DEVELOPMENT AND DISEASE RESISTANCE OF LEAFY REDUCED STATURE MAIZE (*Zea mays* L.)

Yinghai Deng

Department of Plant science
McGill University, Macdonald Campus
Montreal, Quebec, Canada

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Short Title

DEVELOPMENT AND DISEASE RESISTANCE IN MAIZE

Abstract

Ph.D. **Yinghai Deng** **Plant Science**

Previous studies on Leafy reduced-stature (LRS) maize found that it had extremely early maturity and a higher harvest index (HI), leading to high yields for its maturity rating. Whether this apparent high HI is related to its earliness, or can also exist among the medium or late maturity LRS maize has not been previously investigated. It was also of interest to know if the traits that produced the LRS canopy structure have pleiotropic effects on root architecture. Finally, field observations indicated that LRS maize had a lower incidence of common smut. It is not known whether this apparent resistance is specific to smut or includes other diseases.

Using a wide range of the most recently developed LRS hybrids and some conventional hybrids, a two-year field experiment was conducted to examine the HI and disease resistance of LRS maize. HI, yield, and yield components were compared between the two genotype groups (LRS and conventional) under different population densities. The resistance to the natural incidence of common smut and artificially inoculated *Gibberella* ear rot was also tested. Morphology and fractal dimension analyses of roots at an early development stage were conducted in indoor experiments. These analyses were performed with WinRHIZO (version 3.9), an interactive scanner-based image analysis system.

This work showed that: 1) There was no relationship between the HI and maturity; higher HIs can also exist among the medium and late maturity LRS hybrids. 2) While LRS maize hybrids have the potential for high yield this was not realized in the LRS hybrids used in this work. Further breeding and development of optimum management practices are needed to fully exploit this potential. 3). During early development LRS hybrids generally had more branching and more complex root systems than conventional hybrids. 4) Fractal dimension, as a comprehensive estimation of root complexity, was highly related to major root morphological variables, such as root total length, surface area, branching frequency and dry mass. 5) Of the hybrids tested the greatest resistance to both common smut and *Gibberella* ear rot, two major ear diseases, occurred in some of the LRS types.

Résumé

Des études précédentes sur le maïs feuillu à stature réduite (FSR) ont montré qu'il est hâtif et que son indice de récolte (IR) est élevé, ce qui mène à des rendements élevés pour sa catégorie de maturité. La relation entre l'IR et le temps de maturation du maïs FSR n'a pas encore été étudiée. Les expériences aux champs ont montré que l'incidence du carbone sur ce type de maïs est basse. On ne sait pas si cette résistance est spécifique à cette maladie ou non. Finalement, on était interessé à savoir si les traits qui ont produit l'architecture des parties aériennes sur FSR ont des effets pléotropiques sur l'architecture des racines.

Pendant 2 ans, on a utilisé les hybrides FSR les plus récents et quelques hybrides commerciaux dans une expérience au champ pour étudier l'IR et la résistance aux maladies. On a utilisé différentes densités de population pour comparer l'IR, le rendement et ses composantes des 2 groupes génotypiques (conventionnel et FSR). On a aussi testé la résistance au carbon d'incidence naturelle et inoculé. L'analyse de la morphologie et de la dimension fractale des racines au début du développement de la plante a été faite par le biais d'expériences dans un milieu contrôlé. L'analyse a été faite avec le logiciel interactif d'analyse d'images WinRHIZO (version 3.9).

Ce travail a montré que: 1) il n'y a pas de relation entre l'IR et la maturité. Des IR élevés existent aussi parmi les hybrides FSR à maturité moyenne et tardive. 2) Tandis que les hybrides FSR ont le potentiel de donner des rendements élevés, ceci n'a pas été réalisé par les hybrides utilisés dans mon travail. Un travail d'amélioration génétique et un effort de développement de meilleures pratiques culturales sont nécessaires pour exploiter à fond ce potentiel. 3) Au début du développement, les hybrides FSR avaient un

système racinaire plus complexe et avec plus de branchements que le système des hybrides conventionnels. 4) La dimension fractale, qui donne une estimation de la complexité du système racinaire, était fortement reliée à la longueur totale des racines, leur surface, la fréquence des branchements et la masse sèche. 5) Des hybrides qui étaient evalués, des hybrides FSR étaient plus résistants au charbon et à la pourriture de l'épi causée par *Gibberella* que tous les autres hybrides.

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List of Acronyms

ANOVA	Analysis of variance
CHU	Corn heat units
DW	Dry weight
FN	Fork number
GLM	General linear model
HD	High density
HI	Harvest index
LAI	Leaf area index
LD	Low density
LRS	Leafy reduced stature
NLRS	Non leafy reduced stature
RCBD	Randomly complete block design
SA	Surface area
SAS	Statistic analysis system
TL	Total length
TRSA	Total root surface area

Contributions of Co-authors to Manuscripts for Publication

This thesis is organized in a manuscript-based format, which has been approved by the Faculty of Graduate Studies and Research (see the guidelines below).

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"As an alternative to the traditional thesis format, the dissertation can consist of a collection of papers of which the student is an author or co-author. These papers must have a cohesive, unitary character making them a report of a single program of research. The structure for the manuscript-based thesis must conform to the following:

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2. The thesis must be more than a collection of manuscripts. All components must be integrated into a cohesive unit with a logical progression from one chapter to the next. In order to ensure that the thesis has continuity, connecting texts that provide logical bridges between the different papers are mandatory.
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In general, when co-authored papers are included in a thesis the candidate must have made a substantial contribution to all papers included in the thesis. In addition, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. This statement should appear in a single section entitled "Contributions of Authors" as a preface to the thesis. The supervisor must attest to the accuracy of this statement at the doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to clearly specify the responsibilities of all the authors of the co-authored papers."

Chapters 3-5 of this thesis contain three manuscripts which are intended for publication. All of these papers are co-authored by myself, Dr. D. L. Smith, Dr. T. Paulitz, Dr. L. M. Reid, Dr. R. I. Hamilton, Dr. C. Hamel and Dr. C. Costa. Dr. D.L. Smith is my supervisor. He supervised me throughout the program and provided me the necessary funding. His guidance was present in every aspect from the experiment deployment, to data collection, and writing of the thesis. Dr. T. Paulitz, as one of my supervisory committee members, and he provided invaluable guidance and suggestions on the pathological part of this program. Dr. L. M. Reid co-supervised me in the disease-resistance assessment section and provided critical technical support, pathogen inocula and also reviewed the pathology manuscript. Dr. R. I. Hamilton provided all the necessary LRS hybrids, which made this study possible. Dr. C. Hamel offered her laboratory resources for the root studies and provided numerous key suggestions during the process. Dr. C. Costa made significant contributions to the root analysis work and the data processing associated with it. He also shared his valuable experience with LRS corn hybrids throughout this work.

Chapter 1

General Introduction

1.1. Introduction

Maize (*Zea mays* L.) is the third most important cereal crop, after wheat and rice, in the world. Globally there were over 127 million ha planted with maize, producing 589 million tons of grain, in 1997. The maize kernel finds its way into our life as edible and inedible products, including rubber, plastics, fuel, clothing, food additives and adjuncts, and literally thousands of other forms.

Maize production in Canada is restricted to comparatively small regions, with most of the production occurring in southern Ontario, part of southern Quebec. In addition, there are small pockets of production in the Maritime Provinces, southern Manitoba, southwestern Alberta and coastal British Columbia. This geographical restriction is due to insufficient heat and/or moisture to allow most hybrids to reach maturity. Maize produced in the Maritime Provinces and on the Canadian Praries is normally only for silage. However, grain maize is the third largest crop in Canada, in terms of production (8.9 million tons in 1998) and fifth in terms of seeded area (1.1 million ha in 1998). The total Canadian production of grain maize generally accounts for 1.2% of total world production, ranking 12th in the world. Grain maize is the most widely grown annual crop in both Ontario and Quebec.

The main problem for grain maize production in many areas of Canada is that the growing season is not long enough, i.e. does not contain sufficient thermal-time, for the maturing of maize. The accumulated corn heat units (CHUs) during the growing season in these areas is normally less than 2500, a seasonal minimum generally required to mature grain maize. The development of short-season maize hybrids, without significant loss of yield, is desirable for areas with 2500 CHU or less.

Leafy reduced-stature (LRS) maize hybrids incorporate both Leafy and reduced-stature traits into one genotype. These hybrids are equipped with new characteristics which can potentially help to overcome the short season limitations mentioned above. We have observed an earlier maturity date among the LRS maize but with yields similar to their later maturing commercial counterparts (Modarres *et al.*. 1997b, Begna *et al.*. 1997b). Further analysis revealed that a higher harvest index (HI) and possibly improved disease resistance may underlie at least part of the high yield potential of the very early maturing LRS maize.

While the HI of the early maize was about 0.30 before maize hybrids were widely introduced, through much of this century the reported values have been 0.50 (Snyder and Carlson, 1984). This differs from the small grain cereals, where a substantial portion of the increase in yields over the course of this century has been due to increases in HI (from 0.30 to values of over 0.50) (Gifford *et al.*. 1984, Donald and Hamblin 1976). Most of these increases in HI came from the introduction of short stature varieties along with the corresponding agronomic management. Some newly developed LRS hybrids have HIs of approximately 0.60 (Modarres *et al.*. 1997a,b, Begna *et al.*. 1997a,b). Fully understanding the potential advantages of LRS maize hybrids is of great academic and practical significance to maize breeders and producers. It is also conducive to the expansion of maize production in short season areas.

1.2. Hypotheses

1. The high HI found in some of the early maturing LRS maize hybrids can also be present in medium and later maturity LRS hybrids.
2. Among LRS hybrids, high HI is associated with high grain yield.
3. The increased leaf number and leaf number above the ear caused by the Leafy trait will affect the process of LAI establishment in LRS maize.
4. LRS hybrids have greater general disease resistance than conventional hybrids.
5. The Leafy and reduced-stature traits, already shown to strongly modify maize canopy structure, have pleiotropic effects on root architecture.
6. Fractal dimension, as a measurement of root complexity, has strong relationships with conventional root morphological measurements.

1.3. Objectives

1. To determine if elevated HI is a common phenomenon among LRS maize types, regardless maturity date.
2. To examine the pattern of LAI establishment during the vegetative growth period, in order to determine how this has been changed by incorporation of the Leafy and reduced-stature traits.
3. To test the resistance of LRS maize to common smut and *Gibberella* ear rot.
4. To evaluate the morphological changes that occur during early root development of LRS maize.
5. To apply fractal dimension (FD) analysis to a wide range of LRS and conventional maize hybrids to see if there are differences in FD between the LRS and conventional maize hybrids, and how these changes are related to the morphological changes of maize roots.
6. To determine which of the conventionally measured root variables contribute the most to root fractal dimension.

Chapter 2

Literature review

2.1. Yield components and their relationship to yield

Yield components for maize generally consist of number of ears per unit area, number of grains per ear and individual grain weight. There is plenty of evidence to show that these components are interdependent to some degree; that for example a greater number of ears per hectare is counteracted by a smaller number of grains per ear. If yields of current varieties are to be substantially increased this compensatory mechanism must be suppressed (Evans 1977). No single yield component predominates in determining yield. However, combining ears m^{-2} with grains per ear showed that number of grains per unit field area was correlated with yield (Gallagher and Biscoe 1978). Several studies have demonstrated the use of combining the first two of the components of grain yield to give a single composite component, the number of grains per unit area, which is an expression of the capacity of the crop sink for assimilation after anthesis. The observation that grain yield tends to be more closely related to grains per unit area than to individual grain weight (Willey and Holliday 1971, Gallagher *et al.*. 1975, Gales 1983, Sangoi and Salvador 1997) has led several authors to propose that cereal grain yields are sink-limited and that individual grain weight is the most stable of the three basic yield components.

Responses to variation in population density demonstrate that the grain yield of temperate cereal crops can be buffered against variation over a very wide range of seeding rates, within a given growing season (Kirby 1967, Echarte *et al.* 2000). Increased plant density is always associated with a wide range of changes in rate and pattern of development of cereal plants, which can cause changes in the magnitude of each of the three major components of yield, especially ear population density and ear size, which tend to be mutually compensating (Darwinkel 1980). The primary effect of increasing plant population density is to increase competition between adjacent plants; the resulting shading of plant tissues (alteration of both the quantity and spectral composition of radiation incident upon shaded leaves) has profound influences upon the balance of plant growth regulators, recognized in several investigations as an increase in tissue levels of gibberellins (Kirby and Faris 1970). The overall effects of this are the promotion of leaf sheath and blade extension and the acceleration of all crop development processes. Thus closer spacing of cereal plants is associated with larger and more rapidly-growing leaf canopies, since the individual leaves are larger. However, this effect is relatively short-lived because later leaves are smaller and the senescence of the leaf canopy is also faster (Hay and Walker 1989). Stem extension occurs earlier in the life of the crop, at a lower leaf number and at a lower node (Kirby and Faris 1970), but the stem tends to be weaker, leading to increased incidence of lodging at high seeding rates.

Sowing date has a profound influence on grain yield (Otegui *et al.*. 1995). In principle, delay in sowing beyond a given date results in a progressive reduction in the potential yield of a crop because an increasing proportion of the available solar radiation will not be intercepted by the crop canopy (Green *et al.*. 1985, Knop 1985). The acceleration of the development of late-sown crops means that the duration of stages of development is progressively reduced with increasing delay in sowing. The acceleration in the rate of crop development associated with increased plant population density, or with delay in sowing, means that the duration of the spikelet initiation phase is reduced. In the case of population density, the rate of spikelet initiation is relatively unaffected, with the result that ear size declines progressively with increasing seeding rate. The number of leaves per stem declines because the length of the period of leaf initiation decreases. In contrast, variation in sowing date is commonly found to have a negligible influence upon the number of grains per ear (Kirby 1969, Harris 1984). Generally, these modest effects tend to lend support to the proposal that the individual grain weight for a given genotype is a relatively stable character (Gallagher *et al.*. 1975). However, when a delay in the start of grain-filling by a few days coincides with a rapid deterioration in the environment at the end of the season, much larger effects can be anticipated.

The fundamental difference between individual crops in sowing date experiments is that, during the early stages of growth, at least, plant development proceeds under different photoperiods and temperatures (Otegui *et al.*. 1995). Variation in each of these environmental factors can have a profound influence on development and, although considerable progress has been made, it is not yet possible to present a detailed interpretation of their interactions with one another and with other environmental factors. An alternative to the sowing date experiment is to grow cereal crops at different latitudes, but otherwise under identical management. In this way, the crop will be subject to different daylengths from emergence, although differences in temperature and other variables, such as rainfall, disease incidence, etc., will depend upon the size of the difference in latitude as well as the particular pattern of weather during the test season. However, most of the differences between the crops could be explained in terms of temperature alone and it was not possible to identify any specific influence of the rather modest differences in daylength (Ellis and Kirby 1980). Normally it can be concluded that, within limits, the longer the period available for crop development (early sowing, higher latitudes, cool temperature, adequate water supply) and therefore, for the interception of solar radiation, the higher will be the potential yield.

One problem should be noted with respect to the effect of temperature on yield that relates to development rate, and that is, the temperature optimum for development is not the optimum for high grain yields. It has been fairly well established that the longer the grain filling period the higher the grain yields provided a frost doesn't kill the plant before the kernels are filled. Results from phenological studies (Wilson *et al.*. 1973, Stewart *et al.*. 1998) indicate that cool growing seasons help to prolong the subperiods of development, so that cool growing seasons boost yields, particularly when a killing frost doesn't present a hazard. The ideal growing seasons for maize in temperate latitudes are those that are warmer than normal in the spring and early summer, and early fall with a late killing frost date in the fall.

2.2. Leaf area index and Leafy reduced-stature maize

2.2.1. Leaf area index and radiation interception

Williams *et al.*. (1968) reported that photosynthetic efficiency and growth were strongly related to the effect of canopy architecture on vertical distribution of light within the maize canopy. Radiation is transmitted through and between leaves, and its flux density and spectral composition change rapidly with canopy depth (Gardner *et al.*. 1985, Maddonni and Otegui 1996). Canopy light interception and photosynthesis are closely related to leaf area index (LAI) up to a 'critical' LAI, i.e. that required to intercept 95% of the incident irradiance (Pearce *et al.*. 1965). Maize yields have been improved by increasing radiation interception through early planting (Pendleton and Egli 1969), tassel removal (Hunter *et al.*. 1969), reflective surfaces placed between the rows (Schoper *et al.*. 1982), and artificial lighting (Graham *et al.*. 1972).

The development of plant leaf area depends primarily upon four environmental factors:

1. Temperature: affects rate of leaf production, rate and duration of leaf expansion;
2. Nitrogen status: affects leaf size and longevity;
3. Population density: affects early season crop leaf area (e.g. low in widely-spaced crops), competition effects (leaf shading);
4. Water supply: affects leaf size and longevity (less important in many temperate and irrigated areas).

The seasonal patterns of LAI in annual crops were well illustrated by Watson (1947). In cereal crops, leaf growth was depressed by low temperatures during the early growth phases. Sowing date can have a profound influence upon the course of LAI development. In addition, nitrogen fertilizer, harvest date, pests, diseases and environmental stresses are all factors that can act to influence the magnitude or duration of LAI (Radley 1963, Stone *et al.*. 1999). It is important for a crop to be grown in such a way that the annual cycle of LAI matches the seasonal variation in incident solar radiation. If they do not match, potential yield will be lost as a consequence of unintercepted radiation or wasteful investment of dry matter in excessively large leaf canopies during periods of low irradiance (Filter and Hay 1987). It has been found that an LAI of at least 3 is generally required for the interception of 90-95 percent of incoming radiation (Hipps *et al.*. 1983). The concept of optimum leaf area index (L_{opt}) means photosynthesis achieves its maximum value under the prevailing conditions; below L_{opt} growth rate would be dependent upon LAI and would be depressed owing to incomplete interception of the available solar radiation, whereas above $L_{opt,}$ efficiency of photosynthesis would be depressed due to increased respiratory losses (lowered net assimilation rate) (Brown and Blaser 1968).

Leaf area per unit area can be improved in two ways: breeding for increased leaf area per plant and increasing plant density. Increasing plant densities has been investigated as a way of maximizing interception of incoming solar energy in maize canopy (Duncan *et al.*. 1967, Loomis *et al.*. 1967, Duncan 1969, Winter and Ohlrogge 1973, Pepper 1974, Fuenzalida *et al.*. 1999). Increasing plant population density also increases LAI and light capture in the upper canopy, particularly at the ear level, perhaps an advantage in the source-sink relationship (Tetio-Kagho and Gardner 1988a). Dewit (1967) showed that crop canopies convert only 5% of incident solar energy into chemical energy during the crop growing season. Pepper (1974) reported that increased plant densities can promote utilization of solar radiation by maize canopies. The concentration of healthy leaf area at the ear level may explain the responsiveness of maize to increasing plant population density. However efficiency of conversion of intercepted solar radiation into economic maize yields will decrease with high population densities because of mutual shading of plants (Buren 1970). In general, photosynthesis increases until nearly all incident solar radiation is intercepted by photosynthetic surfaces, and any further increase in leaf area only increases shading of the lower leaves with little benefit to the plant (Gardner *et al.*. 1985). Olson and Sander (1988) indicated that higher plant densities are required in more northern areas, in part because the earlier hybrids are smaller with lower leaf areas.

Increased density causes plant stems to become thinner, weaker, and often taller (Duncan 1958, Bleasdale 1967, Willey and Heath 1970, Gardner *et al.*. 1985, Inoue *et al.*.

2000). Thus, strong-stemmed cultivars are required or plant density has to be decreased to reduce lodging. Lodging can increase several-fold with high densities and may result in very high harvest losses that more than negate any yield increase that may have occurred with the higher plant density (Olson and Sander 1988). Lodging also decreases harvestable yield by putting the seeds too close to the ground for equipment to harvest them and decreases absolute yield by degrading leaf display.

2.2.2. Role of the Leafy (*Lfy1*) and reduced-stature (*rd1*) traits in maize

The dominant *Lfy1* trait was first discovered by Robert C. Muirhead, Hughes Hybrid Inc., in 1971 (Shaver 1983). Plants with the *Lfy1* trait have increased numbers of leaves above the ear. Two extra nodes and leaves are produced below the ear placement node. Five or more extra nodes and leaves are produced above the ear node. Expression is somewhat modified by genetic background (Shaver 1983, Troyer 1990, Dronavalli 1992). The action of *Lfy1* can easily double leaf area production, especially for the portion above the ear (Shaver 1983). As a result more photosynthate can be produced and readily deposited into the ear (Eastin 1969). It has been estimated that the successful rate of conversion of existing inbred lines into the *Lfy1* state was only twenty percent, due to the extreme expression of Leafy and the delay of flowering and maturity after the conversion (Shaver 1983). The excessive LAI may have a negative effect on yield (Borojevic and Williams 1982). Conversion of early conventional inbreds into Leafy counterparts is more likely successful because the earliness can offset the *Lfy1*'s negative effect on flowering and maturity.

Leafy genotypes have high yield potential as the increased leaf area above the ear imparted by the *Lfy1* trait contributes more to grain filling than lower leaves (Dwyer and

Stewart 1986). The use of higher populations to increase the leaf area of a canopy may have negative effects on grain yield due to the increase of shading among the lower leaves, which can substantially decrease the productivity of these leaves (Stoskopf 1985, Ottman and Welch 1989). *Lfy1* also increases prolificacy, which in turn increases yield stability due to the greater capacity to reduce the number of barren plants under high population densities or stressful environmental condations (Collins *et al.*. 1965, Hanway and Russell 1969, Prior and Russell 1975, Brotslaw *et al.*. 1988).

The mutant reduced-stature (rdl) gene is recessive, and was first discovered by Nelson and Ohlrogge in 1957 (Coe *et al.*. 1988). Plants bearing the rd1 gene are characterized by short stature with good stalk strength (Daynard and Tollenaar 1983). The potential benefits from the reduced-stature trait also include reduced lodging due to insect and wind damage (Hohenadel 1984), greater tolerance of high population density (Nelson and Ohlrogge 1957, 1961), greater allocation of photosynthate to the grain (Stoskopf 1985) and rapid grain dry-down. The reduced plant size requires less energy and time to complete its development.

2.2.3. Leafy reduced-stature maize

Leafy reduced-stature (LRS) maize genotypes were developed through a collaboration between McGill University's Macdonald Campus and Agriculture and Agri-Food Canada in Ottawa (Begna *et al.*. 1997a,b, Modarres *et al.*. 1997a,b). This work was conducted in two stages. During the first stage the collaborators simply brought the traits together, identified promising inbreds, made crosses and identified good hybrids. The material showed the more rapid leaf development they had hoped for, but also showed more extensive root system development. This led to the second phase of research, in which they investigated production methods and environmental responses of LRS hybrids. They have now shown (Costa, unpublished data) that LRS hybrids are better at extracting soil N, and therefore have higher nitrogen use efficiencies, than conventional hybrids. They have also shown that because of their more rapid leaf production LRS hybrids compete better with weeds than conventional types (Begna *et al.*. 1997b). During the course of the agronomic and environmental work they noted that these hybrids have higher HI than conventional types, which probably explains their unusually high yields, given their early maturities. They also noted that these hybrids seemed to be resistant to smut. The present work seeks to explore the reasons for the high HI, and to determine the extent and utility of the apparent disease-resistance.

The goal in the development of the LRS maize types was to produce maize hybrids that would be more reliable under short season conditions. Maize grown in short-season areas has less leaf area, because it produces fewer and smaller leaves; as a result it has lower yield potential than maize grown in longer season areas. The maximum leaf area indices (LAIs) of maize in short-season areas with normal plant population densities are low, between 2.0 and 2.7; at these LAIs, a maize canopy intercepts only 75% of full sunlight (Hunter 1980, 1977). Grain yield in maize is related to leaf area index and hence canopy structure (Williams *et al.*. 1968). Plants bearing the Leafy trait are characterized by extra leaves above the ear, low ear placement, highly lignified stalk and leaf parts, relatively early maturity for the leaf area developed and high yield potential (Shaver 1983). The semi-reduced-stature, compact (ctl) and reduced-stature (rd) mutants have been shown to be more resistant to population stresses than noncompact and normal-stature hybrids (Nelson and Ohlrogge 1957). As predicted by Buren *et al.*. (1974), these maize types are density tolerant, being characterized by rapid first appearance of ear silk and completion of silk extrusion, rapid growth of the first ear and prolificacy, reduced tassel size, and efficient production of grain per unit leaf area. In addition, the rd1 types have harvest indices slightly higher than conventional types. The newly developed (Modarres *et al.* 1997b) LRS hybrids have harvest indices as high as 0.60 (Modarres *et al.* 1997a,b, Begna *et al.* 1997a,b).

When the original LRS types were developed they were targeted for short season areas. They included three traits: Leafy, reduced-stature and early maturity (Lethbridge gene pool) (Modarres *et al.* 1997a,b). The observed increase in HI (Modarres *et al.* 1997a,b, Begna *et al.* 1997a,b) may be due to the combination of all three of these, or to any two. The combination of Leafy and reduced-stature is most likely responsible, as it is these traits that substantially change the overall shape of the plants, however, this was untested prior to the work in this thesis. A 10% increase in HI means a 20% increase in yield, as long as the total biomass production remains the same.

2.3. Harvest Index

It was not until the early 1960's in Australia that Donald (1962, 1968) first coined the term 'harvest index' for the ratio of grain yield to biological yield or biomass, in his case as applied to wheat. During the following 15 years, HI was mainly employed by Australian scientists. After that, the term HI became more widespread among agronomists and plant breeders. It is now common in the plant science literature.

Donald (1962) first defined HI as the economic grain yield of a wheat crop expressed as a decimal fraction of total above-ground biological yield. Now we use this definition for most crops and especially for the grain crops. The concept of harvest index can also be extended, with varying degrees of success, to a wide range of seed, tuber, fruit and stem crops. It has also been used to quantify the economic yield of primary and secondary metabolic products, and even the partitioning of nutrients, for example the nitrogen harvest index of seed crops.

2.3.1. HI and yield

HI is correlated positively with grain yield and negatively with biological yield in barley (Singh and Stoskopf 1971), oat (Singh and Stoskopf 1971, Takeda *et al.* 1980), rye (Singh and Stoskopf 1971), wheat (Singh and Stoskopf 1971, Luthra *et al.* 1979), soybean (Schapaugh and Wilcox 1980), pigeon pea and mung bean (Singh *et al.* 1980). Thus selecting for higher HIs should increase yield in most cases, and particularly when biological yield is relatively stable.

Several major crops (wheat, barley and rice) have undergone considerable improvement in terms of HI, though the mechanism may be varied. However, maize may be unique among major world crops in that the HI of many commercial genotypes was already quite high in the first decades of this century. While the HI of the earliest maize types was about 30%, through much of this century the reported values have been 50% (Snyder and Carlson 1984). This differs from the small grain cereals, where a substantial portion of the increase in yields over the course of the last 50 years has been due to increases in harvest index (from 30% to values of over 50%) (Donald and Hamblin 1976, Gifford *et al.* 1984). However, the newly developed LRS hybrids (Modarres *et al.* 1997b) have HIs of up to 60% (Modarres *et al.* 1997a,b, Begna *et al.* 1997a,b).

In North America, selection of maize hybrids adapted to intensive cultivation (high population density, high soil fertility, pest and disease control) has resulted in very substantial increases in grain yield potential, mainly caused by increased biomass production rather than increased HI, which has remained relatively stable. However, since selection has largely been for tolerance of high density, the maintenance of high HI has been an implicit breeding objective. Since the number of ears per plant has not varied significantly over this period, the absolute increase in grain yield potential is a result of increased individual grain weight coupled with more modest increases in ear dimensions. As with other crops, the HIs of maize crops are susceptible to severe stress.

2.3.2. The importance of harvest index

The high grain yield and harvest indices in the shorter, modern small grain varieties have come at the expense of stem weight per unit area: the investment of assimilate in leaf production was similar among varieties (Sayre *et al.* 1997). The reduction in competition that would presumably be a consequence of reduced stem weight and height, would therefore allow less restricted development of the ear (Miralles and Slafer 1995). The way in which this apparent relief of source limitation is expressed differs among the varieties. In some cases this may be due to their ability to produce more ears m^{-2}, whereas in others it may be by having larger ears and heavier grains. In winter wheat there is some consistency in varieties possessing the Norin 10 dwarfing gene Gai/Rht2 (for gibberellic acid insensitivity and reduced height), which have more grains per ear than the taller varieties (gai/rht2). Brooking and Kirby (1981) confirmed this characteristic and showed that it was due not to any difference in numbers of spikelets and floret promordia initiated, but to improved floret survival (Fischer and Stockman 1980). This was associated with the partitioning of a greater proportion of total biomass to the ear of Gai/Rht2 lines compared with gai/rht2 lines. There was a direct relationship between the dry weight of the ear at anthesis and the number of grains per ear at maturity.

However, this increased partitioning of dry matter to the ear and the resultant higher HI, was associated not with reduced stem height and weight, but with the possession of the Gai/Rht2 gene. This was confirmed by the comparison of two genotypes, ST (gai/rht2) and TD (Gai/Rht1), which have identical stem weight and similar heights, though the mechanism of this is unclear.

Austin *et al.* (1980) calculated that a reduction in stem and leaf sheath dry matter to half the then current average values and a reallocation of this dry matter to the ear could raise the HI from about 0.5 to 0.62, assuming a constant biomass yield. The problem is whether such a dramatic change is possible or even desirable in view of the stem's role in supporting the ear and maintaining an effective display of leaves for light interception.

Harvest index increased steadily with reduction in plant height (Johnson *et al.* 1986, Edmeades and Lafitte 1993). Under high density stress, the ears of shorter maize cultivars have an enhanced capacity to attract assimilates during flowering and grain filling (Edmeades and Lafitte 1993). The increase in HI (and grain yield) associated with reduced plant height was related to the ability of the plant to allocate a smaller proportion of total dry matter at silking to stem and sheath, and a greater proportion to floret and kernel development, and also increased population tolerance, and decreased barrenness. Leaf area is a major determinant of total accumulation and the quantity of photosynthate available for economic yield (Snyder and Carlson 1984). The genetic control of physiological aspects of leaf area accretion and leaf area duration have not been investigated adequately in most crops.

Considerable additional information on physiological mechanisms that control growth and ultimate size of the individual plant and its potential for economic yield are required for more rapid progress in increasing crop yields. More information is needed regarding the role of specific genes and heritability of morphological and physiological traits, to help breeders operate more efficiently.

2.3.3. Height reduction and its effect on yield and harvest index of maize

Height reductions are achieved by a shortening of each internode. Since a leaf sheath with a leaf blade arises from each internode, reduced-stature plants can have almost the same number of leaves as their tall counterparts and so also have about the same photosynthetic area. Therefore the old tall cultivars and new shorter cultivars do not differ much in the photosynthetic area per plant and their LAIs, i.e., in their source capacity (Borojevic 1990). As a result of changed partitioning within the shoot, assimilates saved by stem reduction are translocated to ear development, resulting most frequently in increased grain setting (Evans 1984). Brooking and Kirby (1981) and Thorne (1982) reported that several short stalked varieties develop heavier ears at anthesis than do those of comparable tall varieties. According to Evans (1981) a key to increased yield potential lies in the greater ability of the differentiating ear to compete with other organs for assimilates. This competition is influenced by the relative sizes of the competing organs, by their relative distance from the source of photosynthate, and by the relative directness and capacity of their vascular connections to it.

2.4. Root morphology and fractal dimension

Root morphology can be described by its diameter, length, root to shoot ratio, branching frequency, surface area, weight and root hair density (Schenk and Barber 1979). Root characteristics such as length, diameter, surface area and mass have been used to describe root systems and estimate their function and size (Murphy and Smucker

1995, Raper *et al.* 1978). Root morphology is influenced by both environmental conditions and genetic factors during its development (Lungley 1973). An improved understanding of root morphological characteristics would be useful to predict the nutrient and water uptake ability and later development of the root. For example, root length, surface area and nutrient concentration in the soil solution are closely related to the amount of nutrients accumulated by a growing plant (Raper *et al.* 1978). The density of rooting within the volume of soil explored by a root system is more important than the length alone (Coutts 1986). In some cases estimates of root length per volume of soil can be used as an indirect parameter in quantifying water and solute uptake (Cowan 1965, Brewster and Tinker 1970).

However, collecting data on root variables has proven to be tedious and somewhat inaccurate (Zoon and van Tienderen 1990). Recently, computer-aided image analysis systems have revolutionized the characterization of root systems (Tagliavini *et al.* 1993, Kaspar and Ewing 1997). Video camera-based image systems (Ottman and Timm 1984, Cunningham *et al.* 1989) and optical scanner-based image systems (Arsenault *et al.* 1995, Kaspar and Ewing 1997) have been developed. The use of these systems has greatly reduced the labor input and increased accuracy for root measurement.

The fractal concept, introduced by Benoit Mandelbrot (1983), designates a rough or fragmented geometric that can be subdivided into parts, each of which is, at least approximately, a reduced-size copy of the whole. Contrary to classical geometry, fractals have provided a new approach for quantifying the geometry of complex or noisy shapes and objects (Mandelbrot 1983, Forutan-Pour *et al.* 1999a), such as soil (Burrough 1981, Peyton *et al.* 1994, Huang 1998, Castrignano and Stellutiu 1999, Oleschko *et al.* 2000, Anderson *et al.* 2000), the branching patterns of fungi (Ritz and Crawford 1990, Jones *et* *al.* 1993); the morphology of root systems (Eghball and Maranville 1993, Spek and Van Noordwijk 1997, Nielsen *et al.* 1997, 1998/1999, Ketipearachchi and Tatsumi 2000, Ozier-Lafontaine *et al.* 1999), shoot systems and canopies of young tree plantations (Morse *et al.* 1985), crop canopy structure (Foroutan-Pour *et al.* 1999b, 2000) and form complexity in plant development (Corbit and Garbary 1995, Critten 1997).

Three categories of methods (Carr and Benzer 1991, Mandelbrot 1983) have been developed to cope with different demands of fractal dimension estimations. The semivarigram and spectral analysis categories are applicable in the estimation of fractal dimension for stochastic fractals, and indicate the similarity of the feature under study to noise. The compass is mainly used to estimate the complexity of shape (Mandelbrot 1983). The box counting method is one type of the compass estimation method. It is the method of preference when dealing with the fractal estimation of concrete physical structures or shapes (Peitgen *et al.* 1992). In this method, each image is covered by a sequence of grids made of squares of descending sizes. For each grid, two values are recorded: the number of squares intersected by the image, N(s), and the side length of squares, s. The regression slope (D) of the straight line formed by plotting log[N(s)] against log(1/s) indicates the degree of complexity, or fractal dimension, which ranges between 1 and 2 ($1 \leq D \leq 2$) (Mandelbrot and Maranville 1983). The linear regression equation used to estimate fractal dimension is: $\log[N(s)] = \log(k) + D\log(1/s)$, where k is a constant and N(s) is proportional to $(1/s)^D$ (Mandelbrot, 1983).

Plant root systems are amenable to fractal description (Tatsumi *et al.* 1989). The fractal dimension of a root is a function of root branching pattern, the proportion of coarse/fine roots and the total length. Changes in any of these components would affect fractal dimension measurement. Fractal dimension could serve to characterize, both quantitatively and qualitatively, the morphology of developing roots (Eghball 1993). It is also helpful in interpreting other root morphological measurements. The fractal dimensions of several crop roots have been shown to fall between 1.48 and 1.58 (Tatsumi *et al.* 1989).

2.5. Ear rot of maize and common smut

The most important disease of maize in Quebec and other parts of eastern Canada is *Fusarium* ear rot caused by *Gibberella zeae* (Schwein) Petch, the sexual stage of *Fusarium graminearum* Schwabe (Sutton 1982). Epidemics of this disease occur every few years, when the environmental conditions are favorable. This disease is characterized by an ear rot that usually starts from the tip, but may also originate from the base of the ear. Pinkish-white mycelium or mold is present on the colonized grains. This same fungus also causes head blights of numerous small grains, including wheat, barley, and oat. *Fusarium graminearum* Type II, present in eastern Canada, readily forms the sexual stage with fruiting bodies called perithecia. This fungus overwinters in crop debris of maize or wheat. The following spring, ascospores produced in the perithecia are ejected, and infect the ear through the silks. Infection can also occur through wounds caused by insects such as the European earworm, or bird damage. The asexual macroconidia may also serve as inoculum.

The main concern about this disease is the production of mycotoxins in the grain and their impact on livestock (Miller and Trenholm 1994). The fungus produces two important mycotoxins-zearalenone and deoxynivalenol (DON or vomitoxin) (Reid *et al.* 1996a). Zearalenone is an estrogen-like compound that causes reproductive disorders in swine (Mirocha and Christenson 1974, Harris *et al.* 1999). The trichothecene DON causes feeding refusal in swine along with decreased weight gains.

At present, there are no effective means of control for this disease. The most feasible from an economic standpoint would be plant resistance. Most of the present maize cultivars do not have much resistance, and work at the Eastern Canada Cereals and Oilseeds Research Center in Ottawa is presently directed at breeding for lines with increased resistance. Standard inoculation techniques and a disease rating system have been developed (Reid 1996 a,b,c).

Common smut is caused by *Ustilago zeae* (Beckm.) or *U. maydis* (DC.). Head smut is caused by the fungus *Sphacelotheca reiliana* (Kuhn) or *Sporisorium holci-sorghi* (Rivolta). The fungus *U. maydis* is a soil-borne organism that infects the meristems of maize. This means that the base of internodes, the base and midrib of leaves, and young ears are particularly susceptible to infection.

The major entrance points of *U. maydis* are maize stigmas (silks) (Snetselaar 1993). The smut fungus *Ustilago maydis* [*U. zeae*] needs the host maize plant for completion of its sexual life cycle (Kahmann *et al.* 1999). Artificial inoculation with *U. maydis* showed that successful infection needs co-presentation of sporidia with compatible alleles at both mating loci (a and b). The infection started after the sporidia mated in pairs through a conjugation tube. Sporidia incompatible at a or b resulted in either slowly growing hyphae or no mating at all (Snetselaar and Mims 1993).

Maize inbreds may differ sharply with respect to resistance to smut (Garber and Hoover 1928). The greatest reduction in yield, owing to smut, among maize plants of the same genotype was brought about by barrenness of the host induced by the fungus. This yield reduction ranged from 7-94% (Jorgenson 1929). At the same time, galls of common smut, caused by *U. maydis* on ears of maize are an edible delicacy known as cuitlacoche in Mexico (Pataky 1991). Inoculation is needed for commercially producing cuitlacoche. Certain fields and cultivars are known to be particularly suitable for maize smut production, and early season drought seems to predispose plants to infection.

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Preface to Chapter 3

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For most cereal crops, increase in HI has been a major contributor to increased yields during the last half century. However, this has not been the case for maize. Recent studies showed that very short season LRS maize had both high harvest index and, for its time to maturity, high yields. In this chapter, the relationships between harvest index and yield, and yield components were investigated in LRS hybrids with a wide range of maturities, in order to determine whether this attribute could be present in maize genotypes of later maturity. The possible contributions to high harvest index and the implications of high harvest index are discussed also.

Previous studies have shown that LRS maize develops faster at the early stages, and has more leaves, especially above the ear. However, no detailed information has been available regarding how these changes were realized and how these changes affect the leaf area development and leaf area present at the different stages of maize development. In this chapter, the total leaf number and the resulting LAI among a wide range of LRS and conventional maize hybrids were examined at several stages between the V3 and silking stages. The comparisons help to characterize genetic differences between the LRS maize and conventional maize hybrids.

Chapter 3

Harvest index and leaf area development in LRS and conventional maize hybrids

3.1. Abstract

Important contributions to the yield potential of the maize crop are the development of leaf area to intercept light, and the final distribution of accumulated biomass between grain and other structures (harvest index; HI). The harvest indices of major crops [e.g., wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and rice (*Oryza sativa*)] underwent considerable increases during the second half of the 20th century. However, this did not occur for maize (*Zea mays* L.). Recently developed Leafy reduced-stature (LRS) maize hybrids have significant changes in plant height and canopy structure and have potential for production in short growing season areas, and also have shown differences in leaf area distribution and higher His, that did not compromise their yield ability. A two-year (1998 and 1999) study with 6 LRS, 1 non-Leafy reduced stature and 3 conventional maize hybrids was conducted. The propensity for high harvest indices in LRS maize hybrids was confirmed, although it was not found in all LRS hybrids. Data from the non-Leafy reduced-stature maize hybrid showed that the reduced-stature trait is the major reason for the higher HIs, however, this hybrid had very low yields. With the combination of both Leafy and reduced-stature traits in one hybrid, it may be possible to have higher harvest indices without sacrificing grain yields. The dynamic changes of LAI, as well as the vertical distribution of the leaf area for LRS maize, during the growing season, were different from those of conventional maize hybrids. The increased leaf number of LRS maize in the vicinity of the ear made LRS maize's above-ear LAI close to that of most commercial hybrids. In addition, the compact size of LRS plants allows higher optimum population densities. Both of these provide effective ways to increase the LAI of maize crops cultivated in short season areas. Our data showed that the more rapid early development and subsequent longer canopy persistence in the later stages of growth were among the main factors contributing to the high HI. Correlation analyses showed that HI was not related to early maturity in LRS hybrids, so that this trait could be introduced into maize hybrids suitable for growth in a wide range of maize production areas.

Key words: Crop canopy, harvest index, Maize (*Zea mays* L.), Leaf area index (LAI), Leafy reduced-stature (LRS) maize.

3.2. Introduction

Donald (1962) first defined HI as the economic grain yield of a wheat crop expressed as a decimal fraction of total above ground biological yield. The concept has since been extended to a wide range of seed, tuber, fruit and stem crops. Harvest index correlates positively with grain yield and negatively with biological yield in such diverse crops as barley (Singh and Stoskopf 1971), oat (Singh and Stoskopf 1971), rye (Singh and Stoskopf 1971), wheat (Singh and Stoskopf 1971, Chaudhary *et al.* 1978), soybean (Schapaugh and Wilcox 1980), pigeon pea and mungbean (Singh *et al.* 1980). Thus selecting for higher harvest indices should increase yield in most cases, particularly when biological yield is relatively stable, as has been seen for most small grain cereal crops.

For maize, throughout much of the last century, the reported harvest index values have changed little, remaining steady at around 0.50 (Snyder and Carlson 1984, Hay 1995), although the harvest index of the earliest maize types was about 0.30. Thus maize differs from the small grain cereals, where a substantial portion of the increase in yields over the last 50 years has been due to increases in harvest index (from 0.30 to values of over 0.50) (Donald and Hamblin 1976, Gifford *et al.* 1984). Most of these increases in harvest index came from the introduction of short stature varieties along with appropriate agronomic management. This has not been applicable to maize due to its large leaves that counter-productively shade each other (Robert *et al.* 1989). Leafy reduced-stature maize hybrids, jointly developed by McGill University's Macdonald Campus and the Eastern Cereal and Oilseed Research Center, Agriculture and Agri-Food Canada, were intended to improve maize production in short season areas of Canada (Dijak *et al.* 1999). The main phenotypic characteristics of LRS maize hybrids are their short statures and unique canopy structures. In LRS hybrids new characters, such as extra leaves above the ear and quick drying of lower leaves when they have completed their roles during the process of early development make them better adapted to short season areas. Some of the newly developed Leafy reduced-stature hybrids were found to have harvest indices as high as 0.60 (Begna *et al.* 1997a,b, Modarres *et al.* 1997a,b).

The main problem for grain maize production in short growing season areas is insufficient heat units for the maturing of maize (Brown 1981). Therefore, the development of extremely early maturity maize hybrids without significant loss of yield is desirable for these areas. Leafy reduced-stature (LRS) maize incorporates both Leafy and reduced-stature traits into one hybrid and is thus equipped with new characteristics potentially helping to meet the needs described above. In addition, LRS maize has been found to mature earlier than most short-season hybrids, but to have yields similar to their later maturing conventional counterparts (Modarres et al 1997b). A higher HI was also found to be associated with the very early LRS maize (Modarres et al 1997b). In this study, LRS hybrids with different thermal-time requirements for maturity were compared with elite conventional hybrids in terms of final HI and yield.

Leaf area index (LAI), i.e. the leaf area per unit land area, is a major determinant of light interception and transpiration (Fortin *et al.* 1994). A LAI value of at least 3 is normally required for the interception of 90-95% of the photosynthetically active radiation (PAR) falling on a crop (Hipps *et al.* 1983), although the specific value varies among crop species and varieties. It is also important to know how leaf area is vertically distributed within a canopy. The ideal type of maize (*Zea mays* L.) was defined as one with erectophile leaves above the ear and plagiophile leaves below the ear, to intercept deeply-penetrating solar radiation (Mock and Pearce 1975). Some early experiments indicated that leaf angles are not necessarily a concern for maize, because it is a C_4 plant with a high photo-saturation point (Trenbath and Angus 1975, Dai *et al.* 1993). Borojevic and Williams (1982) reported that excessive LAI may have a negative effect on yield, since it could upset the balance between vegetative and reproductive growth, in addition to making the heavily-shaded lower leaves "hungry" to the point of being net sinks instead of sources.

Maize grown in short-season areas has less leaf area, because it produces fewer and smaller leaves; this contributes to its lower yield potential than that of maize grown in longer season areas. The maximum leaf area indices (LAImax) of maize in short-season areas with normal plant population densities are low, between 2.0 and 2.7. At these LAIs, a maize canopy intercepts only 75% of full sunlight (Hunter 1977, 1980). Grain yield in maize is related to LAI and hence canopy structure (Williams *et al.* 1968, Andrews *et al.* 2000).

Increasing the population density and increasing the total leaf area of individual plants are two practices used to improve LAI. Caution should be exercised when applying greater population densities to maize to increase the LAI because the benefits of the increased LAI in the upper canopy can cause heavy shading of lower leaves and lodging (Buren 1970, Gardner *et al.* 1985, Andrade *et al.* 1993).

Breeding for increased leaf area per plant is another way to increase the total LAI. Given that leaf number and days to silking have been shown to be positively correlated (Chase and Nanda 1967, Cross and Zuber 1973, Seka and Cross 1995), this strategy may not be suitable for short season areas like Canada as it may shorten the grain filling period. Leafy reduced-stature (LRS) maize is characterized by possession of extra leaves above the ear, a stiff reduced stalk and early maturity (Shaver 1983, Coe *et al.* 1988). It was developed to enhance maize production in short growing season areas (Modarres *et al.* 1997a,b). The potential negative effects of increased leaf number were effectively reduced by careful selection.

The objectives of this study were to determine 1) the dynamic changes of LAI and the leaf expansion rate prior to the silking stage for conventional and LRS maize hybrids, 2) the factors contributing to the LAI advantage of LRS maize hybrids, and 3) whether or not the higher HIs observed in a small number of early maturing LRS hybrids would also be present in hybrids with later maturities. If the latter were true this higher HI could be transferred to a wide range of maize hybrids.

3.3. Materials and Methods

Three conventional hybrids, 6 LRS hybrids, and one NLRS hybrid with a range of maturity dates were chosen for inclusion in the 1998 and 1999 experiments (Table3.1). Both experiments were conducted on a Chicot light sandy loam (mixed, frigid Typic Hapludalf) soil at the E. A. Lods Agronomy Research Centre of the Macdonald Campus of McGill University, Ste Anne de Bellevue, Quebec, Canada (45° 26' N latitude). The planting dates were May 25 in 1998 and May 28 in 1999.

Local climate information was collected from the nearby (15 km) Environment Canada meteorological station (Dorval, Quebec) during the two growth seasons and has been summarized in Table3. 2. Both 1998 and 1999 were unusually warm years, which is generally good for maize growth in this area. Overall, 1998 was warmer than 1999.

The treatments (hybrids) were arranged in a randomized complete block design (RCBD) with 3 blocks. Each block consisted of two sets of the 10 hybrids with two different population densities: 75000 plants ha^{-1} and 125000 plants ha^{-1} in 1998, and 75000 plants ha^{-1} and 96000 plants ha^{-1} in 1999. The high population level was decreased in 1999 as the 1998 work showed it to be too high for all maize hybrid types; at the highest population density in 1998 some of the plants were barren, even in LRS plots. Each plot consisted of 8 rows, 6 m long and 0.75 m wide. All the seeds were hand-planted with the aid of marked strings, to control the within row spacing. In each year 475 kg ha^{-1} of 32-0-18 (N : P_2O_5 : K_2O) compound fertilizer were applied before planting, as recommended by a soil test. Complete hand weeding was carried out three times between seeding and tasseling, and as needed afterward. During the final harvest, 2 m from each of the two centrally located rows of each plot were sampled. Data on harvest index, yield and yield components were collected from this material. The traits measured were kernel rows per ear, kernels per row, 100-kernel weight, ear diameter, ear length, and HI.

Five typical plants in the center of each plot were selected for non-destructive measurement of leaf area and leaf development rates. The individual leaf area was calculated from the following formula: leaf area (La) = leaf length (Ll) x leaf width (Lw) x 0.75 (Montgomery 1991). LAI was measured at the V3, V6, V9, and R1 stages (Ritchie *et al.* 1993) to compare the dynamic changes of LAI between the LRS maize and conventional maize hybrids.

Differences in climatic conditions and population density between the 1998 and 1999 experiments resulted in heterogeneity of variances for the two years. Thus statistical analyses were conducted with the SAS system's GLM procedure (SAS Institute 1994) on a per year basis. Multiple comparisons between variable means were performed by using a GLM protected LSD test (Steel *et al.* 1997). Regression analyses were applied to test for relationships between HI and maturity, and between yield and maturity based on a linear model for each year.

3.4. Results and Discussion

3.3.1. Harvest Index and yield

Though the performances of the 10 hybrids in 1998 and 1999 were not completely consistent, it was clear that many of the LRS maize hybrids had higher harvest index values than the conventional ones (Table 3.1). The year-to-year variation suggests that each hybrid or variety has its own optimum growth conditions in which its genetic potential is fully expressed. Yearly fluctuations in the performance of individual maize hybrids are often due to variation in environmental factors such as moisture availability (Boyer 1970), seasonal temperature (Bird *et al.* 1977), soil fertility (Natr 1972), disease prevalence (Wegulo *et al.* 1997), and the prevalence of other "pests" such as weeds (Zhang *et al.* 1996) and insects (Thome *et al.* 1994). Hybrids may resist negative environmental regimes through traits such as greater disease resistance and lodging resistance (Spike and Tollefson 1991). Both 1998 and 1999 were relatively warm years (Table 3.2). While both the temperature and precipitation in June and September in 1999 were higher than in 1998, the situation was reversed for August. These differences may have resulted in higher grain yields and an average 10 days earlier maturity in 1999 than 1998 (Tables 3.3 and 3.4), because June and September were critical periods for early growth and grain filling, respectively. In addition, there was a heavier incidence of *Gibberella* ear rot and common smut in 1998 than 1999 (See Chapter 5) due to the higher temperature and humidity in August 1998. These diseases, in turn, negatively affected the final grain yields. The environmental influences can also be seen in the evolution of yield components in the two years (Tables 3.3 and 3.4). Most of the yield components as well as the ear length and diameter were greater in 1999 than 1998. It is also clear that LRS maize produced a smaller ear and 100 kernel weight that the conventional hybrids, indicating that increase in ear number per unit area would be the first choice as a method to increase the yield of LRS hybrids.

In 1998, the grain yield of conventional hybrids was lower at the high population density that at the lower one, while it was essentially unchanged for the LRS maize hybrids (Tables 3.3 and 3.4), indicating that LRS hybrids are more tolerant of the high population density, and the stresses associated with this, than the conventional hybrids.

This is in agreement with the findings of Modarres *et al.* (1997a) and Begna *et al.* (1997a,b). The short stiff stalk, reduced height and prolific trait allow the LRS hybrids to be more resistant to lodging, crowding (including competition for light) and nutrient stresses. This made the optimum plant population density of the LRS hybrids higher than that of the conventional hybrids, which could compensate for losses due to reduced ear size for LRS maize. At these higher population densities the LRS hybrids could be able to produce grain yields equal to or greater than the conventional hybrids. However, this was not the case in 1999, during which both the yields of LRS and conventional maize increased under the high population density. One possible reason was that 1999 was a very favorable year for maize growth. Physiological maturity occurred 9 days sooner in 1999 than in 1998 (data not shown) and yields were higher in 1999 than 1998 (Tables 3.3 and 3.4). This allowed both conventional and LRS maize to mature normally, even at the higher population density. In addition, the lower overall stress levels in 1999 than 1998 probably reduced the stresses associated with the high population density, allowing the conventional maize to develop normally even at this density. Finally, the high population density was lower in 1999 than 1998, so that the combination of a lower stand density and better growing conditions made the high population density suitable for even the conventional hybrids in 1999.

Regression analyses between HI and maturity, and between yield and maturity (CHU) among the seven LRS maize hybrids showed no evidence of simple relationships (Table 3.5), indicating that HI and yield do not respond similarly to variation in maturity date of the hybrids, and most importantly, are not negatively correlated. Therefore, it should be possible to combine high HI and high yield in maize hybrids with a wide range of maturities, resulting in the potential production of HI index LRS hybrids over a wide range of maize production areas. The high harvest index was previously shown only for early maturing LRS types by Modarres *et al.* (1997a,b). The current report shows that LRS types of later maturity can also have high harvest indices. This would allow the development of high harvest index type LRS maize for production over a wide range of production areas.

Hybrid 97N-4451 (No.10) (Table 3.1) had the highest harvest index in both years. This hybrid was a reduced-stature type, and did not contain the Leafy trait. Austin *et al.* (1980) calculated that a reduction in stem and leaf sheath dry matter to half the current average values, with relocation of this dry matter to the ear, could raise the harvest index from about 0.5 to 0.62, assuming a constant biomass yield. The question is whether such a dramatic change is possible or even desirable in view of the stem's role in supporting the ear and maintaining an effective display of leaves for light interception. However, this sort of change has proved to be very effective in most small grain cereal crops (Hay 1995). Our data indicated that this can also be true for maize. Most reduced-stature maize hybrids have approximately half the stem biomass of conventional hybrids (Modarres *et al.* 1997a), which means the potential harvest value for these maize hybrids could be approximately 0.6. This was also demonstrated by Modarres *et al.* (1997a,b).

A potential problem is that an increase in harvest index in this way can be associated with reductions in other yield components, and in a worst case scenario, in the yield per plant. High harvest index does not necessarily mean high yield. Thus, the Leafy character was introduced to compensate for any potential photosynthate loss resulting from the introduction of the reduced-stature trait (Modarres *et al.* 1997b). By increasing total leaf number, especially the above-ear leaf number, the Leafy trait may have improved the overall photosynthetic efficiency of LRS canopies. This is the probable reason why some of the LRS hybrids are able to yield as well as some later maturing conventional counterparts (Tables 3.3 and 3.4). However, somewhat lower yields may be acceptable in cases where it means that maize could now be grown in areas where it cannot currently be produced. Theoretically, a higher yield can be expected with a higher harvest index maize genotype as long as the same amount of biomass is produced (Snyder and Carlson 1984). Theoretically, an increase of harvest index from 0.5 to 0.6 would result in the yield increase of 20%, if the total biomass production remained unchanged.

In this work the yields of the LRS hybrids, under the more conventional cultivation regime, were inferior to the best commercial ones. However, when the yields of the conventional hybrids at the low population density and the LRS hybrids at the high population density, which is more appropriate for them, are compared, a few of the tested LRS hybrids look promising. In addition, further hybrid development and improvement of agronomic management for LRS maize types seem certain to lead to yield improvements as some of these types of hybrids have already been shown to have this potential (Begna *et al.* 1997a,b). The combination of reasonable yields and early maturity could make these hybrids very attractive in short growing season areas. The data provided in this manuscript suggest that the LRS canopy architecture, along with higher harvest indices could be incorporated into maize hybrids suitable for production in a wider range of environments.

3.3.2. LAI

In both years, there were few differences among the tested hybrids in terms of leaf area development at the earliest leaf stages (V3) (Tables 3.6 and 3.7). From the V3-V9 stages the LAI of conventional hybrids developed faster than that of the LRS hybrids, when compared within population densities, with the differences diminishing as the LAI reached its maximum. Though leaf size for LRS maize is normally smaller, earlier emergence and faster leaf expansion compensated for this at the early growth stages (Tables 3.8 and 3.9). Later, the leaf size of conventional hybrids gradually became a dominant factor in determining LAI. When all the leaves around the ear were fully spread out, the increased size and number of these leaves resulted in LAI values for LRS maize that were close to those of the conventional maize hybrids (Tables 3.6 and 3.7). If plant height was taken into account (Tables 3.8 and 3.9), the leaf area of LRS maize in a unit volume is much higher than that of conventional maize.

In northern maize production areas, the development of LAI by maize is always insufficient, due to low temperatures and a short growing period. Increasing population density is the first choice of methods to improve LAI. However, the use of higher populations to increase leaf area may increase the shading of lower leaves, reduce the photosynthetic rate of these leaves and hasten their senescence (Ottman and Welch 1989). As respiration by lower leaves can exceed their gross photosynthetic rate, such leaves are more likely to be a net sink instead of a source (Stoskopf 1985). Because of the Lfy1 trait, LRS maize can substantially increase the total leaf area and leaf area around the ear. These leaves have the highest photosynthetic rates and make the largest contributions to grain filling (Dwyer and Stewart 1986), and can be added in LRS plants without adding extra, and perhaps counterproductive, lower leaves (Shaver 1983). The finding that above-ear LAIs of most commercial hybrids was approximately 3 (Dwyer *et al.* 1992) indicates that the increased above-ear LAI would not result in any shading problem as long as the they were kept to values not higher than 3. The compact stature resulting from inclusion of the rd trait allowed the LRS maize hybrids to be more tolerant to high population densities (Begna *et al.* 1999). This, in turn, can increase the productive LAI of LRS maize grown in short season areas.

It was previously shown that LRS hybrids are more tolerant of high population densities than conventional ones (Begna *et al.* 1997a,b), and that they have higher optimum population densities than conventional hybrids (Modarres *et al.* 1997a,b). Thus, commercial production of LRS hybrids would involve the higher seeding density, while commercial production of the conventional hybrids would be at the lower density. This means that a comparison of LAIs for LRS hybrids at the higher population density with conventional hybrids at the lower population density is a fair one. When this comparison is made, the LAI of LRS maize is substantially higher than that of the conventional hybrids (Figures 3.1 and 3.2). This indicates that LRS maize possesses the potential to yield more than the conventional maize hybrids under proper agronomic management.

3.5. Conclusions

There are more high HIs found associated with LRS maize hybrids regardless the maturity date. The NLRS hybrid (97N-4451) consistently had the highest HI in the two-year experiment indicating that the reduced stature trait plays an important role in determining the HI. The LRS hybrids normally produce a smaller ear size than the conventional hybrids and there was no yield advantage for the LRS maize hybrids used in this work in the two-year experiments.

LRS maize hybrids had higher leaf production rates than the conventional hybrids during early development stages. As a result, they produced more leaves, especially above the ear, during the vegetative development period. However the LAIs of LRS maize did not surpass those of the conventional hybrids due to the reduced leaf size of LRS maize. The Leafy and reduced-stature trait renders LRS maize more tolerant to the stress of high population density. If LRS and conventional maize were compared at population densities close to their optimum densities, the LAIs of LRS maize hybrids were much higher than that of the conventional hybrids. This indicates a high yield potential of LRS maize if properly managed.

Table 3. 1: Harvest indices of LRS and conventional maize hybrids in 1998 and 1999

Hybrids	CHU*	Year 1998		Year 1999	
		HI (LD)	HI (HD)	HI (LD)	HI (HD)
1 Pioneer3979	2400	0.47e	0.45f	0.52f	0.54c
2 39R52	2500	0.50b	0.48de	0.54ed	0.54c
3 Z8950	2700	0.48c	0.47e	0.55cd	0.54c
4 LRS I	2500	0.48c	0.47e	0.56cb	0.54c
5 LRS II	2500	0.49b	0.51b	0.55cd	0.55cb
6 97iso-49	2400	0.52a	0.50bc	0.56cb	0.57b
7 97iso-37	2450	0.48d	0.49cd	0.56cb	0.54c
8 97N-4469	2500	0.47e	0.48de	0.57b	0.56bc
9 97iso-29	2600	0.49bc	0.49cd	0.53ef	0.54c
10 97N-4451	2400	0.52a	0.54a	0.62a	0.60a
$LSD_{0.05}$		0.01	0.02	0.02	0.02

Hybrids 1 to 3 are conventional types, hybrids 4 to 9 are Leafy reduced-stature and hybrid 10 is reduced-stature.

Table 3. 2: Average temperature and total rainfall for each month of the growing season in 1998 and 1999, and the 30 year averages, at Ste-Anne-de-Bellevue, Quebec, Canada

Month	1999		1998		30 year average	
	Temp. (°C)	Precip. (mm)	Temp. (°C)	Precip. (mm)	Temp. (°C)	Precip. (mm)
May	16.2	44.2	17.4	50.5	12.9	68.3
June	21.0	88.5	19.5	74.5	18.0	82.5
July	22.6	74.0	21.1	89.5	20.8	85.6
Aug.	20.0	67.0	21.0	92.5	19.4	100.3
Sept.	18.1	194.5	16.1	62.0	14.5	86.5
Oct.	7.7	88.0	9.8	62.5	8.3	75.4

Temp. = mean monthly temperature, Precip. = mean monthly precipitation.

Table 3. 3: Yield components, ear diameter, and ear length for LRS and conventional maize hybrids in 1998

Hybrid	Rows per ear	Yield (t/ha)		100-kernel weight (g)		Kernels per row		Ear diameter (cm)		Ear Length (cm)	
		LD	HD	LD	HD	LD	HD	LD	HD	LD	HD
1 P3979	14	8.58	7.65	32.92	27.5	32.67	25.33	4.12	3.98	15.67	12.17
2 39R52	16	8.58	7.40	30.20	24.4	34.67	31.00	4.13	3.98	15.97	12.18
3 Z8950	16	8.92	7.54	27.98	25.83	41.00	35.33	3.98	3.73	16.73	13.13
4 LRS I	16	8.19	7.68	23.82	21.77	35.67	33.67	3.67	3.58	14.67	13.24
5 LRS II	16	6.95	7.02	22.75	19.57	34.33	32.00	3.68	3.48	14.93	13.02
6 97iso-49	16	6.97	6.86	21.33	20.05	31.00	30.33	3.64	3.51	13.75	11.20
7 97iso-37	16	6.69	6.71	22.20	19.32	33.67	30.67	3.80	3.38	14.6	12.33
8 97N-4469	16	7.36	7.26	20.38	17.97	33.00	31.67	3.75	3.58	13.98	11.67
9 97iso-29	16	7.14	7.22	23.73	20.7	33.67	30.33	3.83	3.43	14.97	12.97
10 97N-4451	14	6.87	6.79	21.25	20.02	29.67	27.00	3.70	3.45	13.72	11.28
$LSD_{0.05}$		0.22	0.18	2.39	1.89	2.66	1.80	0.34	0.33	1.79	1.66
Aver.		7.63	7.21	24.66	21.71	33.94	30.73	3.83	3.61	14.90	12.32

1, 2, 3 are conventional hybrids, 4~9 are LRS hybrids, 10 is NLRS hybrids

Table 3. 4: Yield components, ear diameter, and ear length for LRS and conventional maize hybrids in 1999.

Hybrids	Rows per ear	Yield (t/ha)		100-kernel Weight (g)		Kernels per row		Ear diameter (cm)		Ear Length (cm)	
		LD	HD	LD	HD	LD	HD	LD	HD	LD	HD
1 P3979	14	9.72	10.16	33.42	30.24	33.33	28.00	4.39	3.98	16.54	14.17
2 39R52	16	10.73	10.75	30.48	25.23	35.00	30.33	4.25	3.98	15.97	13.68
3 Z8950	16	11.94	13.09	28.28	24.64	43.67	36.33	4.04	3.73	18.37	15.13
4 LRS I	16	8.48	8.50	25.71	23.11	33.67	31.00	3.91	3.80	16.67	15.13
5 LRS II	16	8.58	8.09	23.70	21.10	35.33	33.33	3.88	3.65	15.36	14.14
6 97iso-49	16	8.21	9.06	22.36	20.92	32.67	30.33	3.73	3.54	14.90	12.62
7 97iso-37	16	8.17	8.40	23.63	21.57	30.67	28.67	3.68	3.47	14.87	12.57
8 97N-4469	16	8.24	8.54	21.32	19.03	32.33	30.33	3.74	3.52	14.38	12.12
9 97iso-29	16	9.69	10.11	25.41	22.66	32.67	28.67	3.92	3.64	15.67	13.26
10 97N-4451	14	6.16	7.52	20.61	19.29	28.00	26.33	3.62	3.48	14.64	12.55
$LSD_{0.05}$		0.41	1.17	1.63	2.18	2.81	2.30	0.52	0.33	1.76	1.49
Aver		8.99	9.42	25.49	22.78	33.75	30.33	3.92	3.68	15.74	13.54

1, 2, 3 are conventional hybrids, 4~9 are LRS hybrids, 10 is NLRS hybrids

Table 3. 5: F value for correlation between harvest index and CHU and between yield and CHU in 1998 and 1999 based on a linear regression model

	R^2 for 1998	R^2 for 1999
HI (LD) vs CHU	0.37	0.52
HI (HD) vs CHU	0.26	0.48
Yield (LD) vs CHU	0.11	0.66
Yield (HD) vs CHU	0.34	0.43

Table 3. 6: Leaf area index (LAI) of the hybrids at different developmental stages in 1998

Hybrids[1]	CHU[2]	V3[3]		V6		V9		R1	
		LD	HD	LD	HD	LD	HD	LD	HD
1 Pioneer3979	2400	0.049	0.092	0.99	1.45	2.04	2.69	3.41	4.47
2 39R52	2500	0.046	0.080	1.05	1.38	1.91	2.60	3.52	4.98
3 Z8950	2700	0.050	0.088	1.11	1.48	2.10	2.83	4.14	4.91
4 LRS I	2500	0.055	0.090	1.00	1.37	2.03	2.73	3.72	4.74
5 LRS II	2500	0.049	0.086	0.82	1.41	1.89	2.29	3.23	4.73
6 97iso-49	2400	0.047	0.093	0.93	1.24	1.87	2.45	3.29	4.33
7 97iso-37	2450	0.046	0.083	1.06	1.38	1.84	2.23	3.33	4.06
8 97N-4469	2500	0.058	0.098	0.90	1.23	2.03	2.45	3.41	4.31
9 97iso-29	2600	0.056	0.100	0.98	1.43	2.00	2.78	3.50	4.53
10 97N-4451	2400	0.050	0.085	0.78	1.04	1.65	2.28	2.63	3.26
$LSD_{0.05}$		0.004	0.017	0.15	0.12	0.19	0.18	0.27	0.33

[1] Hybrid numbers 1-3 are conventional hybrids, numbers 4-9 are LRS hybrids; number 10 is a reduced-stature but non-Leafy hybrid.

[2] CHU = corn heat units to maturity

[3] V3, V6, V9 represent different vegetative; R1 represent reproductive stage I

Table 3. 7: Leaf area index (LAI) of the hybrids at different developmental stages in 1999.

Hybrids[1]	CHU[2]	V3		V6		V9		R1	
		LD[3]	HD	LD	HD	LD	HD	LD	HD
1 Pioneer3979	2400	0.062	0.102	1.11	1.54	2.26	2.78	3.56	4.58
2 39R52	2500	0.057	0.095	0.95	1.45	2.30	2.82	3.64	4.52
3 Z8950	2700	0.055	0.093	1.21	1.59	2.18	2.96	4.05	4.72
4 LRS I	2500	0.058	0.110	0.97	1.48	2.13	2.78	3.58	4.26
5 LRS II	2500	0.052	0.093	0.89	1.41	1.95	2.58	3.53	4.35
6 97iso-49	2400	0.056	0.095	0.95	1.36	1.89	2.50	3.48	4.24
7 97iso-37	2450	0.059	0.091	0.95	1.38	1.96	2.53	3.40	4.38
8 97N-4469	2500	0.053	0.098	1.08	1.40	1.92	2.49	3.52	4.25
9 97iso-29	2600	0.058	0.095	0.85	1.47	2.10	2.73	3.47	4.47
10 97N-4451	2400	0.054	0.090	0.75	1.21	1.78	2.25	2.72	3.45
$LSD_{0.05}$		0.003	0.015	0.08	0.81	0.23	0.19	0.34	0.33

[1] Hybrid numbers 1-3 are conventional hybrids, numbers 4-9 are LRS hybrids; number 10 is a reduced stature but non-Leafy hybrid.

Table 3. 8: Total fully developed leaf number per plant at different developmental stages and plant height in 1998

Hybrids[1]	CHU	V3		V6		V9		V12		R1		Plant height (cm)
		LD	HD	LD	HD	LD	HD	LD	HD	Total	Above ear	
1 Pioneer3979	2400	2.4	2.6	5.6	5.6	8.4	8.6	10.6	11.6	17.0	6.6	258.0
2 39R52	2500	2.0	2.4	5.4	5.6	8.4	8.6	11.6	11.6	17.8	6.4	264.0
3 Z8950	2700	2.0	2.2	5.0	4.8	8.2	8.4	12.0	11.8	17.0	6.0	264.3
4 LRS I	2500	2.4	2.4	5.4	5.6	9.0	9.2	12.2	12.2	17.8	8.4	171.3
5 LRS II	2500	2.4	2.6	5.6	5.8	9.6	9.6	13.4	13.2	18.4	8.0	165.7
6 97iso-49	2400	3.0	3.0	6.2	6.0	9.4	9.4	13.8	13.6	18.2	8.2	160.0
7 97iso-37	2450	3.0	3.2	6.2	6.4	10.6	10.6	14.6	14.8	19.8	8.8	161.0
8 97N-4469	2500	3.0	3.4	6.2	6.4	10.2	10.6	14.8	15.0	20.0	9.0	203.3
9 97iso-29	2600	3.0	2.8	6.2	6.2	10.2	10.6	13.8	14.0	19.6	8.2	200.3
10 97N-4451	2400	2.2	2.4	5.4	5.2	9.6	9.8	13.4	13.2	14.8	5.8	154.7
$LSD_{0.05}$		0.42	0.63	0.61	0.68	1.06	1.09	1.13	1.24	1.67	1.47	10.30

Hybrid numbers 1-3 are conventional hybrids, numbers 4-9 are LRS hybrids; number 10 is a reduced-stature but non-Leafy hybrid.

Table 3. 9: Total fully developed leaf number per plant at different developmental stages and plant height in 1999

Hybrids	CHU	V3		V6		V9		V12		R1		Plant height (cm)
		LD	HD	LD	HD	LD	HD	LD	HD	Total	Above ear	
1 Pioneer3979	2400	2.6	2.4	5.8	6.0	8.4	8.6	11.0	11.2	17.6	7.0	261.3
2 39R52	2500	2.2	2.4	5.6	5.6	8.6	8.8	11.8	11.8	18.0	6.6	266.7
3 Z8950	2700	2.4	2.6	5.4	5.6	8.6	8.6	12.4	12.8	17.4	6.4	270.7
4 LRS I	2500	2.8	2.8	5.8	6.0	9.4	9.4	12.6	12.8	18.4	9.2	176.0
5 LRS II	2500	2.8	3.0	6.0	5.8	9.8	9.8	13.6	13.4	18.8	8.4	168.7
6 97iso-49	2400	3.2	3.0	6.2	6.0	9.4	9.4	13.8	13.8	18.6	8.6	163.0
7 97iso-37	2450	3.4	3.2	6.4	6.6	11.0	11.0	15.0	15.0	20.2	9.2	166.0
8 97N-4469	2500	3.0	3.0	6.4	6.6	10.6	10.6	14.6	14.6	20.4	9.6	206.0
9 97iso-29	2600	3.2	3.4	6.2	6.0	10.2	10.4	14.0	13.8	19.8	8.6	204.3
10 97N-4451	2400	2.6	2.8	5.2	5.4	9.8	9.6	12.6	12.8	15.0	6.0	156.7
$LSD_{0.05}$		0.60	0.68	0.66	0.66	0.85	0.86	1.02	1.10	1.46	1.26	9.34

Hybrid numbers 1-3 are conventional hybrids, numbers 4-9 are LRS hybrids; number 10 is a reduced-stature but non-Leafy hybrid.

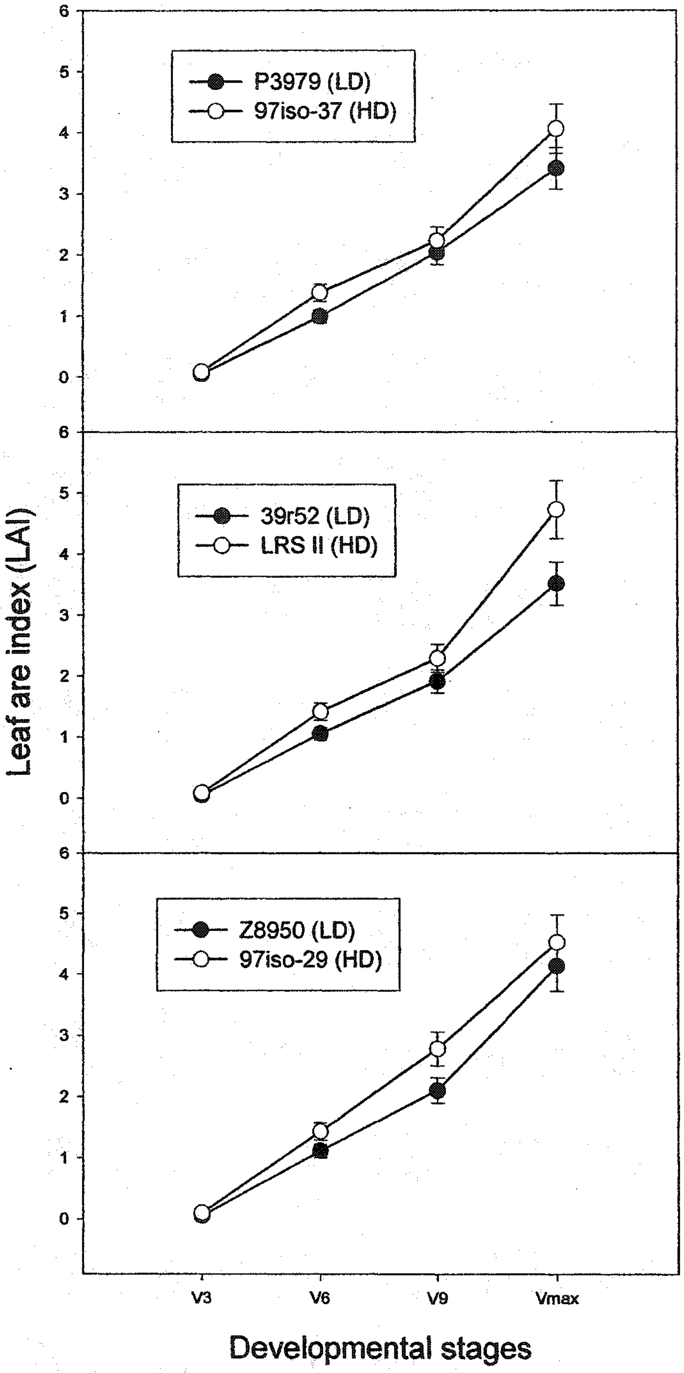

Figure 3. 1: LAIs of LRS maize and conventional maize hybrids with comparable CHU requirements and under different population densities in 1998

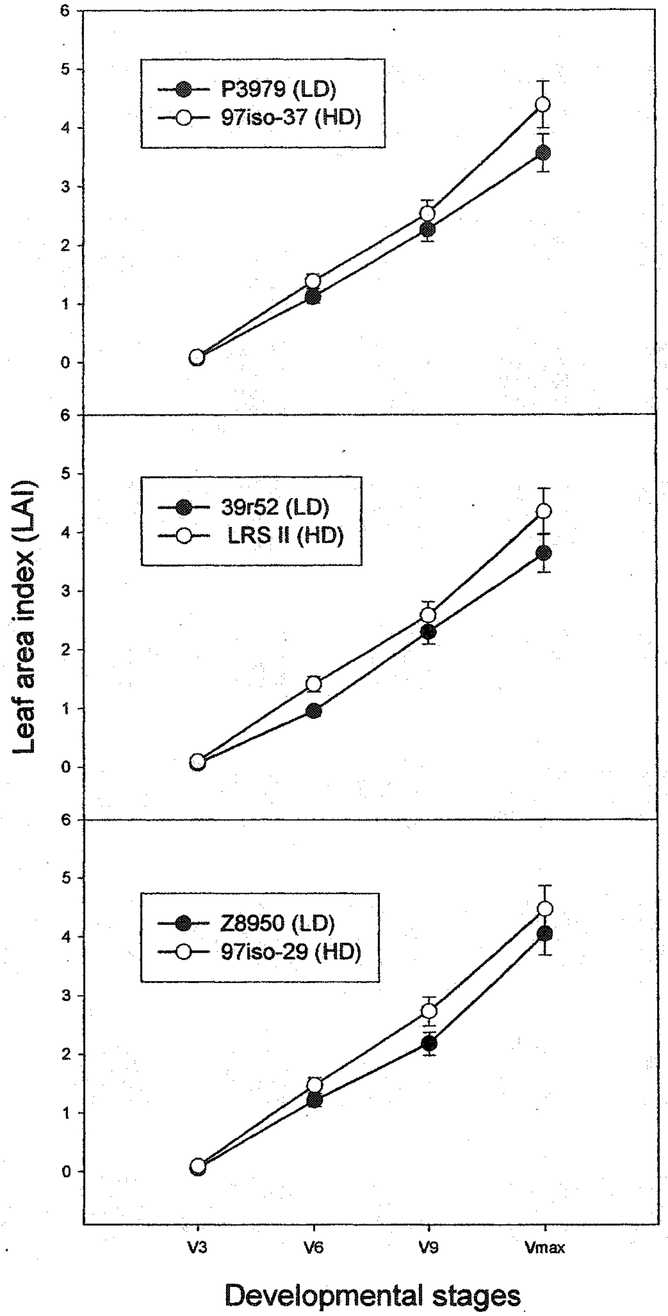

Figure 3. 2: LAIs of LRS maize and conventional maize hybrids with comparable CHU requirements under different population densities in 1999

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Preface to Chapter 4

Chapter 4 is comprised of a manuscript to be submitted for publication to Agronomy Journal in 2001.

In the previous chapter we examined the effects of including the Leafy and reduced-stature traits on maize canopy development and final harvest index. The inference that the Leafy and reduced-stature traits, both present in LRS maize, caused not only profound changes to canopy architecture, but also pleiotropic effects on root structure was tested in this chapter. The improved efficiency and accuracy of computer assisted image analysis systems made it possible for analysis of root morphological variables on a large scale. Comparisons of root morphologies between LRS and conventional maize hybrids were made based on the information acquired from a wide range of genotypes. This also made it possible to determine the general relationships among root morphological variables.

Fractal dimension was introduced to quantitatively describe the complexity of irregular structures and here it is used to quantify the complexity of maize roots. This approach substantially simplifies the comparisons between roots and is potentially useful in root modeling work. The suitability of fractal dimension as description of root complexity and its relationship with other major root morphological variables was measured and discussed.

Chapter 4

Root morphology and fractal dimension analysis of LRS maize at early developmental stages

4.1. Abstract

Incorporation of the Leafy and reduced-stature traits into maize hybrids considerably modifies their canopy structure; however, there has been no previous work to determine possible pleiotropic effects of these traits on maize root systems. Measurements of root system characteristics were conducted on eight Leafy reduced-stature (LRS) maize and three conventional maize hybrids at early development stages using a scanner-based image analysis system. Plants were grown in a greenhouse and the experiment was organized following a completely randomized design with 6 replicates. The results showed that LRS maize hybrids had, on average, a longer root system, larger root diameter, higher branching frequency and greater root dry mass than conventional hybrids. Considerable variability was also found within the LRS group. A close correlation was found between total root length and total surface area ($r = 0.89$), and between total length and number of forks ($r = 0.91$). In general, 70-80% of the length of early maize roots fell into the diameter range 0-0.4 mm. Fractal analysis was conducted on maize roots at early growth stages with the WinRHIZO^{TM} (version 3.9), a computer-assisted and scanner-based image analyzing system. Correlation between the fractal dimension (FD) and other root morphological variables were estimated. The results indicated that roots of Leafy reduced-stature maize hybrids had higher FD values, i.e. greater root complexity, than conventional maize hybrids. Fractal dimension was highly correlated to total root length (R = 0.89), root surface area (R = 0.97) and number of forks (R = 0.93). The correlation between fractal dimension and root dry weight was also significant (R = 0.88). Root total length, surface area, and number of forks were major determinants of root fractal dimension, accounting, collectively, for 56.81% of the variability of root fractal dimension. While the general difference between the LRS and conventional hybrid groups showed the presence of pleiotropic effects of the Leafy and reduced-stature traits on root morphology, no specific relationships were found between early root morphology and elements of later canopy structure.

Key words: Leafy reduced-stature (LRS) maize, root morphology, fractal dimension, *Zea mays* L.

4.2. Introduction

Maize hybrids containing the Leafy and reduced-stature traits have recently been the subject of substantial research efforts (Shaver 1983, Stewart and Dwyer 1993, Modarres *et al.* 1998, Begna *et al.* 1999). These hybrids have considerably altered canopy architectures, with more leaves above the ear, a shorter stature, in some cases, a tendency to produce two ears per plant, and higher harvest indices (Dijak *et al.* 1999). However, little is known regarding potential pleiotropic effects of these traits on elements of root architecture such as length, diameter, surface area, branching frequency and factal dimension.

Root characteristics such as length, diameter, surface area and mass have been used to describe root systems and estimate their function and size (Murphy and Smucker 1995). Roots play important roles in both nutrient uptake and anchorage of the whole plant. Although root morphology is influenced by environmental conditions during its development, genetic control is also important in determining root morphology (Lungley 1973), especially during early development stages (Cahn *et al.* 1989). An improved understanding of root morphological characteristics would be useful in predicting nutrient and water uptake ability and later development of the root. For example, root length, surface area and nutrient concentration in the soil solution, are all closely related to the amount of nutrients accumulated by a growing plant (Raper *et al.* 1978). The density of rooting within the volume of soil explored by a root system is more important than the length alone (Coutts 1986). In some cases estimates of root length per volume of soil can be used as an indirect parameter in quantifying water and solute uptake (Cowan 1965, Brewster and Tinker 1970). However, the measurement of these root variables has proven to be tedious and prone to inaccuracies (Zoon and Van Tienderen 1990).

Several methods have been developed to estimate root variables (Rowse and Phillps 1974, Richards *et al.* 1979, Zoon and Van Tienderen 1990). Scanner-based computer-assisted image analysis has made the measurement of root morphology simpler, faster and more accurate (Collins *et al.* 1987, Cunningham *et al.* 1989, Stutte and Stryjewski 1995, Box 1996). This has made comparisons of the real root length, rather than the weight-based length estimates, possible and informative (Box and Ramseur 1993). Recent work has demonstrated that, when combined with appropriate root staining (Costa *et al.* 2001a) scanner-based computer-assisted image analysis of plant roots becomes considerably more effective.

Most of previous studies of maize root morphology dealt with the influence of fertilizer and other soil factors on root morphology (Eghball Maranville 1993, Feil *et al.* 1991). Costa *et al.* (2001b) first compared the root morphology of LRS maize and conventional maize. The comparison, involving only one LRS and one conventional maize hybrid, indicated that the LRS genotype had a greater root length and surface area than the conventional hybrid, at the silking stage.

The fractal concept was introduced by Benoit Mandelbrot (1983). It designates a rough or fragmented geometric that can be subdivided into parts, each of which is, at least approximately, a reduced-size copy of the whole. Contrary to classical geometry, fractals are not regular in dimension. Fractal geometry has provided a new approach for quantifying the geometry of complex or noisy shapes and objects (Mandelbrot 1983, Foroutan-Pour *et al.* 1999a), such as soil (Burrough 1981, Peyton *et al.* 1994, Huang 1998, Castrignano Stelluti 1999, Oleschko *et al.* 2000, Anderson *et al.* 2000), the branching patterns of fungi (Ritz and Crawford 1990, Jones *et al.* 1993) the morphology of root systems (Eghball *et al.* 1993, Spek and Van Noordwijk 1997, Nielsen *et al.* 1997 1998/1999, Ketipearachchi and Tatsumi 2000, Ozier-Lafontaine *et al.* 1999), shoot systems and canopies of young tree plantations (Morse *et al.* 1985), crop canopy structure (Foroutan-Pour *et al.* 1999b, 2001) and form complexity in plant development (Corbit and Garbary 1995, Critten 1997).

Three categories of method have been developed to cope with different demands of fractal dimension estimations: semivarigram, spectral analysis, and "compass" (Mandelbrot 1983, Carr and Benzer 1991). While the first two are applicable in the estimation of fractal dimension for stochastic fractals, which indicate the similarity of the feature under study to noise, the compass methods are mainly used to estimate the complexity of shape (Mandelbrot 1983). The box counting method is one representative of the compass category of methods. It is the method of preference when dealing with the fractal estimation of concrete physical structures or shapes (Peitgen *et al.* 1992). In this method, each image is covered by a sequence of grids made of squares of descending sizes. For each grid, two values are recorded: the number of squares intersected by the image, N(s), and the side length of squares, s. The regression slope (D) of the straight line formed by plotting log[N(s)] against log(1/s) indicates the degree of complexity, or fractal dimension, which ranges between 1 and 2 ($1 \leq D \leq 2$) (Mandelbrot 1983). The linear regression equation used to estimate fractal dimension is: $\log[N(s)] = \log(k) + D\log(1/s)$, where k is a constant and N(s) is proportional to (1/s)D (Mandelbrot 1983).

Plant root systems, like other branching systems, are amenable to fractal description (Tatsumi *et al.* 1989). The fractal dimension of a root is a function of root branching pattern, the proportion of coarse/fine roots and the total length. Changes in any of these components affect fractal dimension measurement. Fractal dimension can characterize, both quantitatively and qualitatively, the morphology of developing roots (Eghball *et al.* 1993). It is also helpful in interpreting other root morphological measurements. The fractal dimensions of several crop roots have been shown to fall between 1.48 and 1.58 (Tatsumi *et al.* 1989).

Leafy reduced-stature (LRS) maize hybrids are newly developed genotypes of maize which significantly differ in canopy architecture from conventional genotypes. While the aboveground potion of these hybrids has been well characterized (Shaver 1983, Stewart and Dwyer 1993, Modarres et al 1997a,b), there has been little work regarding the effects of Leafy and reduced-stature traits on the architecture of the root systems. Costa et al (2001c) have shown a difference in root fractal dimension between one of these LRS genotypes and a conventional hybrid. While fractal dimension has been examined in a number of plants (Eghball et al 1993, Nielsen et al 1997, Costa et al 2001c), there has been no attempt to relate conventional aspects of root morphology measurement (e.g. root length, diameter, branching frequency) to fractal dimension. The objectives of this study were 1) compare the root morphologies of a wide range of LRS hybrids and a group of conventional hybrids at early developmental stages, using a scanner-based imaging analyzing system, 2) to determine whether root fractal dimension is different between LRS and conventional maize hybrids, 3) to examine the relationships between the root fractal dimension and other root morphological variables.

4.3. Materials and Methods

Three conventional and 8 LRS maize hybrids (Table 4.1) were arranged in a completely random design with 6 replications. The experiment was conducted twice in the research greenhouse of the Macdonald Campus of McGill University. The seeding date for the first experiment was January 20, 2000 and July 11, 2000 for the second. In each experiment, two seeds of each hybrid were seeded in plastic pots (25 cm top diameter, 23 cm bottom diameter and 23 cm height) containing vermiculite. After the seedlings emerged they were thinned to one per pot, retaining the most vigorous seedling in each pot. Plants were watered once every two days with tap water.

All the pots were cultured at 25 ± 2^{o}C for the first experiment and 27 ± 3^{o}C for the second experiment and a relative humidity of 85%. The light regime was maintained at 16:8 (light/dark), with supplemental light provided by 430 Watt Phillips sodium lamps (Phillips, Montreal, Canada), when needed. The plants were harvested 15 days after emergence in the first experiment and 20 days in the second experiment. All the plants were at about the 3 leaf stage at harvest time in the first experiment and at about the 4 leaf stage in the second experiment. Six relatively uniform seedlings of each hybrid were sampled for further root and shoot measurements. All the roots were carefully washed by hand until no rooting medium remained attached. Root samples were stored in 35% ethanol solution to preserve them until measurement. After measurement, all the roots and shoots were dried to a constant weight at 75^{o}C for the calculation of root/shoot ratio.

Root measurements were performed using the WinRHIZO^{TM} (version 3.9) system (Regent Instrument Inc., Quebec, Canada), which consists of one Windows-based PC, one scanner and the WinRHIZO software. All the root measurements were based on scanned images of the real roots. Prior to scanning, root samples were stained for 15 minutes in 0.1% w/v toluidine blue solution (Costa *et al.* 2001a). The root was rinsed under the tap water for about 1 minute and then placed in Plexiglas tray with a 3-4 mm deep layer of water. After untangling the root as much as possible, with the aid of small plastic spatulas, the root was ready to be scanned.

Root fractal measurements were performed using the fractal analysis function of the WinRHIZO^{TM}. The software calculates fractal dimension following the same principle described in Tsunami *et al.* (1989). In a manner analogous to the box-counting method, WinRHIZO automatically sets different grid sizes for the image and records the number of grids intercepted by the root image and the side length of the grid. Choosing appropriate minimum and maximum pixel sizes is equivalent to deciding the minimum and maximum box size in the box counting method and is based on the displayed image pixel size. The minimum pixel size cannot be smaller than the displayed image pixel size. In this study the minimum and maximum pixel sizes were set to 0.1 and 3.0 mm in the first experiment, and 0.25 and 3.0 mm in the second experiment. This covered the entire diameter range of the root images and gave more than 20 measurements of the same root under different grid sizes. Different pixel sizes were used in each experiment as different scanning resolutions were used, based on the root sample size, i.e. because of the later harvest for the second experiment the roots were somewhat larger. The fractal dimensions (FD) were calculated based on these measurements and the linear regression equation $\log[N(r)] = \log(K) - D\log(r)$, where $N(r)$ is the grid number intercepted by root, r is the side length of the grid and k is a constant (Mandelbrot 1983).

Bartlett's test (Steel *et al.* 1997) was used to test the homogeneity of the data from the two experiments. Information on root total length, surface area, average diameter, tip number, fork number and total length distribution over 10 diameter ranges was used to analyze the root's morphological characteristics. Normality tests and ANOVA analyses were conducted with the SAS system's GLM procedure (SAS Institute 1994). Multiple comparisons between variable means were performed by using GLM protected LSD tests (Steel *et al.* 1997). Correlation analysis was applied between FD and other variables to determine their relationships (Steel *et al.* 1997). Stepwise multiple regression between FD and several major morphological variables was conducted by using the SAS system's REG procedure (SAS Institute 1994).

4.4. Results and Discussion

4.4.1. Morphology analysis of maize root at early developmental stages

Homogeneity of variance tests indicated that the variances of root length, surface area, average diameter and the number of tips were homogeneous across experiments. However, this was not true for number of forks. Further analysis showed that, for all variables where the data could be combined across experiments, the main effects of the experiment were significant, while there were no experiment by genotype interactions. Therefore, the data on these root parameters were pooled for analysis (Table 4.2). Although variability existed both between and within the genotype groups, the largest values for almost all variables were for the LRS group. This was consistent with the results of Costa *et al.* (2001b). For example, LRS hybrid 97N-4295 was consistently the highest in terms of root total length, total surface area, number of tips and number of forks, while the non-LRS hybrids P3979 and 39r52 were consistently lower. Most LRS hybrids had higher values of these six major root variables than the non-LRS hybrids. A large amount of variability was also found within the LRS group, indicating relatively wide genetic variation among these root traits. Johnson *et al.* (1998) found considerable variation for root morphological traits among alfalfa cultivars, and concluded that selection for specific root modifications could be effective. Contrasts between the LRS group and conventional group showed that the LRS group had larger values for average diameter, number of tips and number of forks than the conventional group (Table 4.2). A close correlation was found between total length and total surface area (r = 0.89, $P < 0.01$), and between total length and number of forks (r = 0.91, $P < 0.01$).

The root dry mass results followed the pattern described above for the morphology variables. Those roots with larger diameters had heavier dry masses (Tables 4.3 and 4.4). In general LRS hybrids had more root dry mass than the non-LRS groups. The shoot dry weight followed the same pattern as root dry weight, which resulted in a relatively constant root-to-shoot ratio in the first experiment (Tables 4.3 and 4.4). Later, with the rapid development of the shoot, the root-to-shoot ratios decreased to a level determined by both genetic and environmental factors (McCullough *et al.* 1994). Variation among different genotypes was evident (Table 4.4). In our experiment, all the hybrids were grown under the same conditions, therefore the differences among hybrids for evolution of root-to-shoot ratio were genetically based.

Because of the scanning-based techniques used it was possible to classify the total root length into different root diameter ranges. For instance, in our experiments roots were separated into 10 groups according to their actual diameter ranges (Fig. 4.1). This is meaningful for root study, because roots with different diameters have different functions (Peat and Fitter 1994). The absolute root length in each diameter range varied among the 11 hybrids with the highest values consistently being associated with LRS genotypes for each root size grouping (Fig. 4.1). There were also differences among non-LRS genotypes for ranks in root length categories. For instance, P3979 had less root length than the other hybrids in the 0.2-0.4 and 0.4-0.6 mm diameter ranges, however, it had much more root length in the 0.6-0.8 mm diameter range. Root length in any given size category, expressed as a percentage of the total root length, showed few differences among genotypes. Most of the root length occurred in diameter ranges between 0-0.4

mm; these comprised 70-80% of the total length (Fig. 4.2). This trait was quite stable across the tested hybrids.

We attempted to determine whether there were relationships between root traits expressed early in development for pot grown plants and measurements of canopy structure taken in the field at silking (see chapter 3). If such relationships between canopy and root structure were detected they would provide further indication of pleiotropic effects of canopy architecture traits on root architecture. However, no obvious relationship could be established (result not presented). While the differences between the LRS and conventional canopy structure hybrids suggest a general pleiotropic effect of canopy traits on roots, the relationship does not appear to be strong within genotype groups, or was masked between early root growth and later canopy architecture, and/or pot and field settings. The larger and more finely structured early root system measured for the LRS hybrids could allow greater early plant development, and might have a long-term effect on later development. Rapid early root development could be particularly valuable for a short growing season area.

4.4.2. FD analysis of maize roots at early developmental stages

Bartlett's tests showed that the data from the two experiments were homogeneous, therefore, they were pooled for subsequent statistical analyses. Analyses of FD were conducted following a Log_{10} transformation due to non-normal distribution of the data. Differences in FD existed among the hybrids (Table 4.2). Contrast analysis showed a difference between the conventional group of hybrids and the LRS group, indicating that the LRS hybrids have a more complex root system than the conventional hybrids (Table 4.2). This corroborates the single measurement made by Costa *et al.* (2001b) and is consistent with the measurements of other morphological variables. For instance, there was a higher branching frequency in LRS maize hybrids (Table 4.2). Fractal dimension could be a more comprehensive variable when comparing the complexity of two root systems. In addition, it provides a single value estimate of root system complexity and space occupancy that could be useful in developing models of root function. This would parallel recent work on crop canopies (Foroutan-Pour *et al.* 2001).

Correlation analyses showed that fractal dimension is highly related to total root length ($R = 0.89$), root surface area ($R = 0.97$) and forks ($R = 0.93$) (Fig. 4.3). The correlation between fractal dimension and root dry weight was also significant ($R = 0.88$) (Fig. 4.3). The close correlation of FD with these important determinants of root morphology shows that FD provides a comprehensive estimation of root complexity. There have been no previous publications attempting to relate the conventional measures of root morphology to FD. It is clear that variables such as root area and diameter could be correlated with each other. Therefore it would be of interest to know which of these variables were making the major contributions to root fractal dimension.

Stepwise multiple regression analysis found that the contributions of average diameter and number of tips to the fractal dimension were not significant (Table 4.5). After deleting these two parameters from the model, the equation of the fitted model is as follows:

$$FD = 1.41 + 0.000077*TL + 0.000038*Forks - 0.00081*SA$$

Where FD, TL and SA represent fractal dimension, total root length and surface area, respectively (Table 4.5). This model was highly significant ($P < 0.001$) and explained 56.81% of the variability in fractal dimension. It is not surprising that root length and forks should be contributors to this model as, together, they determine how much root there is and how it is potentially branched. Once root length is known surface area provides an indication of how much total root volume is present, which will, again, affect space occupancy and how often, in the box counting method, roots encounter elements of the grid. This represents the first effort to determine which elements of root morphology contribute to fractal dimension.

4.5. Conclusions

LRS maize hybrids normally had larger root systems than the conventional hybrids. This was manifested in the heavier average root dry weight, larger surface area and higher branching frequency for the LRS hybrids than the conventional hybrids.

There were clear differences between the LRS and conventional hybrids for root variables such as surface area and branching frequency. There was also variability among LRS and among conventional hybrids (i.e. within hybrid type) for some of these variables. Selection of an ideal early root system along with other favorable traits is possible. With the much easier and more accurate root measurement methods currently available, root traits should now appear more frequently in breeding objective lists.

High correlation was found between total length and total surface area ($R = 0.89^{**}$), and between total length and number of forks ($R = 0.91^{*}$).

Root length distribution among the different diameter ranges varied between and within genotype groups, but when these length classes were expressed as percentages of total root length there were few differences and this variable appeared to be quite stable across genotypes during this early stage of root development. There were no clear relationships between the early root traits and adult canopy traits. This meant a limited predictive role of early root traits for mature canopy structure in the field. A larger early root system could enhance early shoot development, which could have a long-term effect on the later development.

LRS maize hybrids had a larger root fractal dimension value than the conventional hybrids at the early development stages measured in this work. Fractal dimension was closely related to the root total length, surface area, number of tips, number of forks, and root dry mass. Root total length, surface area, and number of forks were major determinants of root fractal dimension, accounting, collectively, for 56.81% of the variability of root fractal dimension. The results indicated that fractal dimension could be used as a comprehensive, single value, measurement of root complexity.

Table 4. 1: Names, sources and CHU requirement of the 11 maize hybrids used in the two greenhouse experiments.

Hybrids[1]	Source	CHU[2]
P3979	Commercial hybrid	2400
39R52	Commercial hybrid	2500
Z8950	Commercial hybrid	2700
LRS I	[CM174rd1xW117rd1]x1240-6-2	2500
LRS II	[CM174rd1xW117rd1]x1306-6-2	2500
97iso-49	(BRCsynxCO392)	2400
97N-4469	(CO392xCO412)xBRCsyn	2500
97iso-37	CM174rd1xCO412	2450
97iso-29	W117rd1xCO392	2600
97N-4295	[(CO392xCO412)xW117rd1	2700
97N-4451	(w117rd1xCM174rd1)xBRCsyn	2400

[1] 1-3 hybrids listed are conventional maize hybrids; 4 -11 are Leafy reduced-stature.

Table 4. 2: Statistic of data on root morphology and FD of LRS and conventional maize hybrids, for the two greenhouse experiments

Genotypes	Total length (cm)	Total surface area (cm^2)	Average diameter (cm)	Tip number	Fractal Dimension	Fork number[2]	
						1st experiment	2nd experiment
P3979	913.6 d[1]	149.5 e	0.051 efgh	1093.8 g	1.46 d	2676.5h	2937.0 d
39r52	994.8 bcd	153.9 de	0.049 h	1079.4 g	1.47 d	2948.2 ef	3164.2 d
Z8968	1082.7 ab	165.1 cd	0.050 gh	1273.9 cde	1.48 bcd	3113.3 de	3271.5 bcd
LRS I	978.1 cd	151.0 e	0.064 a	1205.1 edf	1.47 cd	2776.0 gh	2992.5 bcd
LRS II	1007.0 bc	166.3 cd	0.053 cdef	1351.9 abc	1.47 cd	3003.0 ef	3261.3 ab
97iso-49	1165.1 a	185.5 b	0.053 cde	1373.8 ab	1.50 ab	3732.8 b	3138.5abc
97N-4469	938.9 cd	146.6 e	0.052 defg	1277.2 bcd	1.46 d	2679.2 h	2862.8 ab
97iso-37	1123.7 a	170.5 c	0.051 fgh	1263.6 cde	1.48 cd	3491.7 c	3338.5 d
97iso-29	1013.6 bc	168.2 c	0.055 bc	1170.8 efg	1.49 abc	3237.3 d	3327.0 cd
97N-4295	1163.6 a	202.8 a	0.057 b	1447.6 a	1.51 a	3928.2 a	3599.7 a
97N-4451	969.0 cd	158.3 cde	0.054 cd	1127.3 fg	1.47 cd	2880.8 fg	3122.5 d
Contrast: Conv. *vs* LRS	ns	ns	*	**	**	**	**

Note: 1-3 are conventional hybrids; 4 -11 are LRS hybrids.

1 - Means in the same column followed by different letters differ significantly(*P* <0.05) using an ANOVA protected LSD test.

2 - Data could not be pooled due to the heterogeneous variances in the two experiments.

* means significant at p<0.05 level; ** means significant at p<0.01 level; **ns** means non-significant.

Table 4. 3: Root, shoot dry mass and root-to-shoot ratio of the 11 maize hybrids harvested at 15 days after emergence (Experiment 1)

	Dry mass (mg)		
Genotypes	Shoot	Root	Root/Shoot
P3979	83.12 d[1]	59.26 de	0.72 c
39r52	75.53 d	65.97 cde	0.87 abc
Z8968	95.54 cd	91.63 ab	0.96 ab
LRS I	87.90 cd	82.18 bc	0.99 ab
LRS II	83.76 cd	55.95 e	0.78 bc
97iso-49	122.01 ab	110.64 a	0.92 abc
97N-4469	86.36 cd	76.91 bcd	0.89 abc
97iso-37	80.15 d	85.50 b	1.09 a
97iso-29	104.94 bc	105.83 a	1.02 ab
97N-4295	129.56 a	110.50 a	0.86 abc
97N-4451	76.79 d	83.66 bc	1.09 a
Contrast			
Conv. vs LRS	*	**	ns

Note: 1 - 3 are conventional hybrids; 4 - 11 are LRS hybrids.

1 means, within the same column, followed by the same letter are not different by an ANOVA protected LSD test ($P < 0.05$).

* means significant at $p < 0.05$ level; ** means significant at $p < 0.01$ level.

ns means non-significant.

Table 4. 4: Root and shoot dry masses, and root-to-shoot ratio of the 11 maize hybrids harvested at 20 days after emergence (Experiment 2)

	Dry mass (mg)		
Genotypes	Shoot	Root	Root/Shoot
P3979	171.00 cd[1]	99.89 de	0.59 f
39r52	112.4 g	89.22 e	0.80 bc
Z8968	138.41 efg	122.56 bc	0.89 a
LRS I	133.46 efg	101.32 de	0.77 cd
LRS II	135.88 efg	103.86 cde	0.77 cd
97iso-49	130.6 fg	113.65 cd	0.87 ab
97N-4469	186.97 bc	117.45 cd	0.64 ef
97iso-37	161.27 cde	121.27 c	0.75 cd
97iso-29	200.91 b	141.36 b	0.71 de
97N-4295	290.69 a	173.34 a	0.60 f
97N-4451	147.82 edf	104.37 cde	0.71 d
Contrast			
Conv. vs LRS	*	**	ns

Note: 1~3 are conventional hybrids; 4~11 are LRS hybrids.

[1] means, within the same column, followed by the same letter are not different by an ANOVA protected LSD test (*P* < 0.05).

* means significant at p<0.05 level; ** means significant at p<0.01 level; **ns** means non-significant.

Table 4. 5: Stepwise backward multiple regression analysis between fractal dimension and other morphological parameters (analysis of variance)

Five variable model (R^2=0.5748)		Three variable model (R^2=0.5682)	
Variables	P-value	Variables	P-value
Total Length	0.0156	Total Length	0.0056
Surface Area	<.0001	Surface Area	<.0001
Average Diameter	0.1865	Forks	<.0001
Tips	0.5299		
Forks	0.0002		
Intercept	<.0001	Intercept	<.0001

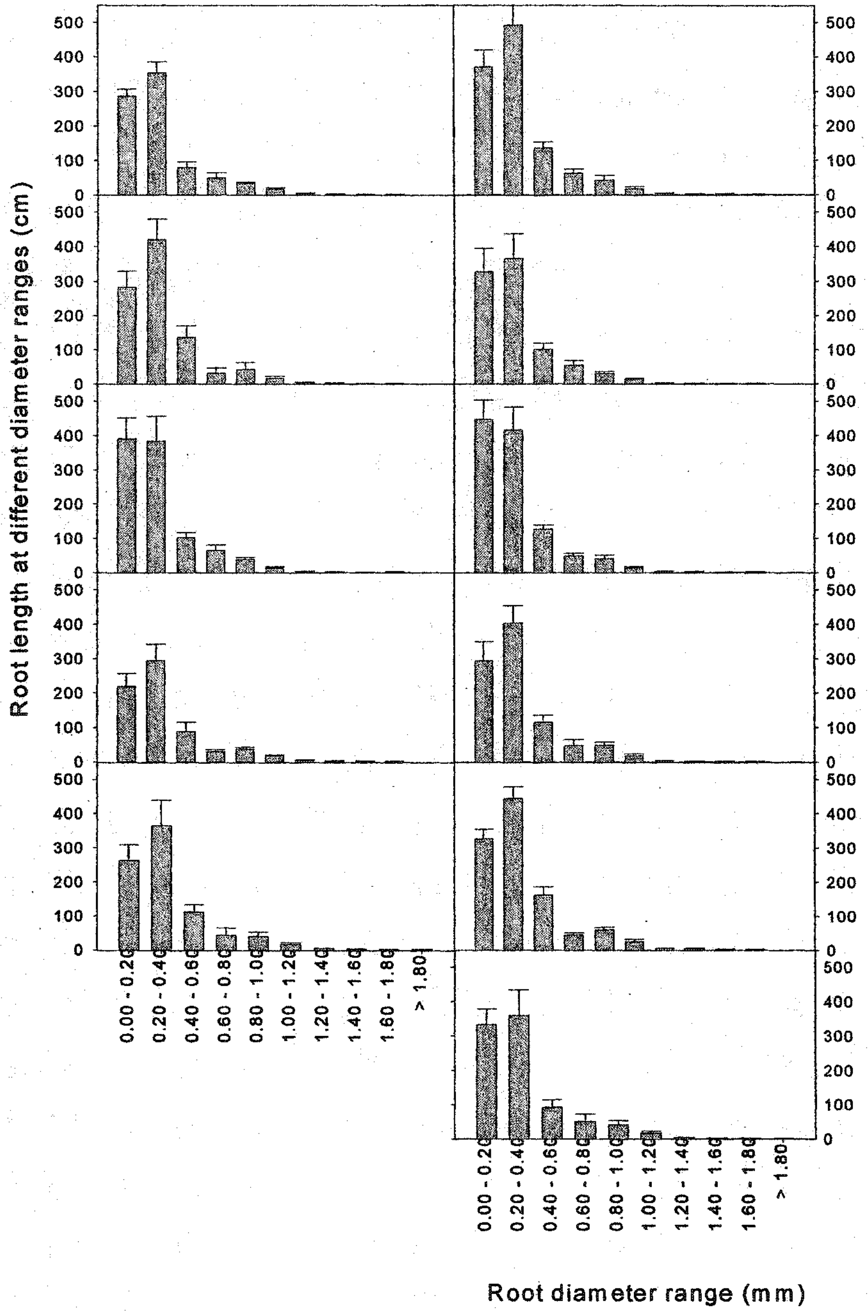

Figure 4. 1: Root total length classified according to diameter ranges in ex[eriment1

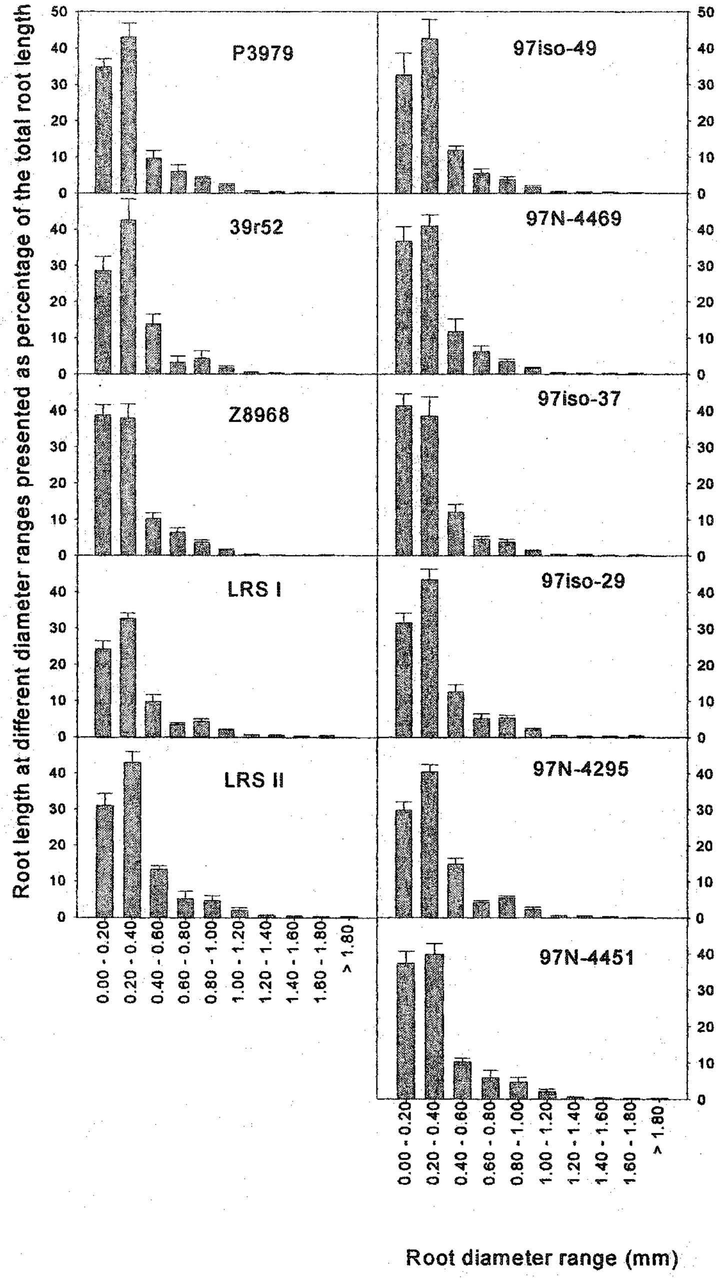

Figure 4. 2: Root lengths belonging to different diameter classes expressed in percentage of the total root length from Experiment 1

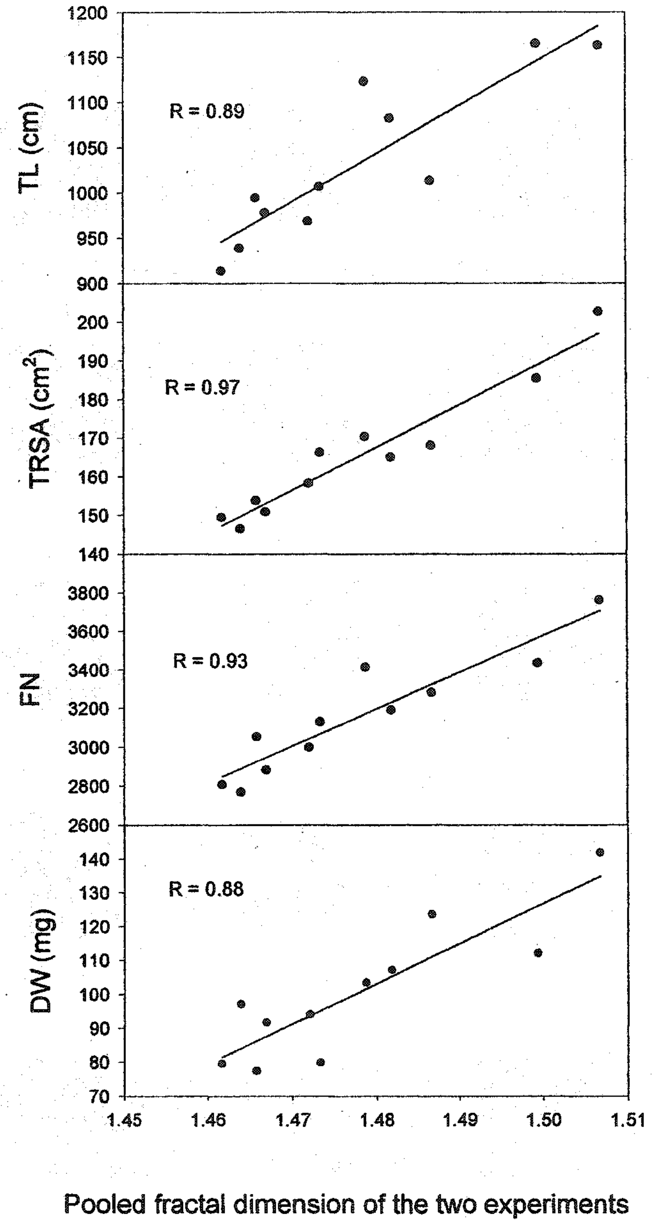

Figure 4. 3: Correlation between the fractal dimension and other morphological variables (Data pooled from the two experiments)

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Preface to Chapter 5

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As promising hybrid candidate for production in short season areas, there is little information on LRS maize regarding disease resistance. However, casual observations during earlier field studies suggested that LRS maize had increased resistance to common smut. In this chapter, resistance of LRS maize to two common ear diseases, *Gibberella* ear rot and common smut, were investigated. The possible reasons for the resistance, along with details of methodology are discussed. This can serve as a start for an overall examination of the disease resistance among the LRS maize hybrids.

Chapter 5

Assessment of resistance of LRS maize to *Gibberella* ear rot and common smut

5.1. Abstract

Four newly developed LRS maize hybrids and four conventional hybrids were evaluated for their resistance to *Gibberella* ear rot in 1998 and 1999. Two inoculation techniques, kernel stabbing and silk channel injection, were used to evaluate kernel and silk resistance, respectively. The natural incidence of common smut was also observed in another experiment with LRS maize hybrids. There were 6 LRS, 1 NLSR and 3 conventional hybrids included in this experiment. The results showed that the kernel stabbing technique was better than the silk channel injection method for detecting differential resistance among hybrids in our experiment. Most of the LRS maize hybrids expressed more resistance to *Gibberella* ear rot than the conventional hybrids. The data on natural incidence of common smut confirmed our previous preliminary observation that LRS maize was less susceptible to common smut than conventional maize.

Key words: common smut, *Gibberella*, Leafy reduced-stature maize, ear rot, *Zea mays L*

5.2. Introduction

Recent studies have revealed a series of improved agronomic characteristics associated with LRS maize, such as early maturity, and higher harvest index, which could increase the reliability of maize production in short season areas (Modarres *et al.* 1997a,b). To date there has been no disease resistance assessment of LRS maize, although preliminary observations have suggested lower levels of common smut [*Ustilago maydis* (DC.) Cda.] than in conventional hybrids. Common smut often enters the ear via the silk by spores landing on the silk, germinating, and the subsequent growth of mycelium down to the silk to the kernels (Pataky *et al.* 1995). In Canada, one of the most important diseases of maize ears, *Gibberella* ear rot, is caused by *Fusarium* spp., which also enter the ear via the silk (Hesseltine and Bothast 1977, Sutton 1982).

F. graminearum Schwabe [teleomorph=*Gibberella zeae* (Schwein.) Petch] and *F. verticillioides* (Saccardo) Nirenberg [=*F. moniliforme* J. Sheldon, teleomorph=*G. fujikuroi* (Sawada) Ito in Ito and K. Kimura] are two major causal pathogens of maize ear rot around the world. In Canada *F. graminearum* ear rot, also called *Gibberella* ear rot, is the major maize ear disease (Sutton 1982). This disease is characterized by an ear rot that usually starts from the tip, but may also originate from the base of the ear. Pinkish-white mycelium or mold is present on the colonized grains. This fungus over-winters in crop debris of maize or wheat. In the following spring, ascospores produced in the perithecia or macroconidia produced on debris are ejected into the air, and infect the ear through the silks. Infection can also occur through wounds caused by insects such as the European maize borer (*Ostrinia nubilalis* Hübna), or bird damage (Attwater and Busch 1983, Sutton *et al.* 1980). Techniques to evaluate maize hybrids for both silk and kernel resistance have been developed (Reid *et al.* 1996b).

The main concern about this disease is the production of mycotoxins in the grain and their impact on livestock (Miller and Trenholm 1994). The fungus produces two important mycotoxins, zearalenone and deoxynivalenol (DON or vomitoxin). Zearalenone is an estrogen-like compound that causes reproductive disorders in swine (Mirocha and Christenson 1974). The trichothecene DON causes feed refusal in swine along with decreased weight gain (Prelusky *et al.* 1994). Deoxynivalenol is also a phytotoxin that causes membrane leakage in some susceptible maize genotypes (Cossette and Miller 1995). At present, there are no effective means of control for this disease. The most feasible control, from an economic standpoint, would be host-plant resistance. Unfortunately, adapted sources of resistance to ear rot are few.

The objective of this study was to determine if the new LRS maize hybrids possess greater resistance to *Gibberella* ear rot and common smut than conventional hybrids.

5.3. Materials and methods

Four LRS and four conventional maize hybrids (Table 5.1) of different maturities were arranged in a randomized complete block design (RCBD) experiment with three blocks. Each plot consisted of eight 6 m long rows with 0.76 m between rows. The population density was 75,000 plants ha^{-1}. Twenty plants from each plot were subjected to a silk channel injection, and another 20 plants to a kernel stabbing inoculation. The natural incidence of common smut was recorded in another experiment which consisted of a wider range of LRS hybrids (Table 5.2) and larger plots (two 8 X 6 m plots for each hybrid), arranged in a RCBD with three blocks. The disease rating in both experiments were conducted at the physiological maturity stage. Inoculated plants were evaluated with the disease severity rating system of Reid *et al.* (1996b). This is a 7-class rating system where 1 = no symptoms, 2 = 1-3%, 3 = 4-10%, 4 = 11-15%, 5 = 16-50%, 6 = 51-75%, and 7 > 75% of kernels on an ear exhibiting visible symptoms of infection. The numbers of visible symptoms of smut in each ear were counted, based on the 500 plants sampled for each hybrid (Table 5.2). Both experiments were conducted in 1998 and 1999 on Chicot light sandy loam (mixed, frigid Typic Hapludalf) soil at the E. A. Lods Agronomy Research Centre of the Macdonald Campus of McGill University, Ste. Anne de Bellevue, Quebec (45° 26' N latitude). The planting date was May 25th in 1998 and May 28th in 1999.

Fusarium inoculum was obtained from Agriculture and Agri-Food Canada, prepared as previously described by Reid *et al.* (1992, 1996b). Macroconidial suspensions of three virulent isolates (DAOM 180378, DAOM 212678 and DAOM 194276), were prepared separately and then mixed to a final concentration of 2 x 10^5

conidia ml^{-1} before inoculation. The silk channel injection was carried out by injecting 2 ml of the conidial suspension into the silk channel of the primary ear 5-6 days after silk emergence. Kernel stabbing inoculation involved wounding the ear with a probe, consisting of 4 nails (1.5 cm) fixed to a cylindrical wooden handle (Chungu *et al.* 1996). Ears were stabbed approximately 15 days after silk emergence, which occurred between August 10 to 20 in the two years. The nails were dipped in the inoculum and then stabbed through the husk, wounding 3 to 4 kernels in the middle of the ear (Chungu *et al.* 1996).

For each experiment the data were analysed separately for each year as Bartlett's test (Steel *et al.* 1997) showed that the variance of the data were not homogenous across years. Therefore the data were analysed separately by using the GLM procedure of SAS (SAS Institute 1994). Simple means comparisons were performed with a GLM protected LSD test ($P < 0.05$).

5.4. Results and Discussion

Both 1998 and 1999 temperatures were warmer than the 30-year average (Table 5.3). The higher precipitation in August and September in 1998 provided favorable conditions for *Gibberella* ear rot development, which was evidenced by the higher severity of ear rot ratings in 1998 (Table 5.1). *F. graminearum* also develops more extensively during wet years (Miller *et al.* 1995). It was also noted that physiological maturity occurred 10 days earlier in 1999 than in 1998. This was probably because of higher temperatures and precipitation in September of 1999 compared to 1998, leading to more rapid grain filling in 1999 (Peters *et al.* 1971).

5.4.1. Resistance to *Gibberella* ear

In both years, the infection rating from kernel stabbing inoculation was higher than silk channel injection (Table 5.1). The results from silk channel injection were highly variable (data not shown). This may have been because silk channel injection was more sensitive to inoculation timing and environmental conditions. In actual practice it was impossible to conduct the inoculations under the same conditions for all hybrids. This was due to the range of maturity dates. For example, if all the hybrids were inoculated 5 days after silking, then the inoculation dates could not be the same, due to the developmental differences among the hybrids. Different inoculation dates would almost certainly result in different environmental conditions at the time of inoculation, which would affect infection development. Conversely, inoculating all hybrids on the same day meant that they were inoculated at different stages of development, which would also affect infection development. In addition, not all the hybrids formed a silk channel, due to a combination of genetic and environmental factors. This resulted in the pathogen developing in micro-environments that differed among hybrids. The kernel stabbing inoculation technique was less affected by environmental factors because the inoculation was under the husk and directly into the kernels, which removed some of the potential environmental influences.

In both years, most LRS maize hybrids, except hybrid 97iso-29, expressed greater kernel resistance to *Gibberella* ear rot than the conventional hybrids (Table 5.1), although the ranking and degree of resistance for individual hybrids changed between years. In 1998, LRS hybrids 5, 6, and 7 were more resistant than the conventional lines 2 and 3. In 1999, the same LRS hybrids (5, 6 and 7) were more resistant than conventional hybrids 1, 2 and 3. The greater resistance may have been due to their more rapid development and faster dehydration in later phases of development (Rao *et al.* 1998).

5.4.2. Resistance to common smut

The natural incidence of common smut was recorded in a wider range of LRS maize hybrids (Table 5.2). Most LRS maize hybrids were more resistant to common smut than the conventional hybrids (Table 5.2), although some LRS hybrids were more susceptible, eg. 97iso-29. In 1998, five of the seven LRS hybrids were more resistant than conventional hybrids 1 and 2. In 1999, six of the same LRS hybrids were more resistant than all three of the conventional hybrids. Increased numbers of husks around the ear, leading to more difficult fungal entry and more rapid development, leading to escape from serious infection, might partially account for this. Hybrid 97iso-29 was susceptible to smut in both experiments and in both years, which suggests some connection between resistance to the two pathogens.

5.5. Conclusions

The LRS maize hybrids included in the experiments above represent the latest achievement in a LRS maize-breeding program. The results of this study showed that some of these LRS maize hybrids have better resistance to *Gibberella* ear rot and common smut, two major ear diseases of maize, than the elite conventional commercial hybrids. At present it is difficult to say whether the improved disease resistance was the result of physiological and biochemical changes or developmental changes associated with the Leafy and reduced-stature traits. However, improved resistance to *Gibberella* ear rot following direct inoculation into the kernels suggests that at least some of the resistance is at the physiological or biochemical level.

Table 5. 1: *Gibberella* ear rot ratings after kernel inoculation, with *Fusarium graminearum*, of four Leafy reduced-stature (LRS) and four conventional maize hybrids in 1998 and 1999

Hybrids	CHU	Ear rot rating[a]	
		1998	1999
1 Pioneer 3979	2400	2.90bc	2.41bc
2 39r52	2500	3.63a	2.69b
3 Pioneer 3902	2600	3.43a	2.69b
4 Z8968	2700	2.61cd	2.17c
5 97iso-49	2400	2.23d	2.24c
6 LRS I	2500	2.49cd	2.26c
7 97N-4469	2500	2.33d	1.62d
8 97iso-29	2600	3.13ab	3.16a
$LSD_{0.05}$		0.51	0.41

Note: 1,2, 3, 4 are conventional; 5, 6, 7,8 are LRSs;

[a] Ear rot rating is based on a scale of 1-7 where 1 = no symptoms, 2 = 1-3%, 3 = 4-10%, 4 = 11-15%, 5 = 16-50%, 6 = 51-75%, and 7 > 75% of kernels on an ear exhibiting visible symptoms of infection.

Means, within the same column, followed by the same letter are not different by an ANOVA protected LSD test ($P < 0.05$).

Table 5. 2: Natural incidence of common smut based on the number of infected plants among 500 evaluated plants

Hybrids	CHU[a]	Incidence / 500 plants	
		1998	1999
1 Pioneer 3979	2400	21.33c	9.33b
2 39R52	2500	40.67a	13.33a
3 Z8950	2700	3.67f	8.67b
4 97iso-49	2400	27.33b	4.33de
5 97iso-37	2450	4.00ef	3.33e
6 LRS I	2500	4.33ef	6.00cd
7 LRS II	2500	8.33de	4.00de
8 97N-4469	2500	11.67d	8.33bc
9 97iso-29	2600	24.33bc	12.67a
10 97N-4451	2400	1.67f	4.00de
$LSD_{0.05}$		4.59	1.81

Note: 1, 2, 3 are conventional; 4~9 are LRSs; 10 is NLRS

Means, within the same column, followed by the same letter are not different by an ANOVA protected LSD test ($P < 0.05$).

Table 5. 3: Average temperature and total rainfall for each month during the growing season in 1998 and 1999, and the 30 year averages.

Month	1999		1998		30 year average	
	Temp. (°C)	Precip. (mm)	Temp. (°C)	Precip. (mm)	Temp. (°C)	Precip. (mm)
May	16.2	44.2	17.4	50.5	12.9	68.3
June	21.0	88.5	19.5	74.5	18.0	82.5
July	22.6	74.0	21.1	89.5	20.8	85.6
Aug.	20.0	67.0	21.0	92.5	19.4	100.3
Sept.	18.1	194.5	16.1	62.0	14.5	86.5
Oct.	7.7	88.0	9.8	62.5	8.3	75.4

Local climate information was collected from the nearby (15 km) Environment Canada meteorological station (Dorval, Quebec).

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Chapter 6

General Discussion

6.1. Development, yield components, and yield

LRS genotypes have more rapid leaf appearance and expansion rates during early developmental stages, and higher above-ear leaf number and area during later stages, than conventional hybrids (Modarres *et al.* 1997a,b, Begna *et al.* 1997a,b). My data on early LAI establishment in the field and on the shoot development in the indoor experiments corroborate these findings. The advantage of the LRS maize is rapid early leaf area development, which could fit very well into a short season environment. However, later maturing conventional hybrids can eventually accumulate as much or more leaf area than LRS maize, as I observed in my work. The smaller leaf size, due to the rd1 trait, and the shorter overall development period, offset the effects of fast leaf production rate on the LAI. In the following vegetative development stages, although LRS maize had more total leaves and more leaves above the ear than the conventional maize, the final LAIs of LRS maize were not greater than that of conventional hybrids.

Because of the shorter LRS stems, the leaf area of LRS maize per unit volume of space, is much larger than that of conventional maize (Costa, unpublished data), which means a larger LAI-to-biomass ratio for the LRS maize. Providing that all the leaf area has the same photosynthetic efficiency, the LRS maize would produce more photosynthate during the season. While the LAIs were similar by the end of the season LRS maize had higher LAI than that the conventional hybrids at the beginning of the season, so that the total LAI-weeks would have been greater over the entire season. The reduced plant size of LRS maize also made more of the photosynthate produced by the leave available to grain filling (Austin *et al.* 1980). The higher harvest index of LRS maize, observed in this study, is an evidence of this. This is of great importance for short growth season areas where LAI is always a limiting factor. This is because, with the exception of LRS hybrids, the shorter the development time for maize hybrids, the fewer leaves they produce (Van Esbroeck *et al.* 1997).

Poor pollination and competition between vegetative and grain filling activities are the major causes of yield decrease when the population density is above optimum (Hashemi-Dezfoli and Herbert 1992, Sowell *et al.* 1961). The compact plant size, shorter vegetative growth period and prolific trait of LRS hybrids made them more tolerant of high population density. The optimum population density of LRS maize is much higher than that of conventional maize (Begna *et al.* 1999). If the LAIs of the two groups were compared at their respective optimum population densities, LRS hybrids would have much higher LAIs than conventional maize. As a result, a higher grain yield should be expected for the LRS maize. This hypothesis was not consistently supported during our two years of field experimentation, in contrast to the findings of Modarres (1997a). In part, this may have been because both 1998 and 1999 were extremely warm years for maize growth, obscuring the potential advantages of LRS hybrids in a short season area. In part, this may have been because of the hybrids used. While all of these hybrids included the Leafy and reduced-stature traits, they had not been selected for yield and so may not have represented the "best" of this group, whereas the commercial hybrids they were compared with are the result of intensive commercial breeding programs with long histories and rigorous selection for high yield. It should also be noted that, when both LRS and conventional maize were placed under an extremely high population density, as in 1998, the yield of the conventional hybrids was reduced substantially, while the yields of the LRS hybrids were increased slightly.

6.2. Shoot and root architecture

Both total leaf number and above-ear leaf number were higher for LRS than conventional maize hybrids, while plant and leaf size were smaller for LRS than conventional maize hybrids. This brought the LAI of LRS maize at different stages close to that of the conventional maize hybrids. The leaves around and above the ear have the highest photosynthetic efficiency and make the largest contribution to grain filling (Dwyer and Stewart 1986). The reduced plant size reduced the energy needed for vegetative growth and the period required to reach maturity. The erectile upper leaves observed in the LRS maize may have increased overall canopy photosynthetic efficiency (Fakorede and Mock 1978) and reduced the shading of lower leaves. This also may have made the LRS hybrids more tolerant of high population density.

The root morphological study, conducted during early development, indicated that LRS maize normally had a larger root system and shoot system than the conventional maize hybrids, at this stage. This may partially explain the higher LAI during early development stages, as the larger root system may have allowed more nutrient and water uptake and, therefore, more growth. The LRS maize, in general, had longer roots, a larger root surface area, more tips and forks, and more dry mass than the conventional maize hybrids. This contradicted the findings of Costa *et al.* (2001), who made a comparison between one LRS and one conventional hybrid. It may be that the LRS hybrid used by Costa was not typical of the group. Fractal analysis also revealed greater complexity for the root systems of LRS hybrids. The root-to-shoot ratio of LRS maize was higher than that of conventional maize hybrids at the beginning. There was also variability among hybrids within the LRS group, indicating that a further improved root system could be achieved through careful genetic selection.

6.3. Fractal dimension (FD) and morphology

Root morphological characters such as total length, surface area, branching frequency and dry mass have been conventionally used to describe a root system (Murphy and Smucker 1995). It is difficult to compare root systems that are quite different with regard to these variables. Fractal dimension is a single unit value that is a function of these variables. It could act as a single-value comprehensive estimation of root complexity. Changes to individual morphological variables would affect the fractal dimension. FD is only one value and without any unit, and is therefore relatively straight forward to use in mathematical exercises such as modeling. For instance, it has been successfully applied to the Beer-Lambert law to estimate light interception by crop canopies (Foroutan-Pour *et al.* 2001).

Contrast analysis showed that fractal dimension was different between the LRS and conventional hybrid groups, with the LRS hybrids showing greater root system complexity. This was consistent with the results of comparisons made between the LRS and conventional hybrids for individual morphological variables. We found Correlations between FD and root total length, root surface area, branching frequency and dry mass were highly significant ($\alpha = 0.01$), supporting the suitability of FD as an objective variable for estimating root complexity. No direct relationship between early root architecture and later canopy architecture development was found; however, similar measurements of root attributes at later stages might reveal such relationships. In general, the root systems of the LRS hybrids were more branched than those of conventional hybrids, in the same way as the LRS stems have more leaves than the conventional ones, indicating a general pleiotropic effect of the LRS condition on the root system.

6.4. Development and disease resistance

Resistance to common smut and *Gibberella* ear rot was tested. These are two important maize ear diseases and no effective control measures are available at present (Schaafsma *et al.* 1997, Du Toit and Pataky 1999). Although the level of resistance varied within the group, The most resistant hybrids were always among the LRS maize. Both diseases can systematically infect a maize plant or enter the ear via the silk, as spores, during the silking stage (Pataky *et al.* 1995, Reid *et al.* 1992).

Two mechanisms were inferred based on the available information regarding LRS maize. First the rapid early development (Chapter 3 of this thesis) might allow some degree of disease avoidance. Earlier silking could be particularly important in this regard, allowing silking to occur prior to the occurrence of maximum inoculum level. Second, the greater number of husks around the ear of LRS maize (Modarres *et al.* 1997a) might deter pathogen entry through the silk channel. It is not clear whether one of these, or a combination of the two, plays an important role in the improved resistance. It is also possible that some linked resistance gene has been introduced along with the Leafy and/or rd traits. The test of *Gibberella* ear rot resistance with the ear stabbing inoculation indicated that more direct resistance to disease might also be a factor, because this exposed the wounded kernel directly to the pathogen. Evidence for a gene for silk resistance to *Fusarium graminearum Schw.* ear rot of maize has been reported (Reid *et al.* 1994).

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Chapter 7

General conclusions

1. Some of LRS hybrids have higher harvest indices (HI) than conventional hybrids. Among the LRS hyrbids there was no relationship between HI and time of maturity. The high HIs previously found in extremely early LRS hybrids were also present in the medium and late-maturity LRS hybrids.
2. Among the LRS hybrids used in this work a high HI was not associated with high yield.
3. LRS hybrids had higher leaf production rates than the conventional hybrids during early development stages. As a result, they produced more leaves, especially above the ear, during the vegetative development period, than conventional hybrids. When LRS and conventional maize were compared at near their optimum population densities, the LAI of LRS maize hybrids was much higher than that of the conventional hybrids.
4. At early development stages LRS maize commonly developed a heavier and more branching root system than conventional maize.
5. High correlations were found between total length and total surface area, and between total length and branch frequency when these relationships were tested across a wide range of maize genotypes. However, no clear relationship could be established between early root architecture and later canopy architecture.
6. The root complexity of LRS maize, assessed through fractal dimension (FD) analysis, was higher than that of conventional maize, at early stages of development. A high degree of correlation was found between FD and each of the following: root length, root surface area, branching frequency and root dry weight. Among the root

morphological variables, root length, branching frequency and root surface area contributed most to fractal dimension.

7. The hyrbids with the greatest resistance to common smut and *Gibberella* ear rot diseases where LRS hyrbids, although variation among hybrid types existed.
8. In view of LRS maize's many new characteristics, as discussed in this thesis, I conclude that LRS maize has high yield potential, especially when grown in short season areas, but needs more careful genetic selection for high yields and more work to identify the best agronomic management.

Chapter 8

Contributions to knowledge

1. The high harvest index (HI) previously observed by other researchers in the extremely early LRS maize hybrids is not related to the maturity date, so that high HI could potentially be expressed in LRS lines with medium and late maturity, i.e. for hybrids potentially produced in a wide range of maize production areas.
2. The measured high leaf production rate and high LAI at early deveopmental stages provides additional evidence as to the rapid early development of LRS maize.
3. During early development LRS maize has a heavier and more branched root system than conventional maize. This thesis demonstrated this to be so over a range of hybrids. There is considerable variability among genotypes within the LRS and conventional hybrids for these root variables. However, the percentages of root length distributed among the specific diameter ranges were quite stable across genotypes. No clear relationship could be established between the early root architecture and elements of later canopy architecture. However, the generally different root structure of LRS vs. conventional hybrids does indicate pleiotropic effects of the Leafy and reduced-stature traits on roots.
4. The fractal dimension (FD) of LRS maize hybrids is higher than conventional maize hybrids, indicating a higher complexity of LRS maize roots. A high degree of correlation was found between FD and root length, root surface area, branching frequency and root dry weight. Root length, branching frequency and root surface area contributed most to fractal dimension in maize root systems.

5. The hybrids with the greatest resistance to common smut and *Gibberella* ear rot were LRS types, indicating that careful select could ensure the presence of this trait in subsequently developed LRS hybrids.

Chapter 9

Suggestions for future research

1. Further explore the yield potential of LRS maize. This needs both careful selection in a breeding program and development of management practices. While some of the work conducted by other students have used LRS hybrids with both high HI and high yield, these two attributes do not always occur together. Developing hybrids that consistently manifest both high HI and high yield remains to be done. Comparisons between LRS maize and conventional maize should be conducted under typical short season area conditions, and under their optimum management conditions.
2. Test the disease resistance of LRS maize to other important diseases such as leaf spot and virus diseases, based on the visual observation that LRS maize might be more resistant to some leaf diseases, since the leaves of LRS maize were often found to remain green even after physiological maturity.
3. Investigate the evolution of root morphology and fractal dimension at later maize development stages. This could reveal more detail regarding pleiotrophic effects of the Leafy and reduced-stature traits and potentially explain some of the changes observed above ground.
4. Research on root topology and nutrient uptake properties under field conditions should be conducted.