-18	14.8	15.0	15.2	14.2	35.3	33.6	34.0	34.2	73.2	68.0	64.3	73.4
I-19	18.9	19.3	19.2	17.9	36.5	34.4	34.3	34.4	75.6	69.2	67.8	68.3
I-20	20.3	20.7	21.3	20.4	34.0	32.5	33.4	33.5	78.7	76.4	75.3	81.5

Table B.2 (Cont.)

Entry	Ear length (cm)				Ear diameter (mm)				Kernel area (mm^2)			
	1993		1994		1993		1994		1993		1994	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-21	16.3	17.8	18.7	18.1	36.2	35.8	34.2	33.4	74.1	74.2	67.8	71.4
I-22	17.0	16.8	17.3	15.4	35.6	33.6	34.4	33.5	84.5	77.4	76.3	81.2
I-23	18.1	19.7	19.0	18.6	36.6	34.9	35.8	36.0	79.8	78.7	76.2	76.9
I-24	16.9	17.6	17.3	16.1	36.9	34.2	35.0	35.8	86.5	71.9	74.8	78.8
I-25	16.4	19.3	18.2	17.5	37.3	34.8	35.8	35.1	82.1	78.4	75.8	78.0
I-26	16.9	17.7	18.8	17.9	35.1	33.9	34.7	34.5	73.0	70.2	75.8	75.2
I-27	18.7	18.4	19.0	19.1	36.1	34.7	35.8	36.7	79.9	77.9	80.8	83.1
I-28	16.6	16.0	17.1	16.1	35.1	32.7	34.9	34.0	78.7	73.1	76.4	75.7
I-29	17.6	19.1	20.0	19.1	33.2	31.6	32.9	31.4	67.2	60.0	63.2	62.1
I-30	17.2	21.0	18.3	18.9	37.1	36.4	36.9	35.7	81.4	83.3	78.7	80.2
I-31	17.4	18.7	19.4	19.0	36.9	34.6	34.9	35.2	81.1	75.4	73.8	74.5
I-32	12.9	17.1	19.2	18.2	36.0	36.9	38.3	36.9	79.3	80.0	80.3	80.1
I-33	16.8	18.3	18.0	18.8	35.6	35.8	36.8	37.8	77.8	81.5	77.2	86.2
I-35	15.1	18.1	16.1	16.0	35.5	34.4	36.9	35.2	77.5	74.6	78.9	78.7
I-36	19.0	20.7	20.9	19.3	37.0	35.5	34.9	35.3	89.4	82.5	78.7	76.5
I-37	12.8	15.8	15.1	15.0	37.3	39.2	38.6	37.1	51.5	54.6	59.0	55.7
I-40	18.7	20.2	19.5	18.2	34.6	35.6	35.3	34.7	75.4	84.3	78.1	77.9
I-42	18.7	19.4	20.4	18.4	36.1	34.7	34.3	35.2	86.6	82.3	77.5	71.0
P3902	17.0	16.6	17.1	17.0	44.2	42.2	43.5	43.9	67.8	69.3	65.4	66.8

Table B.3. Means of three traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994.

Entry	F-Shape (D. min/ D. max.)				Kernel moisture (%)				Lodging (%)			
	1993		1994		1993		1994		1993		1994	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-1	0.81	0.79	0.80	0.79	28.8	34.3	31.2	33.9	30.6	30.3	17.4	16.2
I-2	0.82	0.82	0.83	0.82	34.4	23.3	23.9	30.0	56.3	54.6	5.8	17.2
I-3	0.81	0.80	0.81	0.81	32.1	31.6	29.9	32.4	61.6	19.0	42.0	23.7
I-4	0.80	0.81	0.82	0.82	40.1	27.5	33.0	32.7	42.3	58.3	13.8	23.2
I-5	0.79	0.81	0.81	0.82	40.6	27.6	29.3	27.3	43.3	68.0	26.4	20.3
I-6	0.80	0.80	0.80	0.82	52.1	39.0	35.8	38.3	57.6	46.6	38.4	36.3
I-7	0.76	0.79	0.81	0.77	43.4	31.7	31.9	34.3	24.3	33.6	13.9	17.4
I-8	0.79	0.78	0.79	0.79	34.0	32.1	32.5	26.7	59.0	74.0	37.5	57.1
I-10	0.81	0.81	0.81	0.81	47.4	32.2	34.7	33.7	17.6	44.6	13.4	17.3
I-11	0.82	0.81	0.81	0.82	45.5	35.1	32.6	34.4	34.6	31.6	33.9	31.8
I-12	0.79	0.81	0.82	0.81	45.3	35.6	26.2	28.8	19.3	58.3	19.7	11.4
I-13	0.81	0.81	0.82	0.81	45.1	33.3	31.3	33.6	13.0	42.6	7.7	8.9
I-14	0.78	0.80	0.79	0.81	33.0	25.2	30.0	31.1	48.6	31.6	15.0	8.1
I-15	0.81	0.82	0.81	0.80	45.2	31.7	30.7	32.2	20.6	33.6	9.2	33.0
I-17	0.79	0.77	0.79	0.78	39.9	30.0	33.0	35.6	27.0	55.6	13.8	14.5
I-18	0.81	0.80	0.83	0.81	37.4	34.6	30.5	30.5	35.6	61.3	22.0	15.3
I-19	0.78	0.79	0.79	0.79	39.0	27.2	27.4	27.4	47.3	57.0	18.5	23.3
I-20	0.81	0.82	0.80	0.82	46.8	31.4	31.2	34.0	33.0	34.0	39.8	13.4

Table B.3 (Cont.)

Entry	F-Shape (D. min/ D. max.)				Kernel moisture (%)				Lodging (%)			
	1993		1994		1993		1994		1993		1994	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-21	0.80	0.80	0.81	0.81	37.0	24.8	27.1	28.0	25.6	41.3	35.8	31.7
I-22	0.82	0.80	0.80	0.82	40.9	29.6	29.4	26.5	16.6	47.6	20.6	34.9
I-23	0.82	0.80	0.79	0.79	31.8	26.8	33.7	34.9	38.6	43.3	38.2	13.2
I-24	0.83	0.82	0.81	0.83	41.2	30.3	25.9	28.4	24.0	51.0	11.3	5.3
I-25	0.81	0.81	0.80	0.80	42.8	28.5	29.2	32.6	47.0	51.6	22.8	39.1
I-26	0.80	0.83	0.81	0.81	38.3	28.9	27.0	30.2	64.3	70.0	45.8	36.9
I-27	0.79	0.79	0.81	0.81	42.9	31.0	30.4	33.8	20.3	63.6	5.9	21.8
I-28	0.81	0.82	0.83	0.81	35.4	26.3	25.8	27.9	20.6	47.0	5.2	17.8
I-29	0.82	0.81	0.83	0.81	35.8	24.7	28.1	26.3	27.0	46.3	31.0	15.0
I-30	0.80	0.82	0.81	0.80	45.1	37.4	34.9	29.2	10.3	50.6	19.3	28.8
I-31	0.81	0.81	0.80	0.80	49.3	33.2	30.7	34.1	32.0	56.0	12.4	34.8
I-32	0.80	0.79	0.80	0.82	37.5	33.2	27.3	30.1	29.3	43.0	1.8	5.3
I-33	0.77	0.77	0.77	0.79	50.4	28.6	30.0	33.8	42.3	53.0	37.2	16.7
I-35	0.83	0.82	0.81	0.83	44.1	32.5	31.8	34.2	79.3	55.0	23.5	17.1
I-36	0.78	0.78	0.79	0.77	43.3	30.3	25.8	29.9	23.0	37.6	37.4	20.3
I-37	0.83	0.85	0.82	0.83	44.8	35.4	29.7	34.4	9.0	8.3	7.8	1.8
I-40	0.78	0.81	0.83	0.81	46.7	34.9	33.1	35.9	15.3	38.3	22.4	16.7
I-42	0.81	0.80	0.80	0.80	49.1	33.9	32.3	34.4	28.6	37.3	22.0	4.0
P3902	0.72	0.71	0.69	0.69	32.7	25.1	24.1	25.8	0.0	5.0	0.0	0.5

Table B.4. Means of three traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994.

Entry	Plant height (cm)				Ear height (cm)				Leaf number			
	1993		1994		1993		1994		1993		1994	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-1	268	264	238	271	84	100	77	95	6.2	5.7	6.4	6.2
I-2	248	238	220	242	65	84	52	65	5.7	4.7	5.4	5.1
I-3	239	213	219	244	82	81	68	86	5.4	5.0	5.5	5.0
I-4	230	211	220	240	59	79	60	80	4.6	4.3	5.1	4.5
I-5	258	250	234	253	75	102	66	81	6.0	5.1	5.9	5.7
I-6	269	264	243	271	83	103	66	89	5.4	4.9	5.8	5.4
I-7	255	258	234	276	81	105	70	100	5.3	4.4	5.2	4.9
I-8	246	256	214	233	83	109	74	101	5.4	4.4	5.4	5.1
I-10	266	255	235	265	79	104	73	87	5.1	4.6	5.2	5.4
I-11	282	255	250	281	97	91	78	94	6.3	5.1	5.8	5.4
I-12	229	204	202	228	74	77	57	70	5.3	5.2	5.8	5.8
I-13	254	252	229	262	72	99	64	90	5.6	4.9	5.6	5.4
I-14	247	234	234	253	80	91	72	91	4.7	4.6	4.7	4.9
I-15	-	-	-	-	66	89	67	84	-	-	-	-
I-17	255	268	239	271	86	114	68	101	5.6	4.4	6.4	5.6
I-18	245	208	214	236	69	83	58	72	5.9	5.5	5.6	5.6
I-19	238	227	211	244	74	85	58	78	5.1	5.4	5.6	5.4
I-20	283	261	260	282	94	105	88	108	5.8	4.7	5.6	5.4

Table B.4 (Cont.)

Entry	Plant height (cm)				Ear height (cm)				Leaf number			
	1993		1994		1993		1994		1993		1994	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
1-21	260	256	239	278	75	75	80	101	5.7	5.6	5.4	5.1
1-22	227	206	225	242	62	83	66	87	5.4	4.7	5.5	5.0
1-23	262	248	236	261	81	97	70	78	5.6	5.1	5.9	5.9
1-24	248	226	229	251	73	86	63	70	5.8	4.9	5.8	5.7
1-25	266	258	226	260	78	96	65	90	5.5	5.6	5.3	5.1
1-26	250	232	232	253	77	104	73	89	5.7	4.6	5.5	5.4
1-27	269	257	253	277	79	105	79	85	5.6	4.6	5.7	5.9
1-28	237	230	228	251	65	95	62	83	5.2	4.2	4.9	4.5
1-29	279	251	237	267	93	102	77	96	5.7	4.9	5.3	5.7
1-30	248	244	214	256	72	100	62	92	4.8	4.0	4.6	4.6
1-31	255	232	226	259	73	98	66	87	6.5	4.9	6.6	5.8
1-32	213	205	208	236	66	79	66	85	5.3	4.5	5.5	5.2
1-33	244	248	222	259	77	93	64	85	5.7	5.6	5.8	5.6
1-35	248	251	225	265	76	99	72	86	5.6	5.0	5.5	5.4
1-36	270	268	253	271	74	98	85	92	6.3	5.3	5.6	5.5
1-37	-	-	-	-	81	80	76	75	-	-	-	-
1-40	287	272	253	287	101	121	81	110	5.7	4.9	6.1	5.9
1-42	282	275	252	286	94	113	80	96	6.0	5.7	6.0	5.4
P3902	-	-	-	-	97	121	93	109	-	-	-	-

Table B.5. Means of three traits observed in Ste-Anne-de-Bellevue and Ottawa, in 1993 and 1994.

Entry	Tiller number				Culm diameter (mm)				Shank length (cm)			
	1993		1994		1993		1994		1993		1994	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-1	2.2	1.8	3.1	2.3	18.0	17.5	17.9	18.4	14.0	12.2	15.4	14.6
I-2	2.9	2.6	3.1	2.6	18.2	17.1	17.4	18.6	15.2	12.4	15.1	16.0
I-3	2.4	1.8	3.0	2.3	16.9	16.8	18.3	18.6	8.7	9.0	10.9	11.1
I-4	1.4	1.9	2.7	2.7	16.9	16.6	16.9	18.4	13.8	10.5	13.7	16.1
I-5	1.8	1.9	2.5	2.2	17.4	16.3	17.8	18.5	10.0	10.5	13.8	12.2
I-6	2.7	1.7	2.5	2.0	20.0	18.4	18.6	19.4	10.7	10.2	14.6	11.8
I-7	1.4	2.2	3.2	2.3	17.7	17.8	17.7	17.9	12.3	11.3	15.8	13.4
I-8	1.4	2.0	2.5	2.3	19.4	17.9	17.7	18.7	17.2	14.5	20.1	17.5
I-10	1.9	2.1	2.8	2.4	18.9	18.2	18.2	19.3	15.4	13.6	17.8	16.7
I-11	2.0	1.7	2.5	2.1	17.4	16.9	16.2	17.1	12.4	14.0	14.1	13.5
I-12	0.7	0.9	2.6	2.2	20.1	18.7	20.5	23.9	7.2	7.2	7.9	10.0
I-13	1.6	2.1	2.5	2.5	18.6	18.7	18.7	19.4	14.1	10.8	16.6	13.0
I-14	1.5	2.1	2.6	2.4	17.0	17.5	16.5	17.4	10.8	11.3	12.2	10.1
I-15	1.8	1.8	2.7	1.8	17.4	17.7	17.0	17.0	17.3	13.9	19.0	18.4
I-17	1.5	1.4	2.6	2.1	18.1	17.9	18.9	18.7	8.5	9.6	12.5	11.6
I-18	1.9	2.0	2.7	2.1	15.9	15.2	17.3	16.8	9.7	7.3	9.3	9.0
I-19	1.9	1.9	2.9	2.4	18.4	18.6	18.1	19.1	15.9	13.3	16.5	14.4
I-20	2.7	2.0	3.0	2.7	17.7	17.5	17.5	18.2	10.4	9.0	13.5	12.9

Table B.5 (Cont.)

Entry	Tiller number				Culm diameter (mm)				Shank length (cm)			
	1993		1994		1993		1994		1993		1994	
	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa	Ste-Anne-de Bellevue	Ottawa
I-21	2.5	2.5	2.8	2.6	17.8	18.4	16.7	18.1	11.1	11.8	10.9	14.3
I-22	1.7	1.9	2.6	2.1	16.6	15.8	17.1	17.4	9.1	7.8	9.9	10.7
I-23	1.7	2.0	3.1	2.8	18.9	20.2	18.4	20.2	11.4	14.8	11.3	13.2
I-24	1.6	2.3	2.4	2.6	16.2	16.2	17.3	18.4	9.3	9.8	13.5	15.2
I-25	1.6	2.3	2.7	2.4	18.6	18.2	17.3	19.9	13.5	13.3	16.0	15.0
I-26	2.6	2.5	3.0	2.8	17.6	16.2	16.1	17.9	13.6	11.1	15.7	16.3
I-27	1.9	2.4	3.2	2.5	17.9	18.5	19.1	19.8	13.6	11.1	15.1	15.0
I-28	2.8	1.7	2.8	2.8	17.3	15.4	18.5	18.3	17.1	13.2	17.2	16.7
I-29	2.1	2.3	3.0	2.7	17.8	17.2	17.0	17.3	17.9	15.6	20.3	20.0
I-30	2.1	2.1	2.5	2.7	17.9	17.9	15.9	18.4	11.5	9.9	14.2	12.9
I-31	2.5	2.2	2.6	2.7	19.4	17.2	19.0	20.4	9.4	9.2	9.8	11.0
I-32	1.4	1.7	2.4	2.3	17.0	18.4	19.7	19.7	7.3	7.5	14.8	11.3
I-33	1.8	1.9	2.4	2.0	18.9	18.6	19.6	19.0	13.5	14.8	18.2	15.6
I-35	2.3	2.0	2.8	2.2	19.4	18.9	17.5	19.3	12.7	9.6	12.3	12.2
I-36	2.4	1.9	2.3	1.8	18.8	17.3	16.6	17.8	20.7	14.6	17.4	15.8
I-37	2.2	2.0	2.9	1.5	18.1	19.4	17.5	18.4	10.6	14.3	15.2	14.7
I-40	2.6	1.9	2.3	2.5	20.5	17.4	17.5	18.9	10.5	9.9	13.5	13.0
I-42	2.4	2.3	2.9	2.5	19.4	18.9	18.5	20.7	13.8	10.4	14.9	14.2
P3902	0.03	0.0	1.0	0.1	19.3	17.2	17.5	18.0	25.4	17.1	19.4	17.0