Agronomic and physiological aspects of competition for light between corn hybrids differing in canopy architecture and weeds

by
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Dedication

To my family and my fiancee Wubnesh for their constant love, encouragement, understanding and patience in daily life

Short Title

PHYSIOLOGICAL ASPECTS OF COMPETITION FOR LIGHT IN CORN AND WEEDS

Abstract

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The problems associated with short growing seasons has led to the development of leafy-reduced stature (LRS) corn hybrids. These hybrids have more leaf area above the ear, more rapid leaf area development, shorter stature, earlier maturity, and better responses to high plant populations and narrow spacings than conventional hybrids. Plants grown in a reduced light environment are limited in carbon assimilation and this, in turn, results in reductions in growth and development. A way to supplement the availability of photosynthate is injection of sucrose into plant stems. The objective of this thesis was to determine the ability of LRS corn plants to compete with weeds, and the reactions of weed species to the shade, including the relationships between weed growth (increase in biomass) and development (shape) under shaded conditions. Three years of field experiments (LRS and more conventional corn hybrids with both transplanted and naturally growing weeds) and two years of greenhouse work [weeds alone, C_3 (lamb's quarters and velvetleaf) and C_4 (redroot pigweed) in full sun or deep (75%) shade injected with 15% sucrose or not] were conducted. Yield reductions due to weed pressure were lower for LRS than other hybrids. Biomass production by both transplanted and naturally occurring weeds was up to 85 % less under corn canopies than when grown without competition from corn. The biomass of C_4 weeds was more reduced by competition with corn plants than that of C_3 weeds. In spite of quick and early leaf development, leaves and other plant parts of LRS were not damaged excessively by mechanical (rotary hoeing) weed control. Both C_3 and C_4 weed plants produced more dry matter when injected with sucrose. Dry weights of sucrose injected shaded plants were not different from full sun uninjected plants. However, sucrose injection did not alter shading effects on development (distribution of biomass). Dry matter production and photosynthetic rates of C_4 weeds were more reduced by shading than those of C_3 plants.

Résumé

Les problèmes associés aux courtes saisons de croissance ont mené au développement des hybrides de maïs feuillus à stature réduite (FSR). Comparés aux hybrides conventionnels, les FSR possèdent une plus grande surface foliaire au dessus de l'épi, un développement foliaire plus rapide, et une meilleure réponse aux fortes densités de population et aux rangées étroites. Dans un environnement où la luminosité est réduite, les plantes ont une assimilation limitée de carbone. Ceci résulte en la réduction de la croissance et du développment. L'injection du sucrose dans la tige de la plante est une façon de lui donner un supplément de métabolites photosynthétiques. L'objectif de cette thèse est de déterminer la capacité des FSR de compétitionner avec les mauvaises herbes, la réaction à l'ombre des différentes espèces de mauvaises herbes, incluant les relations entre la croissance des mauvaises herbes (biomasse) et leur développement (forme). Pendant trois ans, nous avons mené des tests aux champs incluant les FSR, les hybrides conventionnels de maïs, des mauvaises herbes naturelles ou transplantées. Pendant deux ans, nous avons aussi mené des tests dans les serres incluant des mauvaises herbes C_3 (chénopode et abutilon) et C_4 (amaranthe à racines rouges), au soleil ou à l'ombre (75%), injectées ou non de 15% de sucrose. La réduction du rendement dûe à la compétition avec les mauvaises herbes était plus faible pour les FSR que pour les hybrides conventionnels. La biomasse des mauvaises herbes sous le maïs était jusqu'à 85% plus faible que celle des mauvaises herbes cultivées sans compétition avec le maïs. La biomasse des mauvaises herbes C_4 a été plus réduite par la compétition avec le maïs que celle des C_3. Malgré le développement foliaire rapide et hâtif, les feuilles et autres organes des FSR n'étaient pas endommagés par le sarcalge mécanique (houe rotative). Les mauvaises herbes C_3 et C_4 ont produit plus de biomassse suite à l'injection de sucrose. La biomasse sèche des plantes injectées cultivées à l'ombre n'était pas différente de celle des plantes non injectées cultivées au soleil. Cependant l'injection de sucrose n'a pas altéré les effets de l'ombre sur le développement (distribution de la biomasse). La production de biomasse sèche et la photosynthèse des mauvaises herbes C_4 ont été plus réduits par l'ombre que ceux des C_3.

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Chapter 1

GENERAL INTRODUCTION

1.1 Corn production levels and use

Cereal grains are and will continue to be important sources of carbohydrates, protein, vitamins and minerals for an ever increasing world population. They constitute the world's major sources of food for humans and feed for livestock. It has been estimated that cereal grains provide 56% of the food energy and 50% of the protein consumed on earth (Christie, 1987). However, the proportion of energy obtained through cereals in the form of human diets varies substantially from location to location (Charlotte and Hazel, 1987).

On a world wide basis the major cereals, in descending order of importance, are wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), corn (*Zea mays* L.), barley (*Hordeum vulgare* L.), and sorghum (*Sorghum bicolor* L.). Wheat, rice, and corn together make up 3/4 of the world grain production. Corn is a major crop for both direct and indirect human consumption as it forms a major energy feed for livestock. In some cultures, corn has been portrayed as the staff of life. In Mexico, close to 98% of the corn crop is consumed in the form of tortillas, the daily bread of the Mexican people (Wellhausen, 1976). Economically, the most important product of corn is the grain which is a valuable source not only of starch but also contains more oil than most other cereals (Langer, 1991)

According to FAO figures 604,012 million metric tons of corn were produced world wide from 137,429 million ha in 1998. Corn production has increased strongly since 1930 due to expansion of production area, genetic improvement and more efficient management practices (especially N-fertilizer additions) (FAO, 1992). Genetic improvement has been largely associated with improved resistance to stalk breakage, root lodging, ear droppage and barrenness, as well as improved yield potential and developing hybrids that are able to exploit suitable cultural practices and normal climatic environments, resulting in steadily increasing yields (Gastlebery et al., 1984). Presently North America produces over 40 % of the world's corn and 97 % of this is produced in USA (FAO, 1998).

Corn has been grown in Canada for many years. The largest production areas are Ontario and Quebec, where the crop is grown extensively for grain and silage. In other parts of the country, principally Manitoba and the Maritime provinces, corn is grown largely for silage, but with more limited success for grain. Corn production area in Canada has increased from 68,000 ha in 1934-1938 to 1.1 million ha in 1998. The yield has increased from 2.5 t ha^{-1} in the 1930s to 7.9 t ha^{-1} in 1998. There are around 300,000 ha of corn produced each year in Quebec; only 25,000 ha of which are for silage. In Ontario there are 800,000 ha of corn of which 120,000 ha are used for silage (Statistics Canada, 1998). In Ontario and Quebec average grain yields were 8.09 and 7.95 t ha^{-1}, respectively in 1998 (Statistics Canada, 1998). During this century the expansion of corn production occurred mainly in Ontario, Quebec and the Red River Valley of Manitoba, largely through the greater popularity which the crop has achieved since the introduction of hybrid corn, the introduction of mechanical harvesters, and the extension of corn production into new areas, made possible by the availability of improved early-maturity hybrids.

1.2 Range of adaptation

The corn crop has a wide adaptation and is able to grow in regions ranging from the semiarid, with an annual rainfall of 20 to 25 cm, to those where annual rainfall may exceed 400 cm. Because of the wide range of climatic conditions over which corn is grown, precise limiting conditions for corn production cannot be set (Benson and Pearce, 1987).

1.3 Physiological and morphological characterization of corn

The yield of any crop represents the summation of numerous physiological processes and overall morphological development. Normally corn plant development is divided into the vegetative and reproductive stages. The vegetative stage can be further divided into stages like planting to germination, germination to emergence, and emergence to tassel emergence, whereas the reproductive stage is divided into tassel emergence to silk emergence, silking (silk emergence) to the onset of grain filling and grain filling to maturity. The effect of temperature on development varies from stage to stage. Therefore it is important to partition the limited heat units available for each stage in order to determine the effects of thermal time on corn yield in a short-season environment.

Vegetative phase duration and leaf area index (i.e. source size) are positively correlated (Muldoon et al., 1984; Corke and Kannenberg, 1989). The ability of a corn crop to generate photosynthate is dependant on leaf area per plant, leaf angle and plant density. Leaf area per plant is often determined by leaf number and size, which are in turn influenced by environmental factors such as temperature and photoperiod (Warrington and Kanemasu, 1983a,b; Hesketh et al., 1989). Genotype affects leaf number and size in corn. Increasing the vegetative phase of the plant leads to delayed flowering and increases in leaf number. Plant height and total leaf number are positively correlated with vegetative phase duration (VPD) and the longer the VPD, the taller the plant height and the greater the leaf number of a corn plant (Cross and Zuber, 1973; Corke and Kannenberg, 1989).

Heat sums (e.g. corn heat units) are one approach used for defining developmental responses to temperature. The use of heat-sum methods for determining the response of flowering time and grain maturity to temperature in corn have been examined extensively (Coelho and Dale, 1980; Major et al., 1991). Heat-sum or thermal-unit methods are now widely used for maturity classification of commercial corn hybrids for particular geographical locations. In particular, they are used for predicting the ontogeny of corn, especially the timing of flowering and harvest maturity. The actual number of days required for corn to reach maturity varies widely with environmental conditions, although cultivars are often designated as having a certain number of days to reach maturity. Different approaches have been used for corn. Brown (1981) developed equations that were used to determine maturity ratings for corn in Ontario, Canada. Plet (1992) also reported the use of CHU for comparison of seasonal thermal indices for measurement of corn maturity in a prairie environment.

Leaf number also serves as an indicator of corn maturity, whereby early maturity corn genotypes have fewer leaves than late maturity genotypes (Tollenaar and Hunter,1983; Stewart and Dwyer, 1994). The contributions of upper leaves and lower leaves to the grain are very different; more contribution is made by the upper leaves than those below the ear; as a result late maturing corn hybrids with more leaf number and greater leaf area above the ear, and produce more yield than early maturing hybrids (Alison and Watson, 1966; Troyer and Larkins, 1985; Troyer, 1990). Therefore an increase in leaf number or size in the upper part of the plant can increase the grain yield of corn (Johnson, 1973). Higher yields have been reported for early maturity corn hybrids that had more leaves above the ear (Modarres et al. 1997b; Modarres et al. 1998; Begna et al., 1997a,b; Begna et al., 1999). By manipulating photoperiod, Hunter (1980) was able to increase the leaf area per plant and the yield of a short-season corn hybrid. He suggested that the yield was increased by a greater assimilate supply from a larger leaf area. This yield increase was also due to a 4-5 day increase in the grain-filling period for plants grown under long photoperiod. Leaf area has been found to be one of the traits most influencing yield of a crop.

Radiation interception percentage in plant systems is determined by leaf area and therefore, this influences plant growth and final yield (Dwyer and Stewart, 1986). A longer vegetative period before flowering increases source size (Beil, 1975; Troyer and Larkins, 1985), while a longer grain filling period after flowering increases sink size in both Corn-Belt and short-season corn hybrids (Corke and Kannenberg, 1989; Troyer, 1990; Dwyer et al., 1994). Hunter (1980) suggested that breeders should select genotypes with rapid leaf area expansion during the pre-silking stage. Grain sink size is strongly associated with kernel number in grain crops, and kernel number is a function of plant dry matter accumulation (Fischer, 1985).

Tasselling and silking times are very weather dependant. Wallace and Bressman (1973) reported that a 115-day cultivar took 74 days from planting to tasselling when the average temperature was 20 ^{0}C, but only 54 days when the temperature was 23 ^{0}C. High temperatures, for example 35 ^{0}C, generally cause stress and they are usually combined with moisture stress. Several researchers (Prine 1971; Tetio-Kagho and Gardner, 1988b; Hashemi-Dezfouli and Herbert, 1992) also found that a poor light environment at very high plant populations could cause ear barrenness. A higher yield was reported for two eared than single eared corn hybrids at high plant density (Brotslaw et al., 1988). At the silking and pollination stages the two-eared hybrid was more tolerant of stress, with a yield reduction of 14%, compared with a 73% reduction for the single-ear hybrid.

The successive stages of seed development are accompanied by reductions in seed moisture, and development of a black layer in the placental-chalazal region of the milky endosperm beginning at the seeds' apex and ending at the base (Daynard and Duncan, 1969; Cross and Kabir, 1989). Harvesting earlier at lower grain moisture results in reduced grain drying costs and lower field losses and while most corn hybrids mature when the grain is at about 30% moisture, the ideal moisture content at which to start combining is considered to be about 25% (Olson and Sander, 1988).

1.4 Limitations of short growing season areas for corn production

The main problems associated with corn production in short season areas are the lower leaf area indices of the plants and insufficient heat units during the growing season. Corn hybrids grown in short-season areas tend to have low final LAIs, mainly due to shorter plant stature, which results in the production of fewer and smaller leaves than hybrids grown in longer season areas (Chase and Nanda, 1967; Hunter et al., 1980; Troyer, 1990). Hunter (1980) reported that the maximum LAIs of corn in short-season areas with normal plant population densities are low, with values not more than 2.7. At these LAIs, a corn canopy can intercept only about 75% of full sunlight. Normally early-maturing corn hybrids are source-limited (limited in assimilate supply to the grain) (Hunter, 1980; Cross, 1991), whereas mid-western hybrids are sink limited (shortage of sink to accommodate assimilate) (Tollenaar, 1977; Hunter, 1980; Cross, 1991).

The second problem for corn production in a short season area is that daily or seasonal thermal heat units are insufficient for the complete grain filling period of the current hybrids, and this in turn becomes critical to yield. Short-season corn growing areas have longer and cooler days at flowering, resulting in both thermal and photoperiod responses which slow maturation at harvest. Troyer (1990) reported that corn production in short-season areas is normally limited by heat units and by the frost free period; current hybrids seldom finish grain filling prior to the first killing frost. Thus earlier flowering corn hybrids are smaller and have longer grain filling periods, while later flowering hybrids are larger and have shorter grain filling periods.

There are two ways of increasing the leaf area of early maturity corn hybrids without delaying the silking time: breeding for increased leaf area per plant and increasing the plant population density. Modarres et al. (1997a,b, 1998) reported more leaf area development for crosses between Leafy-normal and non-leafy reduced-stature inbreeds than for non-leafy reduced-stature and early conventional corn hybrids. It has been suggested that the leafy and reduced-stature traits have potential for use in further studies that may allow the expansion of corn production into areas where it was not previously regarded as economical (Modarres et al., 1997a,b; Modarres et al.1998; Begna et al., 1997a,b)

1.5 The Leafy and reduced-stature traits

Plants bearing the leafy (Lfy1) trait are characterised by extra leaves above the ear, lower ear placement, highly lignified stalks and other plant parts, and higher yield potential than otherwise equivalent genotypes of corn (Shaver, 1983). The Leafy trait confers an increase in leaf number relative to normal hybrids. Leafy-types produce a few more leaves below the ear and almost double the number of leaves above the ear; a normal hybrid will have four or five leaves above the ear, while a leafy hybrid may have eight or nine (Modarres et al., 1997a,b). The net result of this is that Leafy plants show a dramatic increase in the production of leaf area by the time of maturity (Shaver, 1983). Thus, the Leafy morphology increases in LAI and should confer an advantage through increased light interception and photosynthesis, particularly during the grain filling period (Tollenaar and Dwyer, 1990). The considerable potential for yield increases in Leafy corn is due to the action of the Lfy1 trait which can double leaf area production (Shaver, 1983). The leafy trait also increases prolificacy. The limited commercial use of prolific corn hybrids has been attributed to poor stalk quality and plant stand ability (Lonnquist, 1967; Motto and Moll, 1983). Expression of more than one ear per plant may increase competition between the developing ears and the stalk for photosynthate, causing greater reallocation of stalk carbohydrate to the grain sink. Prolific corn has greater yield stability than the non-prolific type resulting from the capacity to alter the number of ears per plant in response to changes in plant population density or environmental conditions (Hanway and Russell, 1969; Prior and Russell, 1975; Brotslaw et al., 1988).

Reduced-stature lines are short with good stalk strength (Daynard and Tollenaar, 1983). These are particularly important traits for short-season environments where plant density could be used as a technique to increase grain yield of the corn plant. The benefits from the reduced-stature trait also include earliness, reduced lodging due to insect and wind damage and greater tolerance of higher plant population densities, which can allow further increase in leaf area index for better light interception competition with weeds.

Several leafy reduced-stature corn hybrids containing leafy and reduced traits have been evaluated along with non-leafy reduced-stature, Leafy normal and non-leafy normal hybrids for their agronomic and physiological aspects in a short-season area of eastern Canada by Modarres et al. (1997a,b, 1998). Leafy reduced-stature hybrids produced more leaf area above the ear and more yield than the non-leafy reduced-stature and early maturing conventional corn hybrids, particularly at a high plant population density (Modarres et al, 1997a,b; Modarres et al, 1998). Begna et al. (1997a,b) has also reported a higher grain yield for the newly developed Leafy reduced-stature corn hybrids than for non-leafy reduced-stature and early maturing conventional corn hybrids. This increase was mainly at high plant densities and in a narrow row spacing.

1.6 Plant population effects

In effective crop production, efficient utilization of available light is considered as an important factor and is strongly affected by crop canopy structure (Daughtry et al., 1983). Photosynthetic efficiency and growth are often related to canopy architecture, and canopy architecture is a function of leaf number, shape, distribution, and orientation, and plant size which collectively determine the vertical distribution of light within the corn canopy (Williams et al., 1968; Girardin and Tollenaar, 1994). Canopy light interception and photosynthesis are closely related to leaf area index and crop yield (Pearce et al., 1965; Tollenaar and Bruuslema, 1988). Corn yields have been increased by increasing light interception through early planting, higher plant density, and narrower row spacing (Pendleton and Egli, 1969; Andrade et al., 1993; Cirilo et al., 1994), tassel removal and reflective surfaces placed between the rows (Schoper et al., 1982).

Based on extensive agronomic research, including crop simulation modelling and remote sensing applications, it is clear that it is important to be able to predict leaf area development, crop canopy photosynthesis, evapotranspiration, dry matter production and final yields. These are all influenced by incident solar radiation and its interception by leaf surface area, which can be calculated once the leaf area development per plant is defined (Warington et al., 1983a,b).

Two components, grain number per unit field area and grain weight, determine the yield of cereals and these in turn are dependant on the leaf area of the plants. Corn grain yields are positively related to leaf area index until an optimum LAI, which is dependent on the plant canopy architecture, is achieved (Williams et al., 1968, Tollenaar and Bruuslema, 1988; Egli, 1988; Muchow et al., 1990, and Welles, 1991). Several researchers (e.g. Karlen and Camp, 1985; Daynard and Muldoon, 1983) suggested that optimum arrangements of leaf area exist for given genotypes, plant population densities, and row spacings, and that the optimum will change in response to any one of these factors.

Increasing plant population densities has been investigated by many plant researchers as a way of improving interception of incoming solar radiation by corn canopies (Duncan et al., 1967; Loomis et al., 1967; Winter and Ohlrogge, 1973; Pepper, 1974; Daughtry et. al., 1983). Agronomists have been using high plant population densities as a technique to increase crop yield per unit area for some time (Karlen and Camp, 1985). Using this method yield per plant decreases with increased plant density, however total light interception by the canopy is maximized and total yield is increased (Hashemi-Dezfouli and Herbert, 1992). Leaf area index distribution and the light capturing capability of the plant canopy, particularly at the ear level, are important parts of the plant canopy in the source-sink relationship and important considerations for short-season corn genotypes for which plant population density can be an important tool for increasing total source potential.

Plant scientists have long speculated about plant densities and researched plant competition to find the optimum plant densities for crops including corn. However, there is no single rule for all conditions because the optimum density is dependant on all unmanageable environmental factors and manageable factors such as soil fertility, corn hybrid selection, seeding date, planting pattern, and harvest time (Nunez and Kamprath, 1969; Brown et al., 1970; Rhoads, 1970; Lutz et al., 1971; Duncan; 1972; Stanley and

Rhoads, 1975; Tetio-kagho and Gardner, 1988b; Carberry et al., 1989; Andrade et.al, 1993). The optimum plant density may not be the same for all hybrids within a maturity group. For example, taller, leafier genotypes with bigger ears may have an optimum plant density that is lower than shorter smaller-eared genotypes (Warren, 1963, Carmer and Jacobs, 1965; Russell, 1985; Tollenaar, 1991). Corn hybrids used in the temperate regions generally have higher optimum planting densities.

Yield-density studies are also useful for evaluating the reactions of plants to their neighbours, and yield-density models are a valuable tool for the assessment of plant interference (Jolliffe et al., 1990). It is also well known that the grain yield of a single corn plant is reduced by the nearness of its neighbours (Duncan, 1984). Single plant yield reduction is mainly due to the effects of interplant competition for light, water, nutrition and other environmental factors. Grain yield per unit area (Prior and Russell, 1975; Karlen and Camp, 1985; Tetio-Kagho and Gardner, 1988b) and plant height (Major and Daynard, 1972; Gardner et al., 1985) increase to a maximum and then start decreasing with increasing plant population density. The response of grain yield per unit area to increasing plant density is parabolic (Karlen and Camp, 1985).

Ear weight, diameter and length, and kernel number per ear were increased, but total yield was decreased by reducing plant population density (Baenziger and Glover, 1980). Number of plants at very low or very high population densities becomes a limiting factor for the yield of corn crops. At low population densities yield is limited by the number of plants whereas at high population densities yield is limited by the number of barren plants (Buren et al., 1974; Daynard and Muldoon, 1983), and a decrease in the number of kernels per ear (Tetio-Kagho and Gardner, 1988b) or both (Hashemi-Dezfouli and Herbert, 1992). Fernando et al. (1993) have also reported shortage of sinks at very low plant density because most contemporary corn genotypes tiller to only a small extent and have low reproductive and foliar plasticity. Reductions in grain yield at higher population densities may have resulted from fewer flower initials being formed prior to flowering, poor pollination resulting from asynchrony of tasselling and silking, or from abortion of kernels after fertilization (Daynard and Muldoon 1983; Karlen and Camp 1985; Heshemi-Dezfouli and Herbert, 1992).

Corn hybrids used in temperate regions generally have optimum planting densities close to 7.0 plants m^{-2} (Russell, 1985; Tollenaar, 1991). It is important to select hybrids that are tolerant of high plant densities. Several researchers (Buren et al. 1974; Cross, 1990) reported that high population tolerant corn hybrids are generally characterized by early maturity, small size, rapid completion of the first ear and first appearance of ear silk, prolificacy, smaller tassel size, and great efficiency in the production of grain per unit leaf area. The semi-reduced-stature, compact (ctl) and reduced-stature (rd1) mutants in inbred backgrounds have been shown to be more resistant to population stress than non compact and normal-stature inbred lines (Nelson and Ohlrogge, 1957). Prolificacy and reduced bareness should be considered as important physiological traits in corn hybrids that are tolerant of environmental stress caused by high plant population density (Tollenaar et al., 1992).

Several researchers have reported that a higher harvest index is not always strongly related to dry matter production (Vattikonda and Hunter, 1983; Allen et al., 1991;

Cox et al., 1994). Tollenaar (1989) reported that recent hybrids maintain a constant harvest index as plant density increases because they are less prone to plant bareness at high densities than older hybrids.

Height reductions can occur through a shortening of each internode. As a result of changed partitioning within the shoot, the assimilates saved by stem reductions 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 comparable tall varieties. A decrease in the height of a plant can lead to increased harvest index (Johnson et al., 1986; Edmeades and Lafitte, 1993). This is the major reason for breeding to reduce vegetative parts to their optimum size and produce short plants (Borojevic, 1990). Borojevic (1990) also reported that reductions in height caused higher harvest indices, more resistance to lodging and, when planted at higher plant population densities, more nutrient uptake, resulting in higher yields per unit area.

Corn heat units from planting to tasselling and to silking and days between tasselling and silking are often changed by plant population density. Days between tasselling and silking increased (Hashemi-Dezfouli and Herbert, 1992). Pollen-shed to silking time is an important indicator of density stress in corn (Edmeades and Lafitte, 1993). Genotypes that are tolerant of high density stress usually display a shorter interval between 50% pollen shed and 50% silk emergence than intolerant genotypes under high plant population densities (Mock and Pearce, 1975; Hashemi-dezfouli and Herbert, 1992; Edmeades et al., 1993; Modarres et al., 1997).

1.7 Planting pattern effects

In the absence of factors such as nutrient deficiencies, temperature extremes, or water stress, solar radiation is the major limitation to growth. Many researchers have related plant biomass production to intercepted photosynthetically active radiation (IPAR) (eg. James and Knievel. 1995). The spacing of corn rows greatly affects plant distribution within the row for any given plant density. Plants compete with each other for nutrients, light and other growth factors. Therefore, it is reasonable that plants spaced an equal distance from each other would provide for minimum competition and maximum yield at any given plant density (Olson and Sander, 1988). Canopy architecture, final leaf area and sun angle are the most important factors affecting the interaction of light with whole plant canopies (Wanjura and Hatfield, 1986; Steiner, 1987).

Incident light is either reflected, transmitted or absorbed by the plant canopy, however the partition of incident radiation by the canopy into these three components mainly depend on the canopy size and radiation wave length (Wanjura and Hatfield, 1986). Rosenthal and Gerik (1991) reported no light transmission coefficients, but cotton cultivar differences in radiation use efficiency through the reproductive period. Therefore accumulated dry weight is a function of accumulated daily absorbed photosynthetically active radiation (PAR) and radiation-use-efficiency (RUE).

Radiation interception by a crop limits productivity when other environmental factors are favourable (Loomis and Williams, 1963; Monteith, 1981; Ottman and Welch, 1989). Radiation-use-efficiency (grams per mega joule) is defined as the above ground dry matter accumulation (grams) per mega joule of photosynthetically active radiation (PAR) absorbed by the plant (Major et al.,1991). In a plant canopy upper leaves are usually radiation saturated or less efficient and lower leaves have reduced photosynthesis, mainly because of shading. Vietor et al. (1977) reported higher photosynthetic rates for upper than lower leaves of a single-cross corn hybrid grown at a single density. Tetio-Kagho and Gardner (1988b) reported more leaf area and light interception at ear level and a shift of level of light interception upward with increasing plant population density. Therefore a more uniform distribution of solar radiation can be advantageous as upper leaves become less light saturated and lower leaves less radiation starved.

Partial redistribution of radiation from the upper to lower leaves can be beneficial because the plant leaf is more efficient at lower irradiance (Loomis and Williams, 1969, Warren, 1981). Planting pattern has an influence on the distribution of radiation within the canopy and the total amount of incident radiation intercepted by a crop (Ottman and Welch, 1989). Ottman and Welch (1989) found interactions among planting pattern, hybrid, and density and suggested that the differences in radiation interception between narrow and wide rows were most pronounced for a hybrid with an erectophile leaf habit planted at a high plant density (99,000 plants ha^{-1}). Therefore, differences found in their studies and any comparable study could be due to hybrid or plant density as well as year, location, and growing conditions.

Plants seeded in narrow rows also intercept more total radiation than in wider rows. Tom and Evans (1990) reported that their light interception model predicted 5 to 10 % more yield for corn planted in 0.38 m rows than 0.76 m rows at 9.45 plants m^{-2}.

This was mainly as a result of more light interception for narrower than wider rows. In the absence of nutrient deficiency and water stress to crop growth, a linear relationship between absorbed incident solar radiation and rate of crop dry matter accumulation was reported by several researchers (Tollenaar and Bruulsema, 1988; Muchow et al., 1990).

Reducing row spacing from approximately 1.0 to 0.5 m has resulted in effects ranging from no changes in yield (Giesbrecht, 1969) to increases of as much as 22% (Stanley and Rhoads, 1971; Ottman and Welch, 1989). Ottman and Welch (1989) also suggested the possibility that interactions between row spacing and management practices affect these results. Modarres (1995) reported a 5 to 10 % increase from row width reduction for an early hybrid but no effect with a full-season hybrid. Rutger and Crowder (1967); Brown et al. (1970); Modarres (1995) reported hybrid differences in response to row spacing. Reducing row width favours small, less leafy hybrids because these hybrids can benefit more than large leaf hybrids from increased energy available per unit leaf area in more equidistant plantings. Early hybrids tend to be smaller than late hybrids making the early hybrids more suitable for planting in reduced row widths. Early planting, as opposed to late planting, also causes a corresponding plant size reduction that favours reduced row spacing. As one would expect, reduced row spacing is most beneficial at high plant population densities (Brown et al., 1970; Modarres, 1995; Modarres et al., 1998; Begna et al., 1997b).

1.8 Effect of mechanical weed control on corn

Interrow cultivation can be an effective form of weed control. Its greatest effect is only after most weeds have emerged (Parks et al., 1995). Adequate information about the timing and rate of weed seed germination and emergence is very important in order to be able to determine the appropriate time for cultivation (Harvey and Forcella, 1993). Integration of herbicides applied at reduced rates in a narrow band over the crop row, and high population plantings of corn may help in achieving both environmental and weed control objectives (Teasdale, 1995). Forcella et al. (1992) showed that good weed control could be obtained with reduced herbicide application rates when crops were planted in narrow rows. An integrated weed management system needs to take all aspects of the cropping system into account: effects of tillage, crop rotation, crop competitiveness, and various methods of weed control (Swanton and Weise, 1991).

Rotary hoeing or inter-row cultivation alone did not control weeds as opposed to herbicides alone or herbicides with interrow cultivation (Burnside et al., 1994; Burnside et al., 1993). Rotary hoeing and inter-row cultivation together can be an effective method of weed control in corn and soybean. More than 70 % weed control in corn and soybean has been reported with only one pass rotary hoeing (Lovely et al., 1958; Mulder and Doll, 1993). Mulder and Doll (1993) also reported that two rotary hoeings alone or together with inter-row cultivation gave additional weed control in corn compared to one rotary hoeing. There was a concern by bean growers in Colorado that rotary hoeing may injure pinto bean plants and reduce yields because these growers usually use a rotary hoe to alleviate soil crusting, but not to control weeds (Vangessel et al., 1995). These same researchers reported that pinto bean hypocotyls and stems were damaged by flex-tine harrow use at both crook and trifoliate stages, while no damage or reduction in stand, yield and seed weight was caused by rotary hoeing. Mohler et al. (1997) found that in two of their three years of experiments cultivation with a rotary hoe or tine weeder reduced weed seedling density by 39 to 74 % , while the same operation reduced corn populations by an average of only 6 %.

1.9 Corn-weed competition and planting patterns

Among plants competition can occur for light, water, nutrients, oxygen, and carbon dioxide, but environmental conditions usually exclude meaningful competition for O_2 and CO_2 (Aldrich, 1987). The relationship between weed population and crop yield vary with environmental and cultural conditions (Wiles and Wilkerson, 1991). In humid or moist regions water and nutrients are usually adequate early in the season, however competition can occur for light. If water and nutrients are sufficient, photosynthesis and growth rates of individual plants in a plant community will be roughly proportional to the light each intercepts (Melvin et al., 1993). James (1994) suggested that in the absence of nutrients or drought stress, the reduction in growth of corn infested with Johnson grass is proportional to the reduction in intercepted solar-radiation per corn plant. Whether competition for light or for soil-supplied resource(s) determines threshold level or area of influence during the latter part of the growing season will depend upon the supply and the use of soil resources and upon conditions affecting the plant's ability to obtain them, and upon relative plant height, shape, and other characteristics which affect the plant's ability to obtain light (Trenbath, 1976; Thomas, 1991). Aldrich (1987) also reported crop row spacing effects on weed growth and weed competitiveness.

Row spacing can influence weed competition greatly; for example, weed weight 16 weeks after planting soybean in 50 cm rows was only 28 % of that in 100 cm rows (Felton, 1976). Some crop species are more competitive toward weeds than others. Planting patterns that favour better light distribution for the crop should favour higher crop biomass accumulation rates and higher yields. Anne and Schreiber (1989) reported 15 and 29 % contributions by pigweed to total leaf area in a soybean crop in 25 cm and 76 cm row spacings, respectively. Challaiah et al. (1986) reported large differences among winter wheat cultivars in terms of their competitiveness toward downy brome (*Bromus tectorum* L.) in Nebraska. Downy brome dry weight when grown with the most competitive cultivar was 41 and 44 % less than when grown with the least competitive cultivar at two locations.

Studies of the effect of growth factor supply on root and shoot growth suggest that canopy size and structure will reflect the combined effects of competition for light, water, and nutrients. Understanding competition is basic to minimizing the impact of weeds. Michael et al. (1992) reported leaf area reduction of each individual leaves of corn plants due to season long weed interference, mainly by increasing the number of senescenced leaves resulting in a reduction of photosynthetically active radiation available to lower leaves and also depleted available soil nitrogen and moisture levels, there by reducing the longevity of lower corn leaves. There were essential differences between species in their capacity to intercept sunlight. Monteith (1981) defined plant growth as the integrated product of intercepted photosynthetic ally active radiation. Swanton and Weise (1991) suggested an enhancement of crop competitiveness against weeds as a key component to decrease ever increasing herbicide use to control weeds. Therefore manipulation of cultivar selection, row spacing, seeding density and mechanical cultivation may provide a means of reducing the impact of weed interference on crop yields. Viram et al. (1993) reported differences in competitive ability against weeds by cultivars of common bean and soybean. They also found significant weed biomass reductions in rows narrower than the traditional 69 cm for white bean. Howe and Oliver (1987) suggested that LAI is a better indicator of weed competition than plant height, net assimilation rate, or relative growth rate. It is very clear that corn suffers severe competition from early germinating weeds because of slow early development and wide row spacings (Kropff et al., 1987). The relative competitiveness of corn can be enhanced by increasing plant density and reducing row spacing. Tollenaar et al. (1994) reported a substantial weed biomass reduction when corn plant population was increased and the lower biomass was largely associated with a higher corn LAI. Radiation is transmitted through and between leaves, and its flux density and spectral composition changes rapidly with depth (Gardner et al., 1985). Jacob and Fishman (1994) suggested height as the most important aspect influencing future growth of individuals in the crowded population because of the importance of light in the plant system.

Photosynthesis and the allocation of photosynthate are very important for seedling survival, growth and also productivity in a plant-soil-water-light management system. Kasperbauer and Hamilton (1984) reported that the reflected far to red (FR) to red (R) light ratio affected leaf shape, thickness, stomatal frequency, chlorophyll concentration, chloroplast structure, and photosynthetic efficiency of soybean and tobacco plants.

Kasperbauer and Karlen (1994) reported that more reflected FR and higher FR to R ratios due to a narrower row spacing, which resulted in corn seedlings with longer and narrower leaves, longer stems, less massive roots, increased shoot size and shoot to root biomass ratio. Kolb and Steiner (1990) reported seedling biomass reduction, but shoot-root ratio and leaf area ratio increases in northern red oak trees in shaded compared to a full sun environment and they gave low light intensity as the explanation for the failure of seedling growth to respond favourably to increased moisture in a shaded fern and grass environment. Normally shoot growth and leaf area development are favoured under shaded conditions, while root growth was favoured in conditions of root competition. Increased inter-plant interference can result in changes in morphological traits such as stem elongation and diameter, and leaf length, width and thickness (Kasperbauer, 1988). Ballare et al. (1990) described the ratio of R to FR as a major environmental signal for plants growing under competitive conditions. Anthanasios and Douglas (1980) reported an effect of decreasing row spacing on the quality and a decrease in the amount of transmitted light through a canopy of greenhouse planted tomato plants and their effects on the increasing losses of lower leaves due to accelerated senescence, resulting in significant amounts of unfiltered light reaching under the closely spaced canopies. They also reported a greater decrease in photosynthesis of the lower leaves than upper leaves due to the narrower spacing. Edward and Myers (1989) reported plants' adjustments to irradiance by decreasing light-saturated photosynthesis, leaf respiration rates, root to shoot ratios, and leaf densities, while increasing leaf area ratio (LAR) because decreases in support tissue to leaf ratios reflect greater partitioning of plant material into leaf tissues that harvest the available PPF, with less biomass diverted to tissues that deplete photosynthate.

Ghersa et al.(1994) suggested that manipulation of the radiation environment (total irradiation, and spectral composition) during the early stages of crop establishment may be a useful tool for weed control and for designing new agronomic practices that take full advantage of the differential responses of specific crop and weed species. The allocation of resources between competing plants will vary with resource levels, densities and spatial arrangements, environmental conditions which affect growth and development of the plants, and the plants' biological characteristics, such as emergence time and growth rate (Radosevitch,1988).

1.10 Light levels and photosynthetic activities

Plants grown under higher light intensities have greater photosynthetic rates per unit leaf area and become light-saturated only at higher intensities. Plants grown in a reduced light environment are limited in carbon assimilation and this, in turn, results in changes to growth (reductions) and development. This is also, in part, as a result of limitations in the photosynthetic induction requirement that develops under low light intensity (Sassenrath-Cole and Pearcy, 1994). Studies of weed species grown under light-limiting conditions have also shown reduced growth, development, and seed production (e.g. Bello et al., 1995; Zangerl and Bazzaz, 1984).

Several researchers reported that plants can adjust to irradiance by decreasing light-saturated photosynthetic rate, leaf respiration rates, stomatal conductance, leaf thickness, root growth, shoot to root ratios, and leaf density, while increasing the leaf area ratio (LAR), which decreases the support tissue:leaf ratio and results in greater partitioning of plant material into leaf tissues that harvest the available PAR, results in less biomass being diverted to tissues that act as sinks for photosynthate (Edward and Meyers 1989; Kephart et al., 1992; Allard et al., 1991; Marler et al., 1994; Ghannoum et at., 1997; Bauer et al., 1997). Many of these physiological and morphological adaptation-to-shade strategies are shared by most plant species regardless of their photosynthetic pathway. However, plant species that differ in their photosynthetic pathway (C_3 vs C_4) are likely to respond at least somewhat differently to light and CO_2 (Patterson, 1984).

Several researchers (e.g. Reeves et al., 1994; Allen et al., 1991; Prior and Rogers, 1995) reported increases in total leaf area, dry weight, and seed number of soybean plants when grown under elevated CO_2 levels. Increases in leaf area and biomass accumulation by weeds and other plants due to elevated CO_2 have been also reported previously (Zangerl and Bazzaz, 1984; Tolley and Strain, 1985; Coleman and Bazzaz, 1992). When greenhouse grown plants are supplied with carbon dioxide as an extra source of carbon, the plants often adjust to such an elevated carbon dioxide enrichment by decreasing the ribulose bisphosphate carboxylase (Rubisco) content (Sassenrath-Cole and Pearcy, 1994; Xu et al., 1994) and stomatal opening (Fay and Knapp, 1995) which can result in photosynthesis levels similar to plants growing without carbon dioxide enrichment. Plants also exhibit numerous other physiological adaptations to low irradiance, including increased quantum yield and reduced dark respiration, light compensation and saturation points (Marler et al., 1994). These researchers also reported that trees under full sunlight had lower ratios of variable to maximum fluorescence (Fv to Fm) than those that were under 25 and 50 % full sun light.

Similarly, researchers have been successful in injecting exogenous substances into plants (e.g stem injection). Using this type of techniques they were able to study the morphological and physiological response of plants to the injected substances.

1.11 Techniques to inject solutions into plants

In the past, methods for supplying nutrients into plants involved additions through roots and leaves (Rending and Crawford, 1985; Tomar et al., 1988). However, the small amount supplied and the short duration of supply made these systems inappropriate for long term physiological studies. During the last 10 years several methods have been developed to inject solutions into plants. The first injection attempts were conducted by Grabau et al. (1986) for soybean and Macknown and Van Sanford (1986) for winter wheat. Grabau et al. (1986) were able to inject an average of 51.2 mL per plant through the stem from the beginning of seed development until physiological maturity. The first workable stem infusion technique for corn was developed by Boyle et al. (1991a,b). Using this technique they were able to supply water-soluble substances into the stems of corn plants. Ma and Smith (1992); Foroutan-pour et al. (1995) reported a method to add nitrogenous solutions to barley plants using an infusion system in which the plants were able to take up to 68 mL of solution during a 20 day injection period through the hollow peduncle internode. Ma et al. (1994b) also developed a variation on the perfusion technique for injection of sucrose solutions into field grown corn, which increased the grain set of some corn hybrids. More recently, Zhou and Smith (1996) developed a pressurized injection technique which allowed solution uptake rates of 5.1 mL per plant per day for a duration of 30 days. In this technique ceramic bricks were placed on the plunger of a syringe, which produced enough pressure to force concentrated solutions into corn stems. Abdin et al. (1998) modified the pressurized injection technique and were able to inject as much as 77.3 mL of 15 % sucrose solution into soybean plants during an 8 week period.

Chapter 2

HYPOTHESIS AND OBJECTIVES

2.1 Hypotheses

1. Because of their more rapid leaf generation and other canopy architecture differences (number and distribution of leaves, size of leaves and plant as a whole), Leafy reduced-stature (LRS) corn hybrids will compete more strongly for light with weeds, will be better able to suppress weed plants, and will be less affected by the presence of weeds than conventional hybrids.

2. Because of more rapid leaf area accumulation and canopy architecture differences, LRS hybrids will be more damaged by rotary hoeing than conventional hybrids.

3. Because weed plants have evolved to compete for light, sucrose supplementation (injection) allow the weeds to overcome shading effects on growth and development.

4. Since C_3 and C_4 weed species are different in terms of photosynthetic pathways, their morphological and physiological responses to light levels and sucrose supplementation will be different.

2.2 Objectives

2.2.1. To study the responses of corn hybrids differing in canopy architecture to plant population, row spacing, weed pressure, and mechanical cultivation. Within the context of these factors to:

A. determine canopy architecture effects on corn dry matter accumulation and yield.

B. determine morphological response differences among hybrids of very different canopy architecture in the presence and absence of weed pressure.

C. determine morphological and yield responses of hybrids with very different canopy architecture and rate of leaf development to chemical and rotary hoeing methods of weed control.

D. measure weed biomass production response to different corn planting patterns and hybrids differing in canopy architecture and light interception by plants as a whole (weeds and corn).

2.2.2. To test the possibility of injecting concentrated solutions of sucrose into stems of three weed species [lamb's quarters (*Chenopodium album*) and velvetleaf (*Abutilon theophrasti* Medic.) both C_3 species and redroot pigweed (*Amaranthus retroflexus*) a C_4 species] under shaded and not shaded regimes and to determine their responses (growth, morphology, and physiology) to increased levels of injected sucrose and shading using a modified injection technique that has been previously used for soybean.

Preface to Chapter 3

This section will form a manuscript to be submitted during 1999 for publication in Crop Science. The format has been changed to be consistent within this thesis. All literature cited in this chapter are listed at the end of the thesis. Each table or figure is presented at the end of this chapter.

In this chapter I address the patterns of dry matter accumulation and partitioning among different plant parts, and leaf area development by corn hybrids of very different canopy architectures using different planting patterns in the presence and absence of weed pressure.

DRY MATTER ACCUMULATION AND PARTITIONING BY CORN HYBRIDS DIFFERING IN CANOPY ARCHITECTURE IN THE PRESENCE AND ABSENCE OF WEEDS

ABSTRACT

More rapid dry matter accumulation during early stages of corn plant development could decrease the impact of stresses associated with weed pressure. Recently, corn hybrids accumulating more leaf area, maturing earlier, yielding better in narrower row spacings and tolerating higher plant populations better than conventional corn hybrids have been developed. Although there have been previous reports regarding the high yield potential of these hybrids in short-season areas, no research has previously been conducted to assess their ability to accumulate dry matter when in competition with weeds. This is of interest because these hybrids develop leaf area more rapidly than conventional types. The objective of this study was to quantify dry matter accumulation and partitioning responses of corn hybrids with a wide range of canopy architectures to the presence and absence of weeds. Experiments were conducted in 1996, 1997, and 1998 at Ste. Anne de Bellevue, Quebec and in 1996 at Ottawa, Ontario. Three corn hybrids were tested: leafy reduced-stature (LRS), late maturing big leaf (LMBL), and conventional Pioneer 3979 (P3979). Each block of the experiment was divided longitudinally into two, one side weed-free and the other weedy. Each hybrid was planted at two plant densities (conventional and high) and row spacings (38 and 76 cm). Both leaf and stem dry matter accumulation increased over time, until the late season maximum, for all three hybrids both in the presence and

absence of weeds. Leaf area index showed the same pattern as leaf and stem dry matter accumulation. Generally dry matter accumulation of leaves at early stages of plant development was higher for LRS and P3979 (especially LRS) than LMBL hybrid and this was so for 1997-1998 under both weed-free and weedy levels. Generally a higher leaf weight ratio in the LRS hybrid at earlier and last harvests indicated greater dry matter partitioning to the leaves of the plants where more light could be intercepted than for the other corn hybrids. Leaf area index was also much higher for the LRS than the other hybrids, in particular at earlier stages of plant development, and especially in the absence of weeds. This increase was partially due to higher plant population densities for LRS and being different in terms of canopy architecture from the other hybrids. Harvest index was higher for LRS than the other hybrids. The more rapid accumulation of leaf dry matter and greater leaf area indices during early stages of the plant development for LRS should have allowed increased light interception, especially at higher plant population densities and narrower row spacings, for better competition with weeds and improved corn productivity in short season-areas.

INTRODUCTION

Dry matter accumulation during the early stages of plant development can have a large impact in decreasing stresses associated with either uncontrollable environmental or controllable agronomic factors, such as seeding time and rate, soil fertility, genotype selection, and weed control. Although each portion of the plant has a role to play, partitioning to leaves is a key factor in plant growth (Tollenaar, 1989; Cross, 1990; Cross, 1991; Girilio, 1994; Stewart and Dwyer, 1994). The rate and duration of leaf area expansion are the key elements in controlling whole plant growth because they control light interception by leaves, which are the major sites of plant photosynthesis (Stewart and Dwyer, 1994). Accumulated dry matter needs to be distributed (partitioned) amongst various plant structures, and how much of it is allocated to each is very important. Among corn hybrids this allocation can be an important factor in canopy architecture.

Canopy architecture is a function of leaf number, shape, distribution, and orientation, and plant size, which collectively determine the vertical distribution of light within the corn canopy (Williams et al., 1968; Girardin and Tollenaar, 1994). Leaf number is also positively correlated with the maturity groups of corn hybrids. Corn plant size (height, weight, and total leaf area) positively correlates with vegetative phase duration (VPD) (Cross and Zuber, 1973; Corke and Kannenberg, 1989). Generally the earliest maturing corn hybrids tend to be much smaller in size than the late maturing ones. Leaf number is also correlated with maturity in corn and influences cultivar adaptation (Stewart and Dwyer, 1994). Corn hybrids used in short-season areas have smaller leaf area indices leading to lower dry matter accumulation than hybrids grown in long-season areas, mainly because of their reduced leaf number and size (Chase and Nanda, 1967; Hunter et al., 1974). Although seed cost is a consideration, very early corn hybrids tend to be faster in dry matter accumulation, more tolerant of higher plant populations and more resistant to lodging due to insect and wind damage than later maturing corn hybrids. Higher population densities could also increase leaf area index leading to better light interception and weed competition (Tollenaar et al., 1994).

Recently, corn hybrids accumulating leaf area faster, particularly above the ear, maturing earlier, yielding well, taking advantage of narrow row spacings and tolerating higher plant population better than the conventional corn hybrids have been reported (Modarres et al., 1997a,b; Modarres et al., 1998; Begna et al., 1997a,b, Begna et al., 1999). The leafy (Lfy1) and reduced-stature (rd1) traits both make contributions to the recently developed "Leafy-reduced stature" hybrids (Modarres et al., 1997a,b; Modarres et al., 1998). The net result of this is that plants bearing the leafy trait show a dramatic increase in the production of leaf area by the time of maturity (Shaver, 1983). Although there have been previous reports regarding better leaf area accumulation and yield potential of these hybrids at higher plant populations and particularly in narrow spacing in short-season areas, no research has been done to compare dry matter accumulation and partitioning of these and other corn hybrids differing in canopy architecture growing in the presence and absence of weeds. The objective of this study was to quantify the accumulation and allocation of dry matter to leaves and stems during early development of corn hybrids varying in canopy architecture in both the presence and absence of weed pressure.

MATERIALS AND METHODS

Experiments were conducted in 1996, and 1997 at the E. A. Lods Agronomy Research Centre of the Macdonald Campus of McGill University, Ste. Anne de Bellevue, Quebec and in the 1996 at the Central Experimental Farm of Agriculture and Agri-Food Canada, Ottawa, Ontario. The 1996 experiment at Macdonald site was on courval sandy soil (fine-silty, mixed, nonacid, frigid Humaquept) while the 1997 and 1998 sites were on clay loam soil (fine, mixed, nonacid, frigid Humaquept). The experiment in Ottawa was on uplands sandy loam (Humo-ferric podzol) soil. Soils at Macdonald were fertilized with 500 kg ha^{-1} of 36-5.3-14.9 NPK in 1996 and 1998. In 1997 soils were fertilized with 400 kg ha^{-1} of 19-8.4-15.8 and 385 kg ha^{-1} of 27-0-0 NPK prior to planting. In Ottawa soils were fertilized with 550 kg ha^{-1} of 36- 5.3-14.9 of NPK. At the Macdonald site weeds were controlled with Primextra [Metolachlor/Atrazine (2:1), 500 g L^{-1}, Ciba-Geigy, Canada Inc.] at a rate of 7.7 L ha^{-1} during all years and at the Ottawa site weed control was through a spring application of Roundup (Glyphosate, 356 g L^{-1}, Monsanto Canada Inc.) at a rate of 2.5 L ha^{-1} and a late June, application of Fusilade (Fluazifop-p-butyl, 125 g L^{-1}, Zeneca Agro) 1 L ha^{-1} as a spot-spray on emerged grasses. In addition to herbicide control hand weeding was also done as required. Weed control was applied only to the weed free plots, while the weedy plots were left uncontrolled. Comparisons between the weed free and weedy plots allowed assessment of the competitiveness of the three corn hybrids with weeds.

Three corn hybrids: Leafy reduced-stature (LRS): (1240-6-2 X 1306-2-2) X PRC LDOP300rd1) and (1240-6-2 X 1306-2-2) X BRC DWARF SYNTHETIC for Ottawa and Macdonald in 1996, respectively, (1306-2-2 X LDOP300rd1) in 1997, and (CO392 X LDOP300rd1) in 1998 for Macdonald; one late maturing big leaf (LMBL):(W117rd1 X CM174rd1) X Galinat] and one conventional commercial type [Pioneer 3979 (P3979)} were used in this experiment. Leafy reduced-stature corn hybrids have become available only recently (Modarres et al., 1997; Modarres et al., 1998). Descriptions of the development of the LRS hybrids have been reported (Modarres et al., 1997). Briefly LRS is a combination of "Leafy (Lfy)" and "reduced-stature (rd1)" traits. The "Leafy" trait increases the leaf number of the plant, especially leaf number above the ear, while the "rd1" trait results in a short statured, early maturing hybrid. The LMBL type was similar in height to P3979 (with an ear leaf of approximately 88 cm long and 10 cm wide at the widest point) but with large leaves (with an ear leaf of approximately 100 cm long and 11 cm wide). The LMBL hybrid was included as its late maturity provides a potential vehicle to measure how much the competitiveness of LRS types with weeds was due to early maturity.

Each block of the experiment was divided longitudinally into two, one side weed free and the other weedy. The weed and weedy treatments were randomly allocated to the north and south sides of each block. The experiment was designed as a split-split-split-plot with the plots arranged in a randomized complete block design with four blocks. The dates of planting for Macdonald site were 24 May, 1996, 21 May, 1997, and 23 May, 1998 and for the Ottawa site it was 29 May, 1996. Each hybrid was planted at two plant densities (100,000; 55,000; 75,000 as conventional and 133,300; 73,300; 100,000 plants ha^{-1} as high density for LRS, LMBL and P3979, respectively) for the 1996 experiment at both sites; however, the high density for LRS in 1997 and 1998 was reduced to 115,000 plants ha^{-1} because we found the previous high density to be too high in as much as the level of interplant competition was sufficient to cause some sterile plants even in the weed-free plots. Weed levels [weed-free (WF), and weedy (W)] formed the main plots, while population density formed the sub-plots and two planting patterns (row spacing of 38 and

76 cm) formed the sub-sub-plots. The 38 cm row width is a narrower arrangement which is better suited for higher plant population densities (Begna et al., 1997). Hybrids formed the sub-sub-sub-plot units. All plots were hand planted. The 76 cm row spacing plots consisted of four rows and the narrow spacing plots of eight rows in the 1996 experiments for both sites, however for the 1997 and 1998 experiments the number of rows for the wide rows were increased to eight so that we could have enough plants for both periodic and final harvests.

The plots were 8 m long for the 1996 experiment and 7 m long for 1997 and 1998 experiments. Plots were over-seeded (20%) and thinned to the required plant densities three weeks after emergence. Regular sampling (two week intervals) began approximately 3 weeks after planting. At each of these harvests two randomly selected corn plants were harvested and dried for dry matter accumulation determination. Before drying the length and maximum width of individual leaves of each of the harvested corn plants were measured and the leaves and stems were dried separately so that the accumulation of dry matter and their distribution to leaves and stems of the plants would be separated. Leaf area of each leaf of a plant was calculated using the formula of leaf area = leaf length (cm) X maximum leaf width (cm) X 0.75 (Montgomery, 1911) for weed-free plots of both sites in 1996 and for weed free and weedy plots in 1997 and in 1998. Dry matter accumulation was expressed on a per m^{-2} basis. Allocation patterns were assessed by calculating leaf and stem weight (g m^{-2}), leaf weight ratio (leaf weight per unit total biomass), and leaf area index (m^2 of leaf area per m^2 of field surface). At physiological maturity, as determined by the black layer method (Daynard and Duncan, 1969; Cross and Kabir, 1989), four plants

(1996) or six plants (1997 and 1998) per plot were randomly selected and cut at ground level. After the fresh weight was taken the sub-samples were dried to a constant weight at 80 ^{0}C for grain and other parts of plant dry weight determination; these samples were used to determine harvest index (dry grain weight divided by the total above ground plant dry weight). Ears were shelled using an electric sheller (SCI1 Corn Sheller, Agriculex, Ont., Canada), grain dry weight was determined and expressed at 15.5 % moisture on a g plant^{-1} basis.

The data of the two sites Macdonald (Site 1) and Ottawa (Site 2) of 1996 or the two years (1997 and 1998 for Macdonald) were pooled when the hypothesis of the homogeneity of variances was tested and accepted by a Bartlett's test (Steel and Torrie, 1980). The statistical analyses were performed using the GLM procedure of SAS (SAS Institute, 1994). Simple means comparisons were made with a GLM protected LSD test ($P<0.05$). Time, weed level, population density, planting pattern and hybrid were examined together to test for interactions between them. The data were later analysed as repeated measures in time and the analysis was carried out using the repeated statement of the GLM procedure (SAS Inc., 1985).

RESULTS AND DISCUSSION

All of the tested factors affected leaf and stem dry matter, leaf weight ratio and leaf area index at all site-years (Tables 3.2, 3.3a and 3.3b). At all site-years under both weed-free and weedy levels there was an increase in leaf and stem dry matter accumulation over time for all three hybrids, until tasselling stage, after which dry matter declined for the early maturing LRS and P3979 hybrids (Figures 3.2, 3.3 and 3.4). Leaf area development followed a pattern similar to leaf and stem dry matter (Figure 3.5). LRS and P3979 reached their maximum much earlier than LMBL hybrid. For LRS and P3979 this was part of the overall pattern of more rapid development and earlier maturity than LMBL.

Leaf and stem dry matter

Generally leaf and stem dry matter accumulation was higher at the narrow and the higher plant population than the wide row spacing and the conventional plant population under both weedy and weed-free conditions (Figures 3.2, 3.3 and 3.4). The maximum accumulation of leaf dry matter occurred at earlier plant development stages for LRS and P3979 (especially LRS) than LMBL both in the presence and absence of weeds at all site-years (Figures 3.2 and 3.3). However, final leaf dry matter accumulation at later stages was much higher for LMBL than the other two corn hybrids. Generally, stem dry matter accumulation at early stages, at all site-years (particularly in 1997 and 1998) was higher for LRS and P3979 than LMBL (Figures 3.2 and 3.4). This occurred both in the presence and absence of weed pressure. Although there was higher stem dry matter for LRS and P3979 at earlier stages of plant development at both row spacings and plant populations under both weed levels, P3979 tended to produce more than LRS. Leaf dry matter accumulation was higher in the narrower row spacing and higher population than the wider spacing and conventional plant population, and this was more pronounced for LRS and P3979 (especially LRS) than for LMBL. This difference was probably as a result of more rapid leaf area accumulation by LRS than by the other hybrids during the early stages of plant growth (Figure 3.5). At all site-years dry matter accumulation in leaves and stems, and leaf area index varied substantially with harvesting times. Dry matter and leaf area accumulation increased with time for all hybrids until the plants reached tasselling stage. At all site-years and in both the presence and absence of weeds, leaf and stem dry weight, and leaf area index at the last harvest were higher for the LMBL than LRS and P3979 corn hybrids. This was probably a function of time to maturity and canopy architecture. The earlier the maturity of a hybrid, the earlier and the quicker was the accumulation of dry matter at early growing stages

Modarres et al. (1997a) reported a higher dead leaf number at tasselling for LRS than for Leafy and non-Leafy normal stature (e.g. P3979) genotypes, which could explain higher leaf dry matter at early stages and lower values at later stage for LRS than the Leafy corn hybrid used in our experiments. Earlier tasselling for LRS, at both low and high plant population densities, than P3979 and Leafy was also previously reported (Modarres et al, 1998; Begna et al., 1999). In 1997 and 1998 generally at later stages of plant development, stem dry matter accumulation, in both the presence and absence of weeds was higher for the LMBLand P3979 than LRS and, for example, in 1997-1998 eight weeks after planting stem dry matter accumulation at the high plant population and in wide rows was 574, 537, and 418 g m^2 for LMBL, P3979, and LRS, respectively (Figure 3.4) and stem dry matter accumulated by LRS was 20-28 % lower than the other corn hybrids. Presumably this was because of differences in canopy architecture and time to maturity. Several researchers have reported differences in canopy architecture (Williams et al., 1968; Girardin and Tollenaar, 1994) and maturity (Stewart and Dwyer, 1994) which would influence on how dry matter should accumulate and partition among different parts of the corn plant. Partitioning of less dry matter into the stem by LRS in 1996 and 1997 was mainly due to its much shorter (by at least 30%) height compared to the other corn hybrids and this could be a benefit for LRS in that it would allocate less assimilate to support stem development leading to improved harvest indices. Probably as a result of big differences in canopy architectures and pattern of dry matter allocations, the harvest index of LRS was generally higher than both of the other corn hybrids (Table 3.4). The over all harvest index was much higher for weed-free (52%) than weedy (28%) levels. In the absence of weed pressure higher harvest indices have been previously reported for LRS corn hybrids (Begna et al., 1997a,b)

Leaf weight ratio

In general, leaf weight ratio declined until eight weeks after planting in 1996 and seven weeks after planting in 1997 and 1998, where after it increased (Figures 3.2 and 3.3). At all site-years under both weed levels at both plant populations the earliest and the last harvest values of leaf weight ratio (especially 1997-1998) tended to be higher for the LRS than any of the other corn hybrids indicating a greater dry matter of the total biomass went to the leaves where it should be an important factor in light interception, and consequently, better competition with weeds, in particular at earlier stages of plant development. Some of the higher value of this variable at an early stage could be partially explained by the faster rate of leaf dry matter accumulation. At late harvests this could be a result of less dry matter partitioning into the stems by LRS than by the other hybrids.

This may also have contributed to its better competitiveness with weeds than the other corn hybrids. Grain yield reduction due to weed pressure was lower for early maturing LRS and P3979 than LMBL hybrid (data not shown). Callaway (1992) reported a greater grain yield reduction for late maturing than early maturing corn hybrids, due to weed pressure. Most probably quicker vegetative growth, in particular at early stages of development, by early maturing corn hybrids help these plants to suppress weeds better than the later ones.

In summary, dry matter accumulation and partitioning and leaf area index were different between hybrids, and this was so both in the presence and absence of weeds at all site-years. LRS, which matures one week earlier than P3979 (Modarres et al., 1997a; Modarres et al, 1998; Begna et al., 1999), generally accumulated leaf dry matter faster and partitioned less dry matter to the stem of the plant which led to a higher harvest index than the other two corn hybrids evaluated in this study. This was so both in the presence and absence of weeds. Leaf area index was also higher for the LRS than the other hybrids at the narrow and higher plant population than the wide row spacing and the conventional plant population, and in particular at earlier stages of plant development in the absence of weeds. This increase was partially due to higher plant population densities for LRS than the other hybrids. The more rapid accumulation of leaf dry matter and greater leaf area index during early stages of the plant development, as demonstrated by higher value of leaf weight ratio of LRS, could allow increased light interception, especially at higher plant population densities and narrower row spacings for better competition with weeds and improved corn productivity in short season-areas.

Table 3.1. A summary of weed species observed during the three years and sites of the experiments.

Weed species	Ottawa 1996	Macdonald 1996	Macdonald 1997	Macdonald 1998
Barnyard grass (*Echinocula crusgali* L.)	H	I	H	H
Giant foxtail (*Setaria faberi* Herm.)	I	H	I	I
Yellow nutsedge (*Cyperus rotundus* L.)	L	H	L	L
Yellow foxtail (*Setaria glauca* L.)	I	H	I	I
Witch grass (*Panicum capillare* L.)	I	H	I	L
Quack grass (*Elytrigia repens* L.)	L	H	H	L
Smooth crabgrass (*Digitaria ischaemum* Schreb.)	I	I	I	I
Lamb's quarters (*Chenopodium album* L.)	H	I	H	H
Redroot pigweed (*Amaranths retroflexus* L.)	H	I	H	H
Canada thistile (*Cirsium arvense* L.)	L	H	H	L
Velvet leaf (*Abutilon theophrasti* Medic.)	L	I	L	L
Purslane (*Portulaca oleracea* L.)	L	H	H	I
Prostrate knotweed (*Polygonum aviculare* L.)	I	I	I	I
Field bindweed (*Convolvulus arvensis* L.)	L	L	H	H
Common ragweed (*Ambrosia artemisiifolia* L.)	L	L	L	L

Population ocurrance (H- high, I- intermidiate, L-low)

Table 3.2. A summary of the univariate procedure of repeated measures analysis of variance for each variable in 1996 (2-sites means).

		Between-subject effect					Within-subject effect		
		Leaf dry matter	Stem dry matter	Leaf weight ratio			Leaf dry matter	Stem dry matter	Leaf weight ratio
Source	df	P-value			Source	df	P-value (Adj G-G)*		
Block (B)	3	0.003	0.0690	0.0654	Time (T)	5	0.0001	0.0001	0.0001
Plant populations (PP)	1	0.0004	0.0044	0.1246	Error T x B	15			
Error (B x PP)	3				T x PP	5	0.008	0.0001	0.2003
Row spacings (RS)	1	0.0001	0.0001	0.5218	Error T x B x PP	15			
PP x RS	1	0.9168	0.8178	0.9867	T x RS	5	0.0009	0.0001	0.7134
Error Bx RS (PP)	6				T x PP x RS	5	0.5109	0.979	0.8549
Hybrids (H)	2	0.0001	0.0003	0.0001	Error T x B x RS (PP)	30			
PP x H	2	0.0913	0.529	0.3881	T x H	10	0.0001	0.0001	0.0034
RS x H	2	0.7597	0.5986	0.8807	T x PP x H	10	0.2235	0.6304	0.0337
PP x RS x H	2	0.3522	0.5496	0.7435	T x RS x H	10	0.3646	0.9724	0.9184
Error	24				T x PP x RS x H	10	0.8567	0.9698	0.9626
					Error	120			

*G-G is Probability values adjusted by using Greenhouse-Geisser estimate of Box's epsilon correction factor.

Table 3.3a. A summary of the univariate procedure of repeated measures analysis of variance for each variable between-subject effects at the Macdonald site in 1997 and 1998.

		Years means (1997-1998)			1997
		Leaf dry matter	Stem dry matter	Leaf weight ratio	Leaf area index
source	df	P -value			
Block (B)	3	0.0006	0.0027	0.4585	0.0844
Weed level (WL)	1	0.0001	0.0001	0.0004	0.0002
Error (B x WL)	3				
Plant populations (PP)	1	0.0001	0.0001	0.6665	0.0001
WLx PP	1	0.1115	0.0607	0.1914	0.3256
Error Bx PP (WL)	6				
Row spacings (RS)	1	0.0001	0.0001	0.2655	0.0143
WLx RS	1	0.0091	0.0071	0.971	0.0001
PP x RS	1	0.1361	0.7176	0.4408	0.4025
WLx PP x RS	1	0.8435	0.7588	0.544	0.9086
Error B x RS (WLx PP)	12				
Hybrids (H)	2	0.0001	0.0001	0.0001	0.0001
WL x H	2	0.0001	0.0001	0.1836	0.0001
PP x H	2	0.0001	0.0001	0.0623	0.0183
WL x PP x H	2	0.0895	0.0071	0.9396	0.0511
RS x H	2	0.0001	0.0001	0.1382	0.0001
WL x RS x H	2	0.0001	0.0001	0.3559	0.0001
PP x RS x H	2	0.0606	0.1274	0.1503	0.2053
WL x PP x RS xH	2	0.8373	0.8475	0.9629	0.8259
Error	48				

Table 3.3b. A summary of the univariate procedure of repeated measures analysis of variance for each variable within-subject effects at the Macdonald site in 1997 and 1998.

		Years means (1997-1998)			1997
		Leaf dry matter	Stem dry matter	Leaf weight ratio	Leaf area index
source	df	P-value (Adj G-G)[+]			
Time (T)	3	0.0001	0.0001	0.0001	0.0001
Error T x B	9				
T x WL	3	0.0001	0.0001	0.0001	0.0038
Error T x B x WL	9				
T x PP	3	0.0001	0.0001	0.0003	0.0644
T x WL x PP	3	0.2937	0.0002	0.7942	0.0001
Error T x B x PP (WL)	18				
T x RS	3	0.0001	0.0002	0.8069	0.6166
T x WL x RS	3	0.0789	0.2291	0.958	0.0942
T x PP x RS	3	0.4831	0.5518	0.6298	0.5631
T x WL x PP x RS	3	0.6318	0.8143	0.6224	0.7066
Error T x B x RS (WL x PP)	36				
T x H	6	0.0001	0.0001	0.0001	0.0001
T x WL x H	6	0.0001	0.0001	0.0001	0.0001
T x PP x H	6	0.0001	0.0017	0.0001	0.098
T x WL x PP x H	6	0.3552	0.0112	0.1587	0.1087
T x RS x H	6	0.0071	0.0001	0.1535	0.0001
T x WL x RS x H	6	0.0017	0.0002	0.114	0.0001
T x PP x RS x H	6	0.7229	0.0312	0.1552	0.8129
T x WL x PP x RS x H	6	0.8807	0.7165	0.8563	0.7682
Error	144				

[+]G-G is Probability values adjusted by using Greenhouse-Geisser estimate of Box's epsilon correction factor.

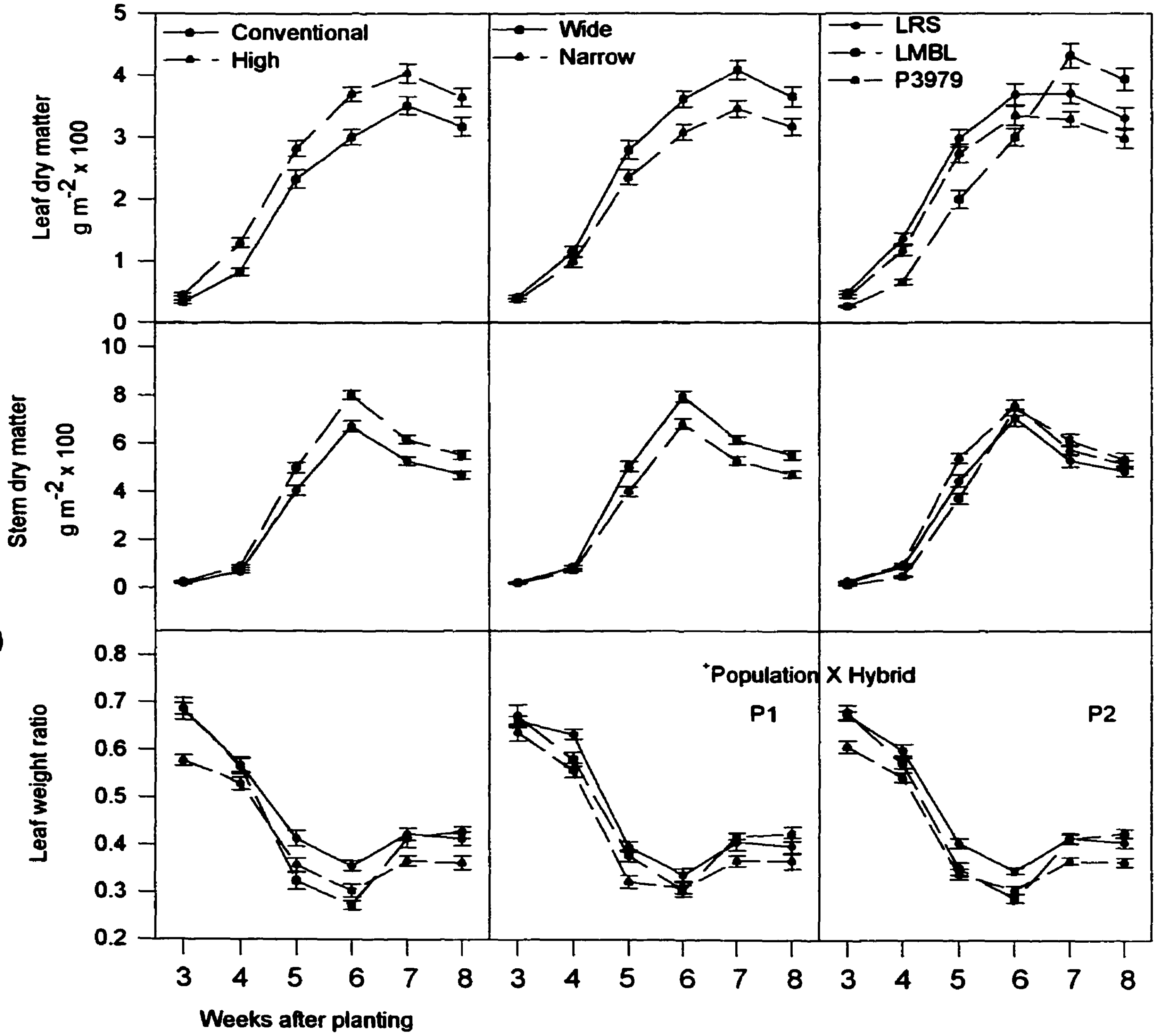
Table 3.3. Multiple pairwise comparisons for main and interaction effects of weed level, plant population and hybrid on harvest index (3-years means).

Weed level	**Plant population**	Harvest index
Weed-free	Conventional	0.51b*
	High	0.53a
Weedy	Conventional	0.27c
	High	0.28c

Hybrid	Harvest index
LRS	0.42a
LMBL	0.38b
P3979	0.40ab

Abbreviations: LRS -Leafy-reduced stature, LMBL-Late maturing big leaf, and P3979-Pioneer 3979. *Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Figure 3.1 Leaf and stem dry matter and leaf weight ratio of corn hybrids at narrow and wide spacings, and at conventional (P1), and high (P2) plant populations in the absence of weed pressure in 1996. [+]For simplicity the interaction effects were presented separately.



Conventional
High
Wide
Narrow
LRS
LMBL
P3979
Leaf dry matter g m-2 x 100
Stem dry matter g m-2 x 100
Leaf weight ratio
*Population X Hybrid
P1
P2
Weeks after planting

Figure 3.2 Leaf dry matter of corn hybrids at narrow (RS1) and wide (RS2) spacings, conventional (P1), and high (P2) plant populations in the presence and absence of weed pressure (Means of 1997 and 1998). +For simplicity the interaction effects were presented separately.

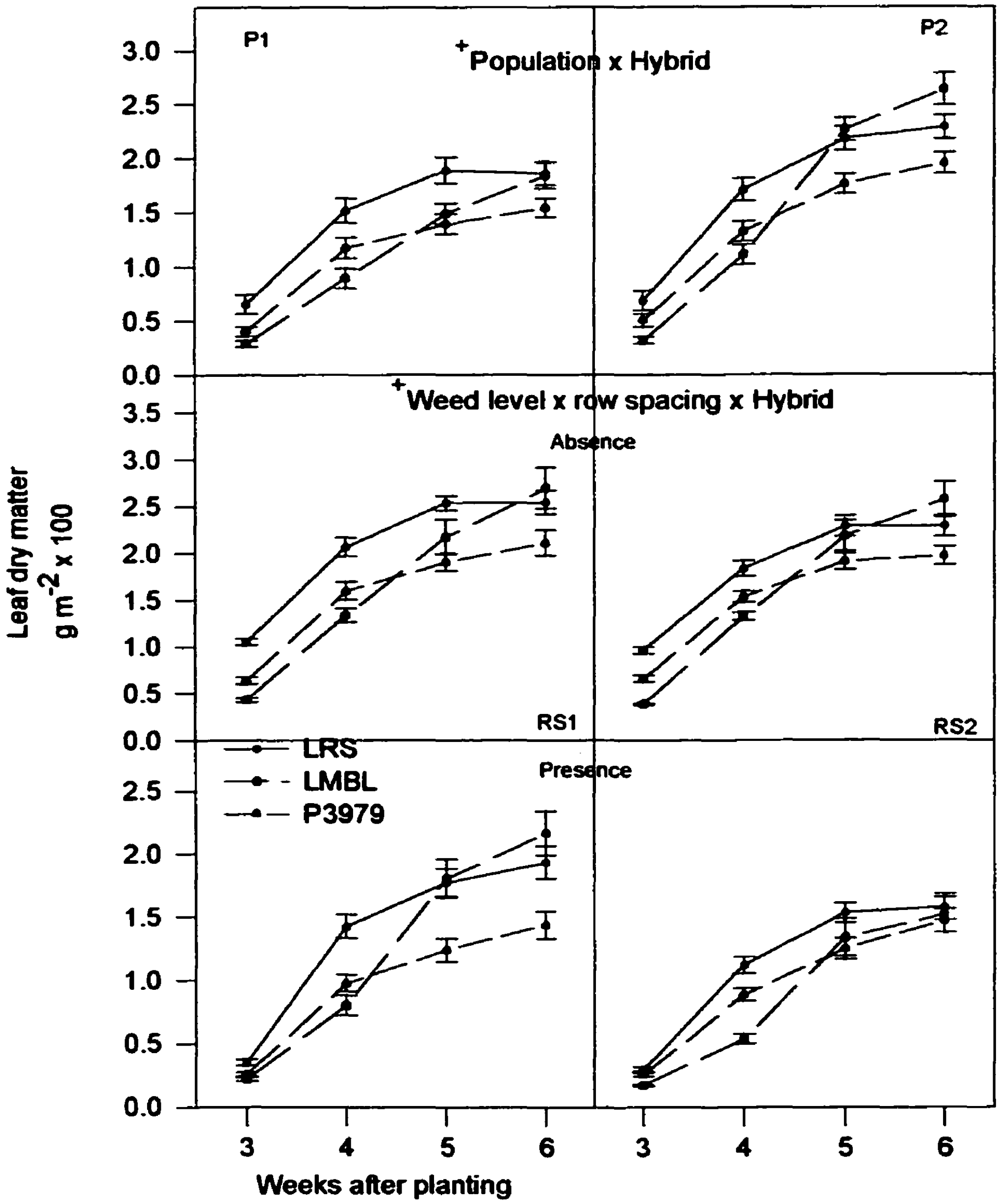
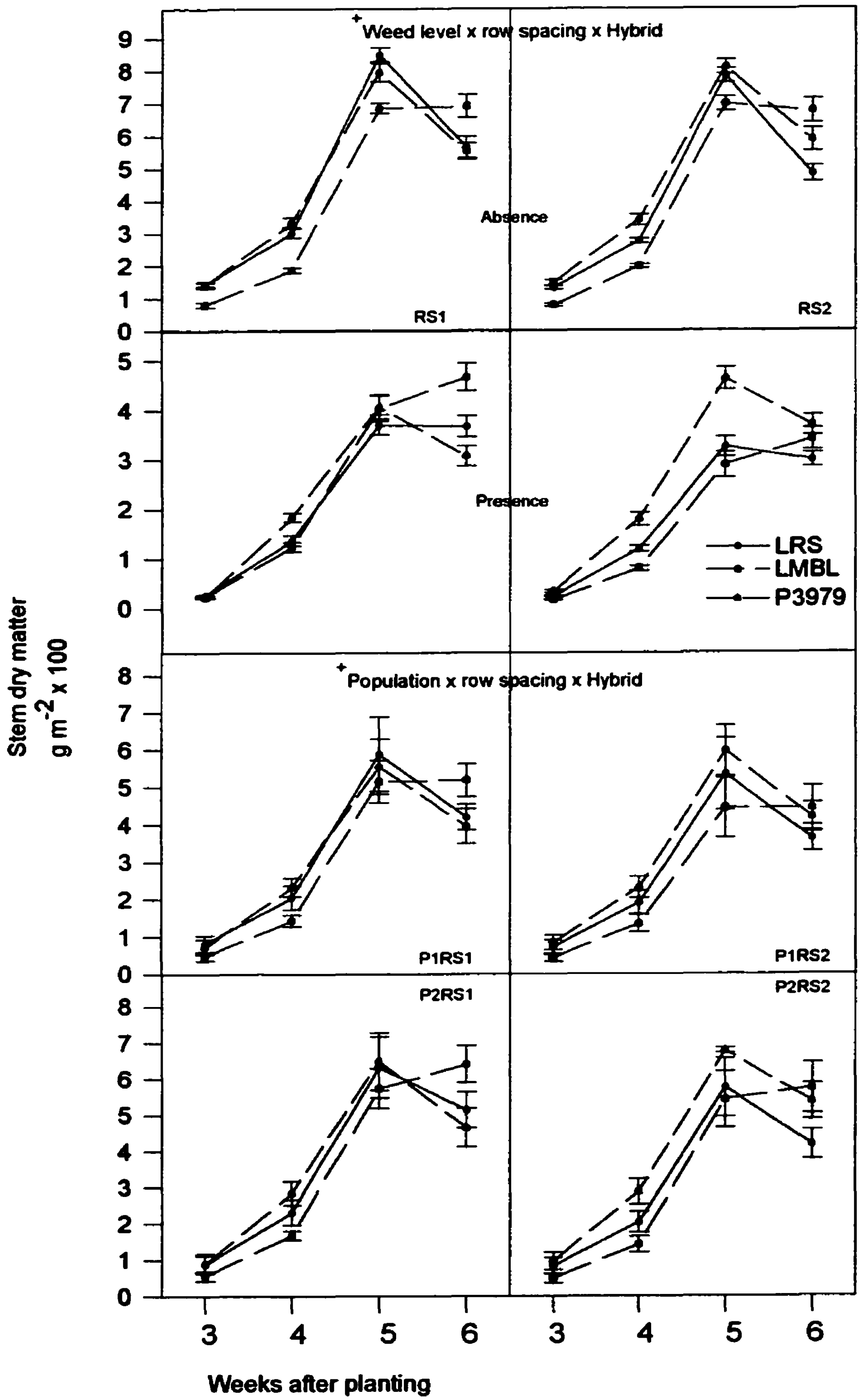
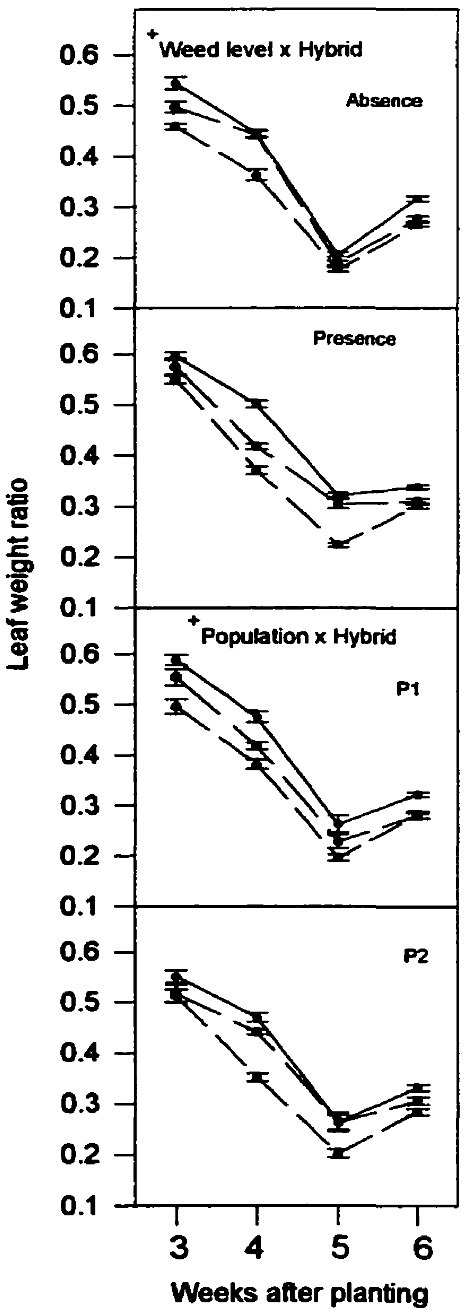

P1
P2
+Population x Hybrid
+Weed level x row spacing x Hybrid
Absence
Presence
RS1
RS2
LRS
LMBL
P3979
Leaf dry matter
g m-2 x 100
Weeks after planting
3.0
2.5
2.0
1.5
1.0
0.5
0.0
3.5
3
4
5
6

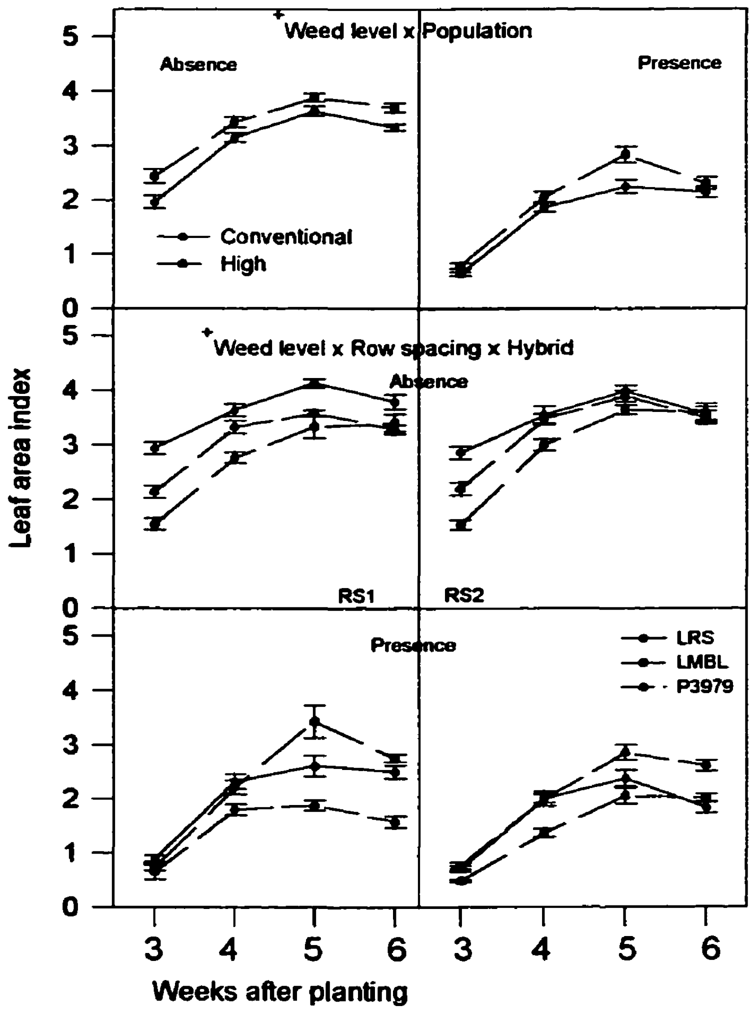
Figure 3.3 Stem dry matter of corn hybrids at narrow (RS1) and wide (RS2) spacings, conventional (P1), and high (P2) plant populations in the presence and absence of weed pressure (Means of 1997 and 1998). +For simplicity the interaction effects were presented separately.



+Weed level x row spacing x Hybrid
Absence
RS1
RS2
Presence
LRS
LMBL
P3979
+Population x row spacing x Hybrid
P1RS1
P1RS2
P2RS1
P2RS2
Stem dry matter
g m-2 x 100
Weeks after planting

Figure 3.4 Leaf weight ratio and leaf area index of corn hybrids at narrow (RS1) and wide (RS2) spacings, conventional (P1), and high (P2) plant populations in the presence and absence of weed pressure (Means of 1997 and 1998). +For simplicity the interaction effects were presented separately.


Leaf weight ratio
+Weed level x Hybrid
Absence
Presence
+Population x Hybrid
P1
P2
Weeks after planting


Leaf area index
+Weed level x Population
Absence
Presence
Conventional
High
+Weed level x Row spacing x Hybrid
Absence
RS1
RS2
Presence
LRS
LMBL
P3979
Weeks after planting

Preface to Chapter 4

This section will form a manuscript to be submitted in 1999 for publication in Agronomy Journal. The format has been changed to be consistent within this thesis. All literature cited in this chapter are listed at the end of the thesis. Each table or figure is presented at the end of this chapter.

In chapter 3, I addressed the patterns of dry matter accumulation and partitioning. and leaf area development by corn hybrids of very different canopy architectures using different planting patterns in the presence and absence of weeds. In this chapter (chapter 4) I investigated grain yield reductions and changes in some morphological traits of these corn hybrids in response to competition from weeds. In addition, I compared the relative competitiveness of these hybrids.

MORPHOLOGICAL TRAITS AND GRAIN YIELD RESPONSE OF CORN HYBRIDS DIFFERING IN CANOPY ARCHITECTURE TO THE PRESENCE AND ABSENCE OF WEED PRESSURE

ABSTRACT

During the course of breeding for corn hybrids better adapted and higher yielding, particularly in short-season areas, morphological traits such as plant height and leaf number have been altered. Recently, corn hybrids accumulating more leaf area, maturing earlier, yielding better in narrower row spacings and tolerating higher plant populations better than conventional corn hybrids have been developed. Although there have been prior reports regarding the high yield potential of these hybrids in short-season areas, no research has been previously conducted to assess their ability to compete with weeds. This is of interest because these hybrids develop leaf area more rapidly than conventional types. The objective of this study was to quantify some of the morphological and grain yield responses of corn hybrids with a wide range of canopy architectures to the presence and absence of weeds. Experiments were conducted in 1996, 1997, and 1998 at Ste. Anne de Bellevue, Quebec and in 1996 at Ottawa, Ontario. Three corn hybrids were tested: leafy reduced-stature (LRS), late maturing big leaf (LMBL), and the conventional hybrid Pioneer 3979 (P3979). Each block of the experiment was divided longitudinally into two, one side weed free and the other weedy. Each hybrid was planted at two population densities (conventional and high) and two row spacings (38 and 76 cm). The decrease in plant height due to weed pressure was smallest for LRS. The overall grain yield of the

LMBL corn hybrid was much greater than the other corn hybrids in the absence, but not in the presence, of weeds. In 1996 and 1997, at both sites, the narrower row spacing increased the yield of the LRS hybrid the most, probably as a result of its smaller size and ability to tolerate high plant densities better than the other hybrids. Grain moisture content, which is an important trait in short growing-season areas, was much lower for LRS and Pioneer 3979 than the late maturing corn hybrid. Early maturing corn hybrids (LRS and P3979) and especially LRS grew and developed faster early in each season. LRS yields were least affected by weed pressure, indicating better tolerance of, and competition with, weed populations.

INTRODUCTION

Corn production has been extended into short-season areas during the course of this century. The selection for better adapted higher yielding corn hybrids has altered morphological traits (e.g plant height and leaf number) that are important components of canopy architecture. The grain yield of any crop represents the summation of numerous physiological processes and overall morphological development. The development which can be divided, in general, into the vegetative and reproductive stages. Corn plant size (height, weight, total leaf area) positively correlates with vegetative phase duration (VPD) (Cross and Zuber, 1973; Corke and Kannenberg, 1989).

In effective crop production, efficient utilization of available light is one of the most important factors and is strongly affected by crop canopy architecture, which, in turn, plays an important role in many canopy processes including the interactions between crop vegetation and its environment (Daughtry et al., 1983; Welles and Norman, 1991). Canopy architecture is a function of leaf number, shape, distribution, and orientation, and plant size which collectively determine the vertical distribution of light within the corn canopy (Williams et al., 1968; Girardin and Tollenaar, 1994). Hybrids used in short-season areas have smaller leaf area indices than hybrids used in long-season areas, mainly because of their reduced leaf number and size (Chase and Nanda, 1967; Hunter et al., 1974). These smaller hybrids mature more rapidly but yield less than larger hybrids. Leaf number is also correlated with maturity in corn and influences cultivar adaptation (Stewart and Dwyer, 1994).

Among corn hybrids differing in canopy architecture there are large grain yield differences in response to higher plant populations, narrower row spacings and competition with weeds. Grain yield and quality of corn can be reduced substantially by weeds with yield decreases of 35-70 %, where weeds are not controlled (Ford and Pleasant, 1994; Teasdale, 1995). Varietal differences in weed suppression ability have been reported for crops such as corn, potato, cotton, and soybean (Callaway, 1992). These differences were largely due to differences in varietal maturity and canopy structure. Staniforth (1961) reported that early maturing corn hybrids had a 6 % yield reduction due to weed presence, while late maturing ones had a 20 % reduction. Callaway (1992) reported greater grain yield reductions due to weed competition for late maturing and larger corn hybrids than early maturing ones. Competition from weeds may be reduced when corn germinates and accumulates leaf area quickly, and forms a canopy that shades emerging weed seedlings. Although seed cost is a potential concern, very early corn hybrids are generally more tolerant of higher plant populations, are less prone to lodging due to insect and wind damage and show a capacity to further increase leaf area index allowing better light interception and competition with weeds.

Recently, corn hybrids accumulating more leaf area, particularly above the ear, maturing earlier, yielding better, taking advantage of narrow spacings and tolerating higher plant populations better than conventional corn hybrids have been reported (Modarres et al., 1997a,b; Begna et al., 1997a,b). The leafy (Lfy1) and reduced-stature (rd1) traits both make contributions to the recently developed "Leafy-reduced stature" hybrids (Modarres et al., 1997a,b; Modarres et al., 1998). The net result of this is that plants bearing the Leafy trait show a dramatic increase in the production of leaf area by the time of maturity (Shaver, 1983). Although there have been previous reports regarding better leaf area accumulation and yield potential of these hybrids at higher plant populations and particularly in narrow row spacings in short-season areas, no research has been conducted to compare their morphological and grain yield responses to weed pressure with that of conventional corn hybrids. The objective of this study was to quantify morphological and grain yield responses of corn hybrids with a wide range of canopy architectures in the presence and absence of weeds.

MATERIALS AND METHODS

Experiments were conducted in 1996, 1997, and 1998 at the E. A. Lods Agronomy Research Centre of the Macdonald Campus of McGill University, Ste. Anne de Bellevue, Quebec and in the 1996 at the Central Experimental Farm of Agriculture and Agri-Food

Canada, Ottawa, Ontario. The 1996 experiment at the Macdonald site was on courval sandy soil (fine-silty, mixed, nonacid, frigid Humaquept) while the 1997 and the 1998 sites were on clay loam soil (fine, mixed, nonacid, frigid Humaquept). The experiment in Ottawa was on uplands sandy loam (Humo-ferric podzol) soil. Soils at Macdonald were fertilized with 500 kg ha^{-1} of 36-5.3-14.9 NPK in 1996 and 1998. In 1997 soils were fertilized with 400 kg ha^{-1} of 19-8.4-15.8 of NPK and 385 kg ha^{-1} of 27-0-0 of NPK prior to planting. In Ottawa soils were fertilized with 550 kg ha^{-1} of 36-5.3-14.9 of NPK. At the Macdonald site weeds were controlled with Primextra [Metolachlor/Atrazine (2:1), 500 g L^{-1}, Ciba-Geigy, Canada Inc.] at a rate of 7.7 L ha^{-1} during all years and at the Ottawa site weed control was through a spring application of Roundup (Glyphosate, 356 g L^{-1}, Monsanto Canada Inc.) at a rate of 2.5 L ha^{-1} and a late June, application of Fusilade (Fluazifop-p-butyl, 125g L^{-1}, Zeneca Agro.) (1 L ha^{-1}) as a spot-spray on emerged grasses. In addition to herbicide control hand weeding was also done as required. Weed control was applied only to the weed free plots, while the weedy plots were left uncontrolled. Comparisons between the weed free and weedy plots allowed assessment of the competitiveness of the three corn hybrids with weeds.

Three corn hybrids: Leafy reduced-stature (LRS): (1240-6-2 X 1306-2-2) X PRC LDOP300rd1) and (1240-6-2 X 1306-2-2) X BRC DWARF SYNTHETIC for Ottawa and Macdonald in 1996, respectively; (1306-2-2 X LDOP300rd1) in 1997, and (CO392 X LDOP300rd1) in 1998 for Macdonald; one late maturing big leaf (LMBL):(W117rd1 X CM174rd1) X Galinat] and one conventional commercial type [Pioneer 3979 (P3979)} were used in this experiment. In 1998 we were short of seeds for LRS, therefore it was necessary to replace the previously used hybrid with another LRS. However, the new one was normal height. Although it was not as short as the previously used LRS material it is still considered to be LRS because leafy hybrids that do not contain the rd1trait are much taller than conventional hybrids (Modarres et al., 1997a). Leafy reduced-stature corn hybrids have become available only recently (Modarres et al., 1997a,b; Modarres et al., 1998). Descriptions of the development of the LRS hybrids have been reported by Modarres et al. (1997a,b). Briefly LRS was a combination of "Leafy (Lfy)" and "reduced-stature (rd1)" traits. The "Leafy" trait increases the leaf number of the plant, especially leaf number above the ear, while the "rd1" trait resulted in a short statured, early maturing hybrid. The LMBL type was similar in height to P3979 (with an ear leaf of approximately 88 cm long and 10 cm wide at the widest point) but with large leaves (with an ear leaf of approximately 100 cm long and 11 cm wide). The LMBL hybrid was included as its late maturity provides a potential vehicle to measure how much the competitiveness of LRS types with weeds has due to early maturity.

Each block of the experiment was divided longitudinally into two, one side weed free and the other weedy. The experiment was designed as a split-split-split-plot with the plots arranged in a randomized complete block design with four blocks. The dates of planting for the Macdonald site were 24 May, 1996, 21 May, 1997, and 23 May, 1998 and for the Ottawa site it was 29 May, 1996. Each hybrid was planted at two population densities (100,000; 55,000; 75,000 as conventional and 133,300; 73,300; 100,000 plants ha^{-1} as high densities for LRS, LMBL and P3979, respectively) for the 1996 experiment at both sites; however, the high density for LRS in 1997 and 1998 was reduced to 115,000 plants ha^{-1} because we found the previous high density to be too high in as much as the level of interplant competition was sufficient to cause some sterile plants even in the weed-free level. Weed levels (weed-free and weedy) formed the main plot, while plant population density formed the sub plots and two planting patterns (row spacings of 38 and 76 cm) formed the sub-sub plots. The 38 cm row width is better suited for higher plant population densities (Begna et al., 1997a,b). Hybrids formed the sub-sub-sub-plot units. The recommended plant population for conventional hybrids in south western Quebec is 65,000 to 75,000 plants ha^{-1}. All plots were hand planted. The 76 cm row spacing plots consisted four rows and the narrow spacing plots of eight rows in the 1996 experiments for both sites, however for the 1997 and the 1998 experiment the number of rows in the wide row plots were increased to eight.

The plots were 8 m long for the 1996 experiments and 7 m long for 1997 and 1998 experiments. Plots were over-seeded (20%) and thinned to the required plant densities three weeks after emergence. The following data were recorded for both weed free and weedy plots at all site-years of the experiments: plant height (soil level to the collar of the top leaf), ear height (soil level to node of the uppermost ear), leaf number (ear leaf and ear leaf number above the ear) at tasselling. These measurements were taken on four randomly selected plants in each plot.

At physiological maturity, as determined by the black layer method (Daynard and Duncan, 1969; Cross and Kabir, 1989), four plants (1996) and six plants (1997 and 1998) per plot were randomly selected and cut at ground level. After the fresh weight was taken the sub-samples were dried to a constant weight at 80 ^{0}C for grain moisture determination.

At all site-years the ears of all plants in a 3 m length of the central portion of the two central rows were hand picked and used for grain yield determination. Ears were shelled using an electric sheller (SCI1 Corn Sheller, Agriculex, Ont., Canada), grain yield was determined and plot yields were expressed at 15.5 % moisture on a t ha^{-1} basis.

The data of the two sites Macdonald (Site 1) and Ottawa (Site 2) of 1996 or the three years (1996, 1997, and 1998 for Macdonald) were pooled when the hypothesis of the homogeneity of variances was tested and accepted by a Bartlett's test (Steel and Torrie, 1980). The statistical analyses were performed using the GLM procedure of SAS (SAS Institute, 1994). Simple means comparisons for each multiple pairwaise were made with a GLM protected LSD test ($P<0.05$). Weed level, population density, planting pattern and hybrid were examined together to test for interactions between them.

RESULTS AND DISCUSSION

Plant and ear height

All of the tested factors, except row spacing at both sites and plant population at the Ottawa site affected plant height, at both the Macdonald and the Ottawa sites in 1996 and 1997 height (Tables 4.2 and 4.3). Plant height for two (1996 and 1997) of the three years at the Macdonald site was greater at the high than the conventional plant population (Tables 4.4 and 4.5). However, in 1998 there was an effect of row spacing on plant height and greater plant height was recorded for the narrow than the wide row spacing (Table 4.7). In 1996, at both sites, ear height was affected only by row spacing with a higher value for the wider than the narrower row spacing (Table 4.8).

Generally, at all site-years interactions between weed level and hybrid existed for both plant and ear height (Tables 4.2 and 4.3). In most cases plant and ear height were higher under weed-free than weedy conditions for all hybrids (Table 4.8). In two (1996 and 1997) of the three years, in both the presence and absence of weeds, the plant height and ear height of the LRS corn hybrids was much lower than the LMBL and P3979 corn hybrids. The LRS corn hybrid was 30 to 40 % shorter than the other corn hybrids (Table 4.4 and 4.8). Similar results have been reported by Modarres et al. (1997a) and Begna et al. (1999) under weed-free conditions. This is mainly because the rd1 trait causes a reduction in the plant height of the LRS hybrids, while the Lfy1 trait increased leaf number (Modarres et al., 1997a). The net result of this has been that plants bearing the Lfy1 trait show a dramatic increase in the production of leaf area by the time of maturity (Shaver, 1983). However, in the 1998 experiment, the height of the LRS plants was similar to the other hybrids. Some combinations of reduced-stature (rd1) and Leafy (Lfy1) may result in approximately normal height hybrids. In as much as Leafy only plants are generally taller than normal hybrids (Modarres et al.1997a), the 1998 LRS hybrid would be still considered to be reduced in stature, although less than the ones used in 1996 and 1997. Plant height, both in the presence and the absence of weeds, was greater for all hybrids at the Ottawa than the Macdonald site (Tables 4.4 and 4.5) for the 1996 experiment. This was probably due to greater total precipitation at the Ottawa site (238.5 mm) than the Macdonald site (171.5 mm), particularly for the months of June and July, during which rainfall together with adequate temperature at Ottawa favoured vegetative growth (Table 4.10).

Leaf number (ear leaf number and leaf number above the ear)

At all site-years, ear leaf number and leaf number above the ear were affected by hybrid, however in 1998 interaction effects existed between weed level and hybrid (Tables 4.2 and 4.3). Although there were greater ear leaf numbers and leaf numbers above the ear for the weed-free than weedy conditions in 1998, in general, this value was the same both in the presence and absence of weeds, but higher values of these variables were recorded for LRS than for LMBL and P3979 for all site-years. The LRS hybrid had at least 2-3 more leaves above the ear than the other two corn hybrids (Tables 4.4, 4.7 and 4.8) under both weed conditions. Although individual leaf size of the LRS hybrid was relatively small (with an ear leaf of approximately 76 cm long and 8.5 cm wide) their numbers were much greater and their appearance was more rapid than either of the other hybrids. In general, variables related to corn plant size (height, weight, leaf number) are positively correlated with vegetative phase duration (VPD) (Cross and Zuber, 1973; Corke and Kannenberg, 1989). However, this is not true for the combination of reduced-stature (rd1) and leafy (Lfy) traits, which resulted in a short plant with a large number of leaves, especially above the ear (Modarres et al., 1997a).

Grain yield and grain moisture content

Grain yield was affected by all of the tested factors and analysis of variance also showed two-way (weed level and plant population) and three-way (weed level, row spacing and hybrid) interactions (Tables 4.2 and 4.3). At all site-years, and especially in wider rows, the grain yield of the LMBL hybrid was higher than either LRS or P3979 in the absence of weeds. However, in the presence of weeds yields were not different among hybrids (Tables 4.6 and 4.8). Grain yield was greater at higher than conventional plant populations under both weed levels. In the presence of weeds the reduction in grain yield was less pronounced for the LRS than the other corn hybrids for all site-years. This was. presumably, due to the earlier, faster growth and development as well as better tolerance to the higher plant populations and weed stresses by LRS than the P3979 and LMBL corn hybrids. The overall reductions in grain yield were 35, 49, and 40 % (Macdonald 1996), 24, 48, and 38 % (Ottawa 1996), and 42, 45,and 46 % (Macdonald 1997) for LRS, LMBL, and P3979, respectively (Tables 4.6 and 4.9). Grain yield reductions of 35-70 % have been reported for corn, where weeds were not controlled (Ford and Pleasant, 1994; Teasdale, 1995). In 1998 the overall reductions in yield due to the presence of weeds were much higher compared to the previous years for all hybrids, and this was especially so for LMBL. The yield decreases in 1998 were 52, 69, and 58 % for LRS, LMBL, and P3979, respectively (Table 4.9). This was probably due to less precipitation for the first three months of the growing seasons in 1998 than for the previous two years (Table 4.10), which may slowed corn plants and favoured weed growth, leading to greater grain yield reductions. Callaway (1992) reported higher grain yield reductions due to weeds for late maturing than early maturing corn hybrids. In both 1996 and 1997 the LRS corn hybrid had the lowest yield reduction due to weed pressure, probably as a result of rapid canopy development and final canopy architecture. In spite of its greater height in 1998 the LRS hybrid still had the lowest yield reductions due to weed pressure, which was probably a result of more rapid leaf area development.

Grain moisture content was affected by hybrid at all site-years, but in 1996 at the Ottawa site there was a row spacing by hybrid interaction (Table 4.2). The LRS hybrid had a higher grain moisture content at the narrow than the wide row spacing, while row spacing did not affect this variable for the other hybrids (Table 4.5). In 1997 grain moisture content was affected by plant population. the value being higher at the high than the conventional plant populations (Table 4.7). Of the three years we found interactions between weed level and hybrid for grain moisture content only in 1998. Grain moisture content varied among hybrids and was much higher for LMBL than the other corn hybrids both in the presence and absence of weeds (Tables 4.4 and 4.5). Under weed-free conditions several researchers (e.g. Major et al., 1991; Dwyer et al., 1994; Modarres et al, 1997b; Modarres et al, 1998; Begna et al., 1997a,b) have reported similar results for late maturing corn hybrids. Although the overall grain yield of the LMBL corn hybrid was higher because they develop, photosynthesize and grain fill for a longer period of time, they have much greater grain moisture contents at harvest, necessitating costly drying. This would make them undesirable in a short growing season area because the grain would not be completely filled at the first killing frost and grain moisture content would be high, possibly too high for mechanical harvest, at harvest time. The other two corn hybrids had 10-13 % less grain moisture than the LMBL, whether weeds were present or not (Tables 4.4 and 4.8). In general the grain moisture of LRS was lower than both P3979 and LMBL under both weed-free and weedy conditions (Table 4.8). This was probably due to earlier tasselling, silking and attainment of physiological maturity (black layer) of LRS than the other hybrids and this was also indirectly shown through its lower grain moisture content. However, in 1998, presumably due to later tasselling and silking than P3979, the LRS corn hybrid had a grain moisture content that was not different from the conventional P3979, although much lower than the LMBL hybrid.

CONCLUSIONS

In 1996 and 1997, the LRS hybrid was much shorter than the LMBL and P3979 hybrids, while leaf number above the ear was higher than the other corn hybrids in all years. Thus, the canopy architecture of LRS hybrid was quit different from the others. For 1996 and 1997, at both sites, plant height of LRS was less affected by the presence of weeds than the other hybrids. This was probably as a result of canopy structure differences and faster leaf area accumulation. The overall grain yield of the LMBL hybrid was greater than the other corn hybrids in the absence, but not in the presence, of weeds. In all site-years, and especially in 1996 and 1997, the narrower row spacing favoured the LRS hybrid, probably as a result of differences in the canopy architecture and their ability to tolerate high plant densities. Grain moisture content, which is an important trait in short growing-season areas, was generally much lower for LRS and Pioneer 3979 than LMBL under both weed-free and weedy conditions. Early maturing corn hybrids (LRS and P3979, and especially LRS) because of their faster growth and development early in the season, and differences in size and canopy architecture, appeared to be more competitive with weeds, resulting in less effect on grain yield due to the presence of weeds.

Table 4.1. A summary of weed species observed during the three years and sites of the experiments.

Weed species	Ottawa 1996	Macdonald 1996	Macdonald 1997	Macdonald 1998
Barnyard grass (*Echinocula crusgali* L.)	H	I	H	H
Giant foxtail (*Setaria faberi* Herm.)	I	H	I	I
Yellow nutsedge (*Cyperus rotundus* L.)	L	H	L	L
Yellow foxtail (*Setaria glauca* L.)	I	H	I	I
Witch grass (*Panicum capillare* L.)	I	H	I	L
Quack grass (*Elytrigia repens* L.)	L	H	H	L
Smooth crabgrass (*Digitaria ischaemum* Schreb.)	I	I	I	I
Lamb's quarters (*Chenopodium album* L.)	H	I	H	H
Redroot pigweed (*Amaranths retroflexus* L.)	H	I	H	H
Canada thistile (*Cirsium arvense* L.)	L	H	H	L
Velvet leaf (*Abutilon theophrasti* Medic.)	L	I	L	L
Purslane (*Portulaca oleracea* L.)	L	H	H	I
Prostrate knotweed (*Polygonum aviculare* L.)	I	I	I	I
Field bindweed (*Convolvulus arvensis* L.)	L	L	H	H
Common ragweed (*Ambrosia artemisiifolia* L.)	L	L	L	L

Population ocurrance (H- high, I- intermidiate, L-low)

Table 4.2. Analysis of variance showing probabilities for the main and interaction effects on plant height, ear height, ear leaf number and leaf number above the ear, grain yield, and grain moisture content at the Macdonald (S1), and Ottawa site (S2) in 1996.

		Plant height		Ear height	Ear leaf and leaf number above the ear	Grain yield	Grain moisture	
		Site 1	Site 2	Mean of sites	Mean of sites	Mean of sites	Site 1	Site 2
source	df				P -value			
Block (B)	3	0.0001	0.4997	0.2660	0.5234	0.5742	0.0742	0.7385
Weed level (WL)	1	0.0001	0.0028	0.1399	0.5866	0.0001	0.4642	0.4815
Error (B x WL)	3							
Plant populations (PP)	1	0.0264	0.1054	0.9010	0.2962	0.0001	0.0581	0.4899
WLx PP	1	1.0000	0.3961	0.5648	0.5844	0.0011	0.3055	0.1614
Error B x PP (WL)	6							
Row spacings (RS)	1	0.1241	0.1926	0.0110	0.7661	0.0011	0.7296	0.3586
WLx RS	1	1.0000	0.9720	0.8525	0.2421	0.4567	0.768	0.9937
PP x RS	1	0.7469	0.8745	0.1283	0.8586	0.2138	0.3033	0.427
WL x PP x RS	1	1.0000	0.9440	0.8139	0.8474	0.8701	0.7347	0.8798
Error B x RS (WLx PP)	12							
Hybrids (H)	2	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
WL x H	2	0.6078	0.0001	0.4138	0.9541	0.0001	0.5731	0.0665
PP x H	2	0.9998	0.7279	0.4537	0.9675	0.0001	0.5376	0.4871
WL x PP x H	2	1.0000	0.5150	0.6235	0.9121	0.9631	0.5642	0.9369
RS x H	2	0.9128	0.989	0.5419	0.5132	0.0001	0.2494	0.0075
WL x RS x H	2	1.0000	0.9085	0.9992	0.7022	0.0001	0.6254	0.7779
PP x RS x H	2	0.8488	0.9968	0.4217	0.2628	0.7234	0.4075	0.8358
WL x PP x RS x H	2	1.0000	0.9855	0.9954	0.9355	0.6125	0.9436	0.8916
Error	48							
CV (%)		9.87	3.81	7.72	3.44	6.39	5.64	3.52

Table 4.3. Analysis of variance showing probabilities for the main and interactions effect on plant height, ear height, ear leaf and leaf number and above the ear, grain yield, and grain moisture content at the Macdonald site in 1996 to 1998.

		Plant height		Ear height		Ear leaf and leaf number above the ear			Grain yield	Grain moisture	
		Means of (1996-1997)	1998	Means of (1996-1997)	1998	1996	1997	1998	Means of (1996-1998)	Means of (1996 & 1998)	1997
source	df	P-value									
Block (B)	3	0.0176	0.003	0.065	0.009	0.3892	0.9839	0.0265	0.0507	0.1588	0.2921
Weed level (WL)	1	0.0006	0.0001	0.2299	0.0122	0.6628	0.6132	0.029	0.0001	0.3435	0.1233
Error (BxWL)	3										
Plant populations (PP)	1	0.0134	0.2334	0.7826	0.0228	0.612	0.7788	0.8527	0.0007	0.1225	0
WL x PP	1	0.7023	0.83	0.9685	0.7245	0.6692	0.5669	0.7277	0.0296	0.7663	0.4463
Error Bx PP (WL)	6										
Row spacings (RS)	1	0.5871	0.0188	0.6961	0.0934	0.6471	0.9401	0.1519	0.0069	0.6789	0.0608
WL x RS	1	0.9943	0.9795	0.9899	0.9862	0.4127	0.4639	0.5978	0.8449	0.5708	0.8436
PP x RS	1	0.8293	0.9631	0.1383	0.9585	0.8503	0.2068	0.9551	0.6145	0.2634	0.7632
WL x PP x RS	1	0.9886	0.5917	0.9899	0.9862	0.8213	0.6443	0.7558	0.9417	0.5812	0.8887
Error B x RS (WCx PP)	12										
Hybrids (H)	2	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.001	0.0001	0
WL x H	2	0.0045	0.0001	0.1722	0.0032	0.9812	0.8566	0.0296	0.0001	0.3512	0.0393
PP x H	2	0.9857	0.9648	0.5276	0.8866	0.64	0.9176	0.6574	0.0561	0.6663	0.3928
Wl x PP x H	2	0.9822	0.9422	0.7759	0.9764	0.7664	0.5048	0.9213	0.2005	0.4651	0.1702
RS x H	2	0.9529	0.9904	0.6548	0.9961	0.1664	0.7394	0.9566	0.0001	0.397	0.7832
WLx RS x H	2	0.9997	0.9979	0.9996	0.9288	0.425	0.9361	0.8902	0.0259	0.5785	0.6119
PPx RS x H	2	0.9181	0.9792	0.4466	0.9884	0.175	0.5301	0.9729	0.9607	0.5918	0.4773
WL x PP x RS xH	2	0.9994	0.9586	0.9558	0.9507	0.9664	0.7195	0.911	0.9715	0.8292	0.7988
Error	48										
CV (%)		7.39	3.31	7.59	5.62	5.32	6.87	2.48	6.35	3.16	2.72

Table 4.4. Multiple pairwise comparisons of overall main effects of weed level, plant population, row spacing and corn hybrid on plant height, ear height, ear leaf and leaf number above the ear, and grain moisture at the Macdonald (S1), and Ottawa (S2) site in 1996.

	Plant height (cm)	Ear height (cm)	Ear leaf and leaf number above the ear	Grain moisture (%)
	Site 1	Means of sites		Site 1
Hybrid				
LRS	134.50b*	38.38c	8.83a	26.10b
LMBL	245.11a	74.58b	6.69b	40.26a
P3979	242.56a	92.22a	5.78c	27.19b

Weed level	Plant height (cm) Site 1
Weed-free (W F)	212.72a
Weedy (W)	202.06b

Plant population	Plant height (cm) Site1
Conventional	204.20b
High	210.58a

Row spacing	Ear height (cm) Mean of sites
Narrow	67.16b
Wide	69.63a

* Values, in the same column, followed by the same letter are not different ($p< 0.05$) based on an ANOVA protected LSD test.

Table 4.5. Multiple pairwise comparisons for interaction effects between weed level and corn hybrid on plant height, and between row spacing and corn hybrid on grain moisture content at the Ottawa site (S2) in 1996.

		Plant height (cm)
Weed level	**Hybrid**	Site 2
Weed-free	LRS	144.69d*
	LMBL	273.25a
	P3979	270.50a
Weedy	LRS	133.56d
	LMBL	247.56b
	P3979	238.44c
		Grain moisture (%)
Row spacing	**Hybrid**	Site2
Narrow	LRS	27.25b
	LMBL	39.43a
	P3979	26.85b
Wide	LRS	25.11c
	LMBL	38.80a
	P3979	28.00b

Abbreviations: LRS -Leafy-reduced stature, LMBL-Late maturing big leaf, and P3979-Pioneer 3979. *Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Table 4. 6. Multiple pairwise comparisons interaction effects between weed level, plant population, row spacing and corn hybrid on grain yield at the Macdonald and Ottawa sites in 1996.

Weed level	**Row spacing**	**Hybrid**	Grain yield ($t\ ha^{-1}$) Means of sites
Weed-free	Narrow	LRS	10.38c*
		LMBL	11.60b
		P3979	11.95b
	Wide	LRS	8.78d
		LMBL	13.28a
		P3979	10.21c
Weedy	Narrow	LRS	6.87ef
		LMBL	6.44efg
		P3979	7.19e
	Wide	LRS	6.15g
		LMBL	6.85ef
		P3979	6.40fg

Weed level	**Plant population**	Grain yield ($t\ ha^{-1}$) Means of sites
Weed-free	Conventional	10.18b
	High	11.88a
Weedy	Conventional	6.45d
	High	6.86c

Abbreviations: LRS -Leafy-reduced stature, LMBL-Late maturing big leaf, and P3979-Pioneer 3979. *Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Table 4.7. Multiple pairwise comparisons of overall main effects of plant population, row spacing and corn hybrid on plant height, ear height, ear leaf and leaf number above the ear, and grain moisture content at the Macdonald site in 1996 to 1998.

	Ear height (cm)	Ear leaf and leaf number above the ear		Grain moisture (%)
	Means of (1996-1997)	1996	1997	Means of (1996 &1998)
Hybrid				
LRS	39.30c*	8.63a	9.94a	25.75b
LMBL	72.36b	6.78b	7.03b	39.03a
P3979	88.92a	5.40c	6.06c	24.93b
	Plant height (cm)	Ear height (cm)	Grain moisture (%)	
Plant population	Means of years (1996-1997)	1998	1997	
Conventional	196.50b	75.77b	30.99b	
High	201.37a	78.00a	32.99a	
	Plant height (cm)			
Row spacing	1998			
Narrow	209.62a			
Wide	206.92b			

Abbreviations: LRS -Leafy-reduced stature, LMBL-Late maturing big leaf, and P3979-Pioneer 3979. *Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Table 4.8. Multiple pairwise comparisons interaction effects between weed level and corn hybrid on plant height, ear height, ear leaf number and leaf number above the ear, and grain moisture, at the Macdonald site in 1996 to 1998.

		Plant height (cm)		Ear height (cm)	Ear leaf number and leaf number above the ear	Grain moisture (%)
Weed level	**Hybrid**	Means of (1996-1997)	1998	1998	1998	1997
Weed-free	LRS	134.91c*	231.75a	68.38d	9.59a	27.21d
	LMBL	248.74a	217.81b	73.25c	6.84c	38.18b
	P3979	240.78a	214.56bc	94.31a	5.95d	29.12c
Weedy	LRS	131.03c	211.25c	69.31d	9.08b	26.91d
	LMBL	220.80b	180.27	67.00d	6.86c	40.31a
	P3979	217.34b	193.97d	89.06b	5.63d	30.19c

Abbreviations: LRS -Leafy-reduced stature, LMBL-Late maturing big leaf, and P3979-Pioneer 3979. *Values, in the same column, followed by the same letter are not different ($p< 0.05$) based on an ANOVA protected LSD test.

Table 4. 9. Multiple pairwise comparisons interaction effects among weed level, row spacing, and hybrid and between weed level and plant population on grain yield at the Macdonald site.

Weed level	Row spacing	Hybrid	Grain yield ($t\ ha^{-1}$) Means of (1996-1998)
Weed-free	Narrow	LRS	9.65b*
		LMBL	9.80b
		P3979	10.14b
	Wide	LRS	8.54d
		LMBL	11.02a
		P3979	9.13c
Weedy	Narrow	LRS	5.82e
		LMBL	4.84f
		P3979	5.51e
	Wide	LRS	5.03f
		LMBL	5.25ef
		P3979	4.87f

Weed level	Plant population	Grain yield ($t\ ha^{-1}$) Means of (1996-1998)
Weed-free	Conventional	9.02b
	High	10.41a
Weedy	Conventional	4.95d
	High	5.49c

Abbreviations: LRS -Leafy-reduced stature, LMBL-Late maturing big leaf, and P3979-Pioneer 3979. *Values, in the same column, followed by the same letter are not different ($p< 0.05$) based on an ANOVA protected LSD test.

Table 4. 10. Monthly temperature and accumulated rainfall during the three years and sites of the experiments

Months	Mean temperature (^0C)				Rainfall (mm)			
	Ottawa	Macdonald			Ottawa	Macdonald		
	1996	1996	1997	1998	1996	1996	1997	1998
May	12.2	12.3	10.7	17.4	53.2	92	76	50.5
June	19.1	18.6	20.1	19.5	89.2	65.5	105	74.5
July	20.1	20.2	20.6	21.1	149.3	106	135	89.5
August	20.2	20.4	19	21	83	22.5	106	92.5
September	16.6	16.3	14.6	16.1	124.4	115.1	91.5	62
October	8.2	8.1	8	9.8	87.2	74.5	30.5	62.5

Preface to Chapter 5

This section will form a manuscript to be submitted in 1999 for publication in the Journal of Agronomy and Crop Science. The format has been changed to be consistent within this thesis. All literature cited in this chapter are listed at the end of the thesis. Each table or figure is presented at the end of this chapter.

In chapter 3, I addressed the pattern of dry matter accumulation and partitioning, and leaf area development, while in chapter 4 I investigated grain yield reductions, morphological responses and canopy architecture differences due to weed pressure. In chapter 5 I investigated general grain yield and morphological responses of corn hybrids varying in leaf area and dry matter accumulations and canopy architectures to mechanical (rotary hoeing) and chemical methods of weed control.

MORPHOLOGY AND YIELD RESPONSE OF CORN HYBRIDS DIFFERING IN CANOPY ARCHITECTURE TO CHEMICAL AND MECHANICAL (ROTARY HOEING) WEED CONTROL

ABSTRACT

Weed interference with growth and yield of corn plants could be influenced by both mechanical and chemical means of weed control. Recently, corn hybrids accumulating more leaf area, maturing earlier, yielding better in narrower row spacings and tolerating higher plant populations better than conventional corn hybrids have been developed. Because these hybrids produce more leaf area during the earliest stages of canopy development they may be more susceptible to damage due to mechanical weed control. Although there have been previous reports regarding the high yield potential of these hybrids in short-season areas under weed-free conditions, no research has been conducted to compare their morphology and grain yield responses to chemical and mechanical (rotary hoeing) weed control with that of conventional corn hybrids. The objective of this study was to assess the response of corn hybrids with a wide range of canopy architectures to these weed control practices and with an emphasis on quantifying morphology and grain yield responses. Field Experiments were conducted in 1997, and 1998 at Ste. Anne de Bellevue, Quebec. Three corn hybrids were tested: Leafy reduced-stature (LRS1 and LRS2), and the conventional hybrid Pioneer 3979 (P3979). The following variables were measured: dry weight (leaf and stem), leaf area (total and ear leaf and above ear leaf area), plant and ear height, grain yield, grain moisture content and harvest index. Rotary hoeing

alone had very little effect, while herbicide treatment reduced the interference of weeds with growth and grain yield of all hybrids. Corn hybrid P3979 had more total leaf area than LRS1 and LRS2, but the percentage of leaf area distributed to the above ear portion was much higher for LRS hybrids (70%) than for P3979 (51%). In both years the grain yield reduction due to weed presence in plots not treated with herbicide were well above 50 % for all hybrids. In both years LRS1 had a greater harvest index than LRS2 and P3979. Generally, LRS hybrids were much shorter than P3979, contributing to the large differences in canopy architecture between the LRS hybrids and P3979. However, morphology and grain yield response of hybrids to rotary hoeing and herbicide weed control were not different.

INTRODUCTION

In the production of agricultural crops, weeds are an important economic and ecological variable. Herbicides have played an important role in weed control during the last 50 years. This is primarily because they are a quick and effective form of weed control. However, they have two disadvantages that have become concerns for researchers and the public. First, herbicides can become contaminates of ground and surface waters (National Research Council, 1986). Second, they are expensive and, as a result, they have come to represent a major cost for producers (Lybecker et al., 1988).

Interrow cultivation can be an effective form of weed control. Its greatest effect is only after most weeds have emerged (Parks et al., 1995). Adequate information about the timing and rate of weed seed germination and emergence is very important in order to be able to determine the appropriate time for cultivation (Harvey and Forcella, 1993). Integration of herbicides applied at reduced rates in a narrow band over the crop row, and high population may help in achieving both environmental and weed control objectives for corn (Teasdale, 1995). Forcella et al. (1992) showed that good weed control could be obtained with reduced herbicide application rates when crops were planted in narrow rows. An integrated weed management system needs to take all aspects of the cropping system into account: effects of tillage, crop rotation, crop competitiveness, and various methods of weed control (Swanton and Weise, 1991).

Rotary hoeing or inter-row cultivation alone did not control weeds as well as herbicides alone or herbicides with interrow cultivation (Burnside et al., 1994; Burnside et al., 1993). Rotary hoeing and inter-row cultivation together can be an effective ways of weed control in corn and soybean. More than 70 % weed control in corn and soybean has been reported with only one pass of a rotary hoe (Lovely et al., 1958; Mulder and Doll, 1993). Mulder and Doll (1993) also reported that two rotary hoeings alone or together with inter-row cultivation gave additional weed control in corn. There was a concern by bean growers in Colorado that rotary hoeing may injure pinto bean and reduce yields; these growers usually use a rotary hoe to alleviate soil crusting but not to control weeds (Vangessel et al., 1995). Pinto bean hypocotyls and stems were damaged by flex-tine harrowing at both crook and trifoliate stages, while no damage or reduction in stand, yield and seed weight was caused by rotary hoeing (Vangessel et al., 1995). Mohler et al. (1997) found that in two of three years cultivation with a rotary hoe or tine weeder reduced weed seedling density by 39 to 74 %, while the same operation reduced corn populations by an average of only 6 %.

Recently corn hybrids accumulating more leaf area, particularly above the ear, maturing earlier, yielding better, taking advantage of narrow spacings and tolerating higher plant populations better than conventional corn hybrids have been reported (Modarres et al., 1997a,b; Modarres et al., 1998; Begna et al., 1997a,b; Begna et al., 1999). The leafy (Lfy1) and reduced-stature (rd1) traits both make contributions to the recently developed "Leafy-reduced stature" hybrids (Modarres et al., 1997a; Modarres et al., 1998). As a result of this combination, canopy architectures of the corn plants have been changed. The net result of this is that plants bearing the Leafy trait show a dramatic increase in the production of leaf area by the time of maturity (Shaver, 1983). There have been previous reports regarding better leaf area accumulation and yield potential by these hybrids at higher plant populations and in narrow row spacings in short-season areas, these have been conducted only with herbicide control of weeds. Because of more rapid leaf area accumulation and canopy architecture differences, LRS hybrids will be more damaged by rotary hoeing than conventional hybrids. No research has been conducted to compare their morphological and grain yield responses to chemical and mechanical (rotary hoeing) weed control with that of conventional corn hybrids. The objective of this study was to assess the response of corn hybrids with a wide range of canopy architectures to herbicide and rotary hoeing weed control practices, with the emphasis on quantifying morphology and grain yield responses.

MATERIALS AND METHODS

Experiments were conducted in 1997 and 1998 on two sites at the E. A. Lods Agronomy Research Centre of the Macdonald Campus of McGill University, Ste. Anne de Bellevue, Quebec. The 1997 experiment was on a clay-loam soil (fine, mixed, nonacid, frigid Humaquept), while the 1998 experiment was on the same clay-loam soil type as 1997 (fine, mixed, nonacid, frigid Humaquept) for site 1and a courval sandy soil (fine-silty, mixed, nonacid, frigid Humaquept) for site 2. Soils were fertilized with 186 kg N ha^{-1} (NH_4NO_3), both in 1997 and 1998, just prior to planting. For all site-years herbicide weed control treatments were through the application of Primextra [Metolachlor/Atrazine (2:1), 500g L^{-1}, Ciba-Geigy, Canada Inc.)] at a rate of 7.7 L ha^{-1} before planting. This was applied only in weed-free plots. Mechanical weed control was conducted with a rotary hoe. The rotary hoe (John Deere model 400, Canada) was operated at approximately 8 km/h, with the gangs set at a 5-cm spacing in both years. In 1997 hoeing was done parallel to the rows, while in 1998 since the plants were at much earlier growth stages than the 1997ones, the operation was perpendicular to the rows (. In both years the rotary hoeing was a one pass operation conducted at the 4-6 and 2-4 corn leaf-stages for the 1997 and 1998 experiments, respectively. Single pass rotary hoe operations are common and can provide adequate weed control (Lovely et al., 1958; Mulder and Doll, 1993). The earlier hoeing in 1998 allowed the operation to be conducted over the corn seedlings.

Three corn hybrids: two leafy reduced-stature [LRS1:(1306-2-2 X LDOP300rd1) both in 1997 and 1998, while LRS2:(1306-2-2 X 91L210-2 X 9lL190-1) in 1997 and

(CO392 X LDOP300rd1) in 1998] and one conventional [Pioneer 3979 (P3979)] were tested. Leafy reduced-stature corn hybrids have become available only recently (Modarres et al., 1997a,b). Descriptions of the development of the LRS hybrids have been reported (Modarres et al., 1997a,b). Briefly LRS is a combination of "Leafy (Lfy)" and "reduced-stature (rd1)" traits. The "Leafy" trait increases the leaf number of the plant, especially leaf number above the ear, while the "rd1" trait results in a short statured, early maturing hybrids. In 1998 we were short of seeds for LRS2, therefore it was necessary to replace the previously used LRS2 hybrid with another one. The new one proved to be approximately normal height. Although it was not as short as the previously used LRS material it is still considered to be reduced in stature because leafy hybrids that do not contain the rd1trait are much taller than conventional hybrids (Modarres et al., 1997).

The experiment followed a split-split-plot randomized complete block design with four blocks. Herbicide weed control formed the main plots (applied or not applied) and rotary hoeing (hoeing or no-hoeing) formed the subplots. Hybrids formed the sub-sub-plot units. The dates of planting were 21 May, 1997, and 23 May, 1998. The corn was planted at 120,000 and 80,000 plants ha^{-1}, for LRS hybrids and P3979, respectively for both 1997 and 1998 experiments. The hybrids were LRS planted in a narrow row spacing (38 cm), while P3979 was planted in a wider (76 cm) row spacing. Selection of plant population and row spacings was based on their canopy architectures and performance at different plant populations and row spacings; LRS hybrids perform better at higher plant populations and narrower spacings than the conventional P3979 hybrid (Begna et al., 1997a,b). All plots were hand planted. The 76 cm row spacing plots consisted four rows and the narrow spacing plots of eight rows in both 1997and 1998 experiments. The plots were 3 m long.

The following data were recorded for all combinations of weed control in all plots at all site-years of the experiment: Visual observation of corn seedlings were taken immediately after rotary hoeing in order to assess damage to the crop plants, dry matter accumulation was determined at tasselling (four corn plants were harvested). Prior to drying leaf area (length and maximum width of individual leaves) of the four collected plants were measured and the leaves and stems were dried and weighed separately. The leaf area of each leaf was calculated using the formula: leaf area = leaf length (cm) X maximum leaf width (cm) X 0.75 (Montgomery, 1911). Dry weight was expressed on a per plant basis. Allocation patterns were assessed by calculating leaf and stem weight (g $plant^{-1}$) and leaf area (total leaf area and ear leaf area, and above the ear leaf area were expressed as cm^2) Plant height (soil level to the collar of the top leaf) and ear height (soil level to node of the uppermost ear) at tasselling were also taken on four randomly selected plants from each plot.

At physiological maturity, as determined by the black layer method (Daynard and Duncan, 1969; Cross and Kabir, 1989), four plants per plot were randomly selected and cut at ground level. After the fresh weight was taken sub-samples of the plants were dried to a constant weight at 80 ^{0}C for grain moisture determination. These same samples were also used to determine harvest index. At all site-years the ears of all plants of the two central rows were hand picked and used for grain yield determination. Ears were shelled using an electric sheller (SCI1 Corn Sheller, Agriculex, Ont., Canada), grain yield was determined and plot yields were expressed at 15.5 % moisture on a t ha^{-1} basis.

All data were subjected to analysis of variance on a site-year basis with the PROC GLM Procedure of SAS (SAS Institute, 1994). The data of the two 1998 experiments were pooled when the hypothesis of homogeneity of variances was tested and accepted by the Bartlett's test (Steel and Torrie, 1980). Simple means comparisons for each multiple pairwaise were made with a GLM protected LSD test at the 0.05 level probability. Effects of herbicide, cultivation (rotary hoeing) and hybrids were examined jointly to test for interactions between the three factors.

RESULTS AND DISCUSSION

Growing conditions varied between the two years the experiments were conducted. The average monthly temperature was slightly lower in 1997 than in 1998 and rainfall accumulation for 1997 was much higher than for 1998. For example in the month of July, 1997, the accumulated rainfall was 135.0 mm, while for the same month of 1998, it was only 89.5 mm (Table 5.1). Presumably as a result of differences in rainfall accumulation between the years most values of the measured variables were higher for 1997 than 1998.

All corn hybrids responded positively to the use of both rotary hoeing and herbicide methods of weed control although there was greater effect due to herbicide ($P<0.05$) than rotary hoeing ($P>0.05$). Except for grain moisture and ear height all measured variables were affected by herbicide. Most variables were also positively affected by hybrid. In both years there was a two way interaction between herbicide and hybrid for stem dry weight, total leaf area and plant height (Table 5.2) where higher values for plots treated with herbicide than untreated plots were recorded for all hybrids.

Dry matter and leaf area

In both years of the experiment rotary hoeing did not cause any differences in dry matter and leaf area as compared to the weedy plot, while herbicide treatment increased leaf and stem dry weight of all corn hybrids. Generally, leaf and stem dry weights of P3979 were higher than LRS1 and LRS2 (Tables 5.3, 5.5, and 5.6). Although higher leaf and stem dry weights per plant were expected for P3979, mainly due to canopy architecture differences, some of the increases may have been due to plant population and row spacing differences, where lower plant populations and wider row spacings favour higher leaf and stem dry weights on a per plant basis. Several researchers have reported higher above ground dry matter per plant for corn when planted at lower than higher populations (e.g. Jolliffe et al., 1990; Tollenaar et al., 1994). Plant size differences had larger effects on stem than leaf dry weight. For example in the 1997 experiment the stem dry weight of P3979 in herbicide treated plots was 94.3 g, which was more than twice of that of LRS1 (36.8 g) and LRS2 (46.3 g). The same was true in rotary hoed plots where P3979 weighed 77.7 g, while LRS1 and LRS2 weighed only 33.7 and 44.9 g, respectively (Tables 5.3 and 5.6).

Total plant leaf area, ear leaf area and leaf area above the ear were influenced by rotary hoeing (P=0.3) and herbicide treatments (P=0.002), but with a significant influence by the rotary hoeing than the herbicide. Plots that received the herbicide treatment had greater total leaf area than the no-herbicide control plots with an increase in total leaf area due to herbicide of 38-43 % (Table 5.6). In both years the herbicide treated plots of P3979 had more final leaf area than herbicide treated LRS1 and LRS2 plots. While the final leaf area for P3979 was greater than the LRS hybrids, P3979 had the smallest percentage of the total leaf area distributed above the ear. For example in 1997 average leaf area above the ear for the LRS hybrids was 70 %, while for P3979 it was only 51% (Table 5.4).

Plant height

Plant height and ear height were not affected by rotary hoeing although the variables were affected by herbicide treatment. Herbicide treatment resulted in taller plants than no-herbicide treatment. In general, plant height and ear height of the LRS hybrids were less than P3979 in both herbicide treated and no-herbicide plots. Both LRS1and LRS2 in 1997 and LRS1 in 1998 were 30 to 40 % shorter than P3979 (Tables 5.3 and 5.6). Similar results have been reported under weed-free conditions (Modarres et al.,1997a; Begna et al., 1999). This was mainly because of the rd1 trait which reduced the height of LRS hybrids, while the Lfy1 traits increased leaf number (Modarres et al., 1997a; Modarres et al., 1998). The net result of this has been that plants bearing the Leafy trait show a dramatic increase in the production of leaf area by the time of maturity (Shaver, 1983). Generally this made LRS hybrids very different, in terms of canopy architecture, from P3979. Regardless of their differences in canopy architecture hybrid responses to rotary hoeing and herbicide treatment followed the same general pattern.

Grain yield, grain moisture content, and harvest index

In both years, grain yield was not increased by rotary hoeing while it was increased by herbicide treatment. Grain yield of all hybrids were much higher in plots that were treated with herbicide than plots not treated with herbicide. The reduction in grain yield due to weed interference in the herbicide untreated plots was as much as 50-60 % (Table 5.5). Similar grain yield reductions due to weed presence have been reported by other researchers (eg.s Ford and Pleasant, 1994; Teasdale, 1995). However, when weeds were not treated with herbicide, grain yield reduction due to weed presence was higher for P3979 than for the LRS hybrids. This was, presumably, due to the earlier, faster growth and development as well as better tolerance of higher plant populations (Modarres et al., 1997a,b; Modarres et al., 1998; Begna et al., 1997a,b; Begna et al., 1999) and probably weed stresses by the LRS hybrids than P3979.

Grain moisture content was affected by neither rotary hoeing nor herbicide treatments. However, when grain moisture content was averaged over rotary hoeing and herbicide treatments corn hybrids were different. Of the three factors tested in our study only herbicide and hybrids affected harvest index. When this value was averaged over rotary hoeing and hybrids, harvest index in the herbicide treated plots was more than twice of that of the herbicide untreated plots. Harvest index of LRS1 was higher than LRS2 and P3979 in both years (Tables 5.4). Presumably this was due to differences in canopy architecture among the hybrids, whereby the LRS hybrids allocated the smallest amount of assimilates to support stem development. Higher harvest index has previously been reported for LRS hybrids under weed-free conditions (Modarres, 1995; Begna et al., 1997a,b).

CONCLUSIONS

Rotary hoeing did not reduce the interference of weeds with growth and grain yield of any hybrid while chemical weed control was effective for all hybrids. However, we assume that more passes with a rotary hoe, or, perhaps a different timing of its use would provide effective weed control as numerous other authors have reported this. In spite of more rapid early leaf production and, therefore, greater potential damage due to rotary hoeing, LRS hybrids were not more adversely affected by this form of mechanical cultivation for weed control than a conventional hybrid.

Table 5.1. Monthly temperature and accumulated rainfall during the two years of the experiments.

	Temperature (^0C)		Rainfall (mm)	
Months	1997	1998	1997	1998
May	10.7	17.4	76	50.5
June	20.1	19.5	105	74.5
July	20.6	21.1	135	89.5
August	19	21	106	92.5
September	14.6	16.1	91.5	62
October	8	9.8	30.5	62.5

Table 5.2. Analysis of variance showing probabilities for main and interactions effects of herbicide (H), rotary hoeing (R),and hybrids (HY) on leaf and stem dry weight, total leaf area, ear leaf area and above the ear, plant and ear height, grain yield, grain moisture and harvest index in 1997 and 1998.

Source	CV	H	R	H x R	HY	H x HY	R x HY	H x R x HY
	%	P-value						
Leaf dry weight								
1997	15.8	0.0064	0.2443	0.7356	0.0001	0.0713	0.8243	0.6613
1998	11.4	0.0142	0.0643	0.6954	0.0001	0.3566	0.9768	0.9887
Stem dry weight								
1997	9.5	0.0347	0.0716	0.5104	0.0001	0.0001	0.9516	0.8893
1998	11.7	0.0063	0.0575	0.5513	0.0001	0.0012	0.6680	0.8518
Total leaf area								
1997	12.2	0.0018	0.1850	0.9347	0.0001	0.0158	0.9221	0.9777
1998	8.4	0.0003	0.1290	0.7930	0.0001	0.0001	0.9760	0.9755
Ear leaf area and above the ear								
1997	21.2	0.0065	0.3928	0.9595	0.0359	0.5633	0.9807	0.9599
1998	12.6	0.0010	0.3851	0.7749	0.0001	0.8596	0.9140	0.8735
Plant height								
1997	11.7	0.0038	0.2168	0.9832	0.0001	0.0044	0.9970	0.9937
1998	5.2	0.0166	0.1975	0.9157	0.0001	0.0005	0.9960	0.9977
Ear height								
1997	13.9	0.0932	0.7082	0.9515	0.0001	0.9922	0.9522	0.9815
1998	7.3	0.2797	0.0748	0.8869	0.0001	0.9599	0.9951	0.9678
Grain moisture								
1997	10.2	0.0908	0.9752	0.9917	0.0325	0.8952	0.8812	0.9045
1998	12.7	0.7659	0.7398	0.5438	0.0021	0.8811	0.9824	0.9682
Grain yield								
1997	8.9	0.0001	0.4767	0.9691	0.1075	0.2423	0.8967	0.9827
1998	7.4	0.0001	0.2473	0.9660	0.0083	0.6695	0.9533	0.9529
Harvest index								
1997	8.0	0.0006	0.6693	0.6693	0.0250	0.7985	0.8553	0.9273
1998	6.9	0.0001	0.5303	0.9660	0.0104	0.1239	0.9404	0.9797

Table 5.3. Multiple pairwise comparisons of overall main effects of rotary hoeing treatment on leaf and stem dry weight, total leaf area, ear leaf area and above the ear, plant and ear height, grain yield, grain moisture, and harvest index in 1997 and 1998.

			Dry weight (g plant $^{-1}$)		Leaf area (cm^2 plant $^{-1}$)		Height (cm)		Grain moisture	Grain yield	Harvest index
Year	Rotary hoeing	Hybrid	Leaf	Stem	Total	Ear leaf and above the ear	Plant	Ear	(%)	(tha^{-1})	
1997	Applied	LRS1	15.09b*	33.68b	2596.92c	1788.14b	113.44b	35.19b	25.53b	6.99a	0.43a
		LRS2	20.08a	44.92b	3066.78b	2120.72a	122.00b	37.00b	28.25a	7.23a	0.41ab
		P3979	22.55a	77.66a	3530.81a	1836.51b	215.38a	98.13a	28.01a	7.38a	0.40ab
	Not applied	LRS1	14.39b	31.86b	2399.83c	1683.76b	108.63b	35.50b	25.91b	6.65a	0.42a
		LRS2	18.43a	42.09b	2880.77b	2063.79a	116.25b	38.63b	28.52a	7.03a	0.41ab
		P3979	20.61a	75.01a	3428.80a	1731.59b	210.19a	95.06a	27.47a	7.24a	0.39b
1998	Applied	LRS1	11.43b	58.51c	2255.05b	1637.16b	110.21b	41.57c	22.15b	6.38a	0.41a
		LRS2	15.32a	102.44b	3317.85a	2612.99a	225.32a	69.76b	26.22a	6.87a	0.38b
		P3979	17.42a	134.26a	3269.87a	1748.36b	207.00a	87.94a	23.37b	6.41a	0.38b
	Not applied	LRS1	10.57b	56.00c	2117.59b	1602.29b	106.86b	39.46c	21.80b	6.13a	0.40a
		LRS2	14.67a	98.86b	3212.90a	2581.82a	222.34a	67.87b	26.16a	6.71a	0.37b
		P3979	16.78a	124.61a	3132.26a	1650.75b	203.43a	85.69a	23.41b	6.25a	0.38b

Abbreviations: LRS-Leafy-reduced stature, P3979-Pioneer 3979, * Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Table 5.4. Multiple pairwise comparisons of overall main effects of corn hybrids on leaf dry weight, ear leaf area and above the ear, ear height, grain moisture, grain yield, and harvest index in 1997 and 1998.

		1997					
		Leaf dry weight (g plant^{-1})	Area of the ear leaf and leaves above the ear (cm^2 plant^{-1})	Ear height (cm)	Grain moisture (%)	Grain yield (t ha^{-1})	Harvest index
Year	**Hybrid**						
1997	LRS1	14.74c*	1736.00b	35.34b	25.72b	6.82b	0.42a
	LRS2	19.25b	2092.30a	37.81b	28.38a	7.13ab	0.41ab
	P3979	21.58a	1784.10b	94.09a	27.74ab	7.31a	0.39b
1998	LRS1	11.99c	1619.73b	40.51c	21.97b	6.25b	0.40a
	LRS2	14.99b	2597.40a	68.82b	26.19a	6.79a	0.37b
	P3979	17.01a	1699.56b	86.82a	23.39b	6.31b	0.38b

Abbreviations: LRS-Leafy-reduced stature, P3979-Pioneer 3979, * Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Table 5.5. Multiple pairwise comparisons of overall main effects of herbicide treatment on leaf dry weight, ear leaf area and above the ear, grain yield, and harvest index in 1997 and 1998.

	1997				1998			
Herbicide	Leaf dry weight (g plant^{-1})	Area of the ear leaf and leaves above the ear (cm^2 plant^{-1})	Grain yield (t ha^{-1})	Harvest index	Leaf dry weight (g plant^{-1})	Area of the ear leaf and leaves above the ear (cm^2 plant^{-1})	Grain yield (t ha^{-1})	Harvest index
Applied	21.80a*	2266.60a	10.16a	0.56a	16.27a	2320.29a	8.91a	0.51a
Not applied	15.25b	1474.90b	4.01b	0.26b	12.46b	1624.16b	4.00b	0.25b

Abbreviations: * Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Table 5.6. Multiple pairwaise comparisons interaction effects between herbicide and hybrids on stem dry weight, total leaf area and plant height in 1997 and 1998.

		1997			1998		
		Stem dry weight (g plant^{-1})	Total leaf area (cm^{2}plant^{-1})	Plant height (cm)	Stem dry weight (g plant^{-1})	Total leaf area (cm^2 plant^{-2})	Plant height (cm)
Herbicide	**Hybrid**						
Applied	LRS1	36.75c*	3002.58c	113.50c	65.30d	2667.98c	114.87e
	LRS2	46.31c	3640.97b	123.94c	111.08b	4012.13b	242.21a
	P3979	94.28a	4387.27a	235.94a	153.37a	4192.71a	225.64b
Not applied	LRS1	28.78c	1994.17e	108.56c	49.2d	1704.66e	102.20f
	LRS2	40.70d	2306.58d	114.31c	88.21c	2518.62c	205.45c
	P3979	58.39b	2572.34d	189.63b	105.51b	2209.42d	184.79d

Abbreviations: LRS-Leafy-reduced stature, P3979-Pioneer 3979; * Values, in the same column, followed by the same letter are not significantly different ($P<0.05$) based on an ANOVA protected LSD test.

Preface to Chapter 6

This section will form a manuscript to be submitted in 1999 for publication in Weed Téchnology. The format has been changed to be consistent within this thesis. All literature cited in this chapter are listed at the end of the thesis. Each table or figure is presented at the end of this chapter.

In the previous chapters (chapter 3. 4, and 5) I addressed grain yield and morphological responses of corn hybrids with very different in canopy architectures with in combination of planting patterns to weed pressure. The canopy architectures and planting patterns should also cause changes in light distribution through the canopy. In chapter 6 I investigate the light level changes caused both by manipulation of planting patterns and choice of hybrids on biomass production by both transplanted (lamb's quarters and redroot pigweed) and naturally growing weeds.

WEED BIOMASS PRODUCTION RESPONSE TO DIFFERENT CORN PLANTING PATTERNS AND HYBRIDS DIFFERING IN CANOPY ARCHITECTURE

ABSTRACT

Weed biomass production is strongly affected by the degree of competition from the crop and this can be manipulated through selection of crop, plant population, row spacing and genotype. A combination of higher population densities and narrower row spacings could increase leaf area index leading to better crop light interception. This should lead to less weed biomass production. Recently, corn hybrids accumulating more leaf area, maturing earlier, yielding better in narrower row spacings and tolerating higher plant populations better than conventional corn hybrids have been developed. Although there have been previous reports regarding better leaf area accumulation and yield potential of these hybrids at higher plant populations, particularly in narrow spacings, in short-season areas, no research has been previously conducted to compare their ability to compete with weeds. The objective of this study was to quantify light interception by weeds and corn hybrids varying in canopy architecture in a range of planting patterns (row width and population combinations) and their effect on weed biomass production. Experiments were conducted in 1996, 1997, and 1998 at Ste. Anne de Bellevue, Quebec and in 1996 at Ottawa, Ontario. Three corn hybrids were tested: Leafy reduced-stature (LRS), late maturing big leaf (LMBL), and Pioneer 3979 (P3979), a conventional hybrid. Each block of the experiment was divided longitudinally into two, one side with weeds of transplanted lamb's quarters (*Chenopodium album* L.) in 1996, and lamb's quarters and redroot pigweed (*Amaranthus retroflexus* L.) in 1997 and 1998 and the other with naturally occurring weeds (weedy plot). Comparisons between the two sections allowed assessment of biomass production by transplanted and naturally occurring weeds under the corn hybrids. Each hybrid was planted

at two plant populations (conventional and high) and row spacings (38 and 76 cm). At all site-years the decrease in biomass production by both transplanted and naturally occurring weeds was more pronounced due the narrower row spacing than the higher plant population for all hybrids. There was at least a 3-5 % increase in light interception due to changes in planting pattern, in particular in reduced row spacings. Biomass produced by both transplanted and naturally occurring weed populations under all hybrids were 5-8 times less than the biomass produced in the corn-free control plots. A narrower row spacing favoured the LRS hybrids. probably as a result of differences in their canopy architectures, faster growth, and ability to tolerate higher plant densities and weed pressure. Weed biomass production response to all possible plant spacing combinations under early maturing corn hybrids (LRS and P3979), appeared to be more affected than under LMBL corn hybrids.

INTRODUCTION

Weed biomass production is strongly affected by the degree of competition from the crop and this can be manipulated through choice of crop, plant population, row spacing and genotype. The relationship between weed population and crop yield varies with environmental and cultural conditions (Wiles and Wilkerson, 1991). Planting pattern has a large influence on the distribution of radiation within the canopy and the total amount of incident radiation intercepted by a crop (Ottman and Welch, 1989). Ottman and Welch (1989) have found interactions among planting pattern, hybrid, and plant density and suggested that the differences in radiation interception between narrow and wide rows were most pronounced for a hybrid with an erectophile leaf habit planted at a high plant density. They also suggested that differences found in their studies and any comparable study could be due to hybrid or planting pattern as well as year, location, and growing conditions.

Planting patterns that favour better light distribution for the crop should favour higher crop biomass accumulation rates and higher yields. Tollenaar et al. (1994) reported a substantial weed biomass reduction when corn plant density was increased and the lower biomass was associated with a higher corn LAI. Generally narrower row spacings favour crop than weed leaf area production. Anne and Schreiber (1989) reported 15 and 29 % contributions by pigweed to total leaf area of soybean in a 25 cm and 76 cm row spacing, respectively. Row spacing can influence weed competition. For example, weed weight 16 weeks after planting soybean in 50 cm rows was only 28 % of that in 100 cm rows (Felton, 1976). Radiation is transmitted through and between leaves, and its flux density and spectral composition changes rapidly with depth (Gardner et al., 1985). Therefore manipulation of cultivar selection, row spacing, seeding density and mechanical cultivation may also provide means of reducing the impact of weed interference on crop yields without being heavily dependant on herbicide use, which has become an important environmental concern.

Some crop species are more competitive toward weeds than others. The relative competitiveness of corn can be enhanced by increasing plant density and reducing row spacing. There are essential differences between crop and weed species in their capacity to intercept sunlight. Ghersa et al. (1994) suggested manipulation of the radiation environment (total irradiation, and spectral composition) during the early stages of crop establishment may be a useful tool for weed control and for designing new agronomic practices that take full advantage of the differential responses of specific crop and weed species. The allocation of resources between competing plants will vary with resource levels, densities and spatial arrangements, environmental conditions which affect growth and development of the plants, and the plants' biological characteristics, such as emergence time and growth rate (Radosevitch, 1987).

In humid to moist regions water and nutrients are generally adequate early in the growing seasons, however competition can occur for light. If water and nutrients are sufficient, photosynthesis and growth rates of individual plants in a plant community will be roughly proportional to the light each intercepts (Melvin et al., 1993). James (1994) suggested that in the absence of nutrients or drought stress, the reduction in growth of corn infested with Johnson grass is proportional to the reduction in intercepted solar-radiation per corn plant. Whether competition for light or for soil-supplied resource(s) determines threshold levels or areas of influence during the latter part of the growing season will depend upon the supply and the use of soil resources and upon conditions affecting the plant's ability to obtain them, and upon relative plant height, shape, and other characteristics which affect the plant's ability to obtain light (Trenbath, 1976; Thomas, 1991).

Canopy architecture is a function of leaf number, shape, distribution, orientation, and plant size which collectively determine the vertical distribution of light within the corn canopy (Williams et al., 1968; Girardin and Tollenaar, 1994). It is also believed to be positively correlated with the maturity groups of corn hybrids. Corn plant size (height, weight, and total leaf area) positively correlates with vegetative phase duration (VPD) (Cross and Zuber, 1973; Corke and Kannenberg, 1989). Earlier maturing corn hybrids are generally smaller than later maturing ones. Leaf number is also correlated with maturity in corn and influences cultivar adaptation (Stewart and Dwyer, 1994). Corn hybrids used in short-season areas have smaller leaf area indices leading to lower dry matter accumulation than hybrids grown in long-season areas, mainly because of their reduced leaf number and size (Chase and Nanda, 1967; Hunter et al., 1974). Although seed cost is a consideration, very early corn hybrids tend to be faster in dry matter accumulation, more tolerant of higher plant populations, responsive to narrower spacings and resistant to lodging due to insect and wind damage than latter maturing corn hybrids. A combination of higher population densities and narrower row spacings could increase leaf area index leading to better light interception that would eventually result in less biomass production by weeds.

Recently, corn hybrids accumulating leaf area faster, particularly above the ear, maturing earlier, yielding well, taking advantage of narrow row spacings and tolerating higher plant populations better than the conventional corn hybrids have been reported (Modarres et al., 1997a,b; Modarres et al., 1998; Begna et al., 1997a,b; Begna et al., 1999). The leafy (Lfy1) and reduced-stature (rd1) traits both make contributions to the recently developed "Leafy-reduced stature" hybrids (Modarres et al., 1997a; Modarres et al., 1998). The net result of this is that plants bearing the leafy trait show a dramatic increase in the production of leaf area by the time of maturity (Shaver, 1983). Although there have been previous reports regarding better leaf area accumulation and yield potential of these hybrids particularly at higher plant populations, and in narrow row spacings in short-season areas, no research has been done to compare their effect on weed biomass productions. The objective of this study was to quantify light interception by weeds and corn hybrids varying in canopy architecture under different plant spacings and their effect on biomass production of transplanted and naturally occurring weeds.

MATERIALS AND METHODS

Experiments were conducted in 1996, 1997, and 1998 at the E. A. Lods Agronomy Research Centre of the Macdonald Campus of McGill University, Ste. Anne de Bellevue, Quebec and in the 1996 at the Central Experimental Farm of Agriculture and Agri-Food Canada, Ottawa, Ontario. The 1996 experiment at the Macdonald site was on courval sandy soil (fine-silty, mixed, nonacid, frigid Humaquept) while the 1997 and the 1998 sites were on clay loam soil (fine, mixed, nonacid, frigid Humaquept). The experiment in Ottawa was on uplands sandy loam (Humo-ferric podzol) soil. Soils at Macdonald were fertilized with 500 kg ha^{-1} of 36-5.3-14.9 NPK in 1996 and 1998. In 1997 soils were fertilized with 400 kg ha^{-1} of 19-8.4-15.8 NPK and 385 kg ha^{-1} of 27-0-0 NPK prior to planting. In Ottawa soils were fertilized with 550 kg ha^{-1} of 36-5.3-14.9 of NPK. At the Macdonald site weeds were controlled with Primextra [Metolachlor/Atrazine (2:1), 500g L^{-1}, Ciba-Geigy Canada Inc.)] at a rate of 7.7 L ha^{-1} during all years and at the Ottawa site weed control was through a spring application of Roundup (Glyphosate, 356g L^{-1}, Monsanto Canada Inc.) at a rate of 2.5 L ha^{-1} and a late June, application of Fusilade (Fluazifop-p-butyl, 125g L^{-1}, Zeneca Agro) (1 L ha^{-1}) as a spot-spray on emerged grasses. In addition to herbicide control hand weeding was also done as required. Weed control was applied only to the plots where there were transplanted weeds (i.e. before transplantation), while the weedy plots were left uncontrolled. Comparisons between plots with transplanted and weedy plots (with naturally occurring weeds) allowed assessment of the competitiveness of the three corn hybrids with weeds and corn plans effect on weeds biomass production.

Three corn hybrids: Leafy reduced-stature (LRS): (1240-6-2 X 1306-2-2) X PRC LDOP300rd1) and (1240-6-2 X 1306-2-2) X BRC DWARF SYNTHETIC for Ottawa and Macdonald in 1996, respectively; (1306-2-2 X LDOP300rd1) in 1997, and (CO392 X LDOP300rd1) in 1998 for Macdonald; one late maturing big leaf (LMBL):(W117rd1 X CM174rd1) X Galinat] and one conventional commercial type [Pioneer 3979 (P3979)} were used in this experiment. In 1998 we were short of seeds for LRS, therefore it was necessary to replace the previously used hybrid with another LRS. However, the new one was normal height. Leafy reduced-stature corn hybrids have become available only recently (Modarres et al., 1997a,b; Modarres et al., 1998). Descriptions of the development of the LRS hybrids have been reported (Modarres et al., 1997a). Briefly LRS is a combination of "Leafy (Lfy)" and "reduced-stature (rd1)" traits. The "Leafy" trait increases the leaf number of the plant, especially leaf number above the ear, while the "rd1" trait results in a short statured, early maturing hybrid. The LMBL type was similar in height to P3979 (with an ear leaf of approximately 88 cm long and 10 cm wide at the widest point) but with large leaves (with an ear leaf of approximately 100 cm long and 11 cm wide). The LMBL hybrid was included as its late maturity provides a potential vehicle to measure how much the competitiveness of LRS types with weeds has due to early maturity.

Each block of the experiment was divided longitudinally into two, one side weed free and the other weedy. The weed-free and weedy treatments were randomly allocated to the north and south sides of each block. The experiment was designed as a split-split-split-plot with the plots arranged in a randomized complete block design with four blocks. The dates of planting for the Macdonald site were 24 May, 1996, 21 May, 1997, and 23 May, 1998 and for the Ottawa site it was 29 May, 1996. Each hybrid was planted at two plant densities (100,000; 55,000; 75.000 as conventional and 133,300; 73,300; 100,000 plants ha^{-1} as high densities for LRS, LMBL and P3979, respectively) for the 1996 experiment at both sites; however, the high density for LRS in 1997 and 1998 was reduced to 115,000 plants ha^{-1} because we found the previous high density to be too high since the level of interplant competition was sufficient to cause some sterile plants even in the weed-free level Weed level [plots with transplanted weed (PTW), and plots with naturally occurring weed (PNOW)] formed the main plots. Plant population formed the sub-plots and two planting patterns (row spacings of 38 and 76 cm) formed the sub-sub-plots. The 38 cm row width is better for higher plant population densities (Begna et al., 1997). Hybrids formed a sub-sub-sub-plot unit. All plots were hand planted. The 76 cm row spacing plots consisted four rows and the narrow spacing plots of eight rows in the 1996 experiments for both sites, however for the 1997 and the 1998 experiments the number of rows in the wide row plots was increased to eight. The plots were 8 m long for the 1996 experiments and 7 m long for

1997 and 1998 experiments. Plots were over-seeded (20%) and thinned to the required plant densities three weeks after emergence.

Greenhouse grown weeds lamb's quarters in 1996, and lamb's quarters and redroot pigweed in 1997and in 1998 were transplanted into one randomly chosen row of each plot of the weed free sections and control plots without corn. There were one metre intervals between transplanted weeds and 18 or 36 cm between the transplanted weeds and the corn plants depending of the row spacings used. There were a total of 16, 12, and 12 transplanted weeds per plot for the 1996, 1997, and 1998 experiments, respectively. These weed seedlings (4-6 leaf stage) were transplanted when corn was at the 2-4 leaf stage. The transplanted weeds were watered as required in order to ensure good establishment. However, in 1997, as a result of very dry weather at the beginning of the growing season, we were able to successfully establish only enough weed plants for two of the six planned harvests; one harvest was made before canopy closure and the other four weeks after tasselling. The purpose of these weeds was to study the effect of plant density, row spacings and the selected corn hybrids on the biomass production of individual plants of selected weed species in a more controlled fashion (without random levels of competition from other weeds) while the weedy plots allowed us to study the biomass of weed population developing naturally from the existing seed bank propagule sources. Because of the small number of transplanted weeds, they have no effect on corn yield and so these plots could be considered as "weed-free".

For the weedy parts of the 1997 and 1998 experiments, weed harvest was done using a quadrate (76 cm X 100 cm). Except for the weedy plots of the 1996 experiments where there was a harvest at mid August using a quadrate of 25 cm X 25 cm, the harvests in 1997 and 1998 were taken after tasselling stages of the LRS and P3979 hybrids. Harvested weeds were dried to a constant weight at 80 ^{0}C and the biomass production was expressed on a per m^{-2} basis for naturally occurring weeds and on a per plant basis for transplanted weeds.

Light measurement (using a linear quantum sensor, Li-191SB, LI-Cor, Inc., Lincoln, NE) above the canopy, sensor inverted upward and downward, and another one at ground level were taken. The one measured above the canopy sensor facing upward provided a measurement of the total light falling on the plants, while measurement with sensor facing downward provided an estimate of light reflected by both the canopy and the soil surface. The measurement at ground level provided an estimate of light penetrating the entire canopy. Total light intercepted by the plants was calculated by subtracting light reflected by the plants and soil surface from the total light falling on the canopy and expressed on a percentage basis.

The data of the two 1996 sites [Macdonald (Site 1) and Ottawa (Site 2)] or the three years (1996, 1997, and 1998 for Macdonald) were pooled when the hypothesis of the homogeneity of variances was tested and accepted by a Bartlett's test (Steel and Torrie, 1980). The statistical analyses were performed using the GLM procedure of SAS (SAS Institute, 1994). Simple means comparisons for each multiple pairwaise were made with a GLM protected LSD test at the 0.05 level probability. Simple means comparisons for each multiple pairwaise were made with a GLM protected LSD test at the ($P<0.05$) level.

RESULTS AND DISCUSSION

Biomass produced by both transplanted and naturally occurring weeds and light interception by the plants as a whole (corn and weeds) were affected substantially by both planting pattern and hybrid type at all site-years (Table 6.2). Generally all measured weed variables were reduced by high corn plant population to a lesser, and narrow row spacing to a higher degree at all site-years.

Weed biomass production

Interactions between weed level and hybrid existed at all site-years. Less biomass was produced by naturally occurring weeds under LRS and P3979 than LMBL. Row spacing by hybrid interactions were found for lamb's quarters and naturally occurring weeds in 1998, and redroot pigweed and naturally occurring weeds at the Macdonald site both in 1997 and 1998 (Table 6.2). Biomass production under all hybrids were lower with narrow than wide row spacings (Tables 6.3 and 6.6). There was also an interaction between plant population and hybrid for both transplanted lamb's quarters and naturally occurring weeds in 1998 and for transplanted redroot pigweed and naturally occurring weeds both in 1997 and 1998 at the Macdonald site (Table 6.2). Less biomass was produced by weeds at the high than the conventional plant population under all hybrids.

The reduction in weed biomass production due to the narrow row spacing was 15-20 % at both sites in 1996 (Table 6.3). Biomass production by both transplanted and naturally occurring weeds was higher at the Ottawa site than the Macdonald site. Some of the absolute differences between sites might be accounted by differences in rainfall accumulation, as there was more rainfall at the Ottawa site than the Macdonald site (Table 6.9). The biomass production of weeds, and particularly the naturally occurring population, was higher under LMBL than under LRS and P3979. For example, in 1997 the biomass produced by naturally occurring weeds under LRS and P3979 was only 433.5 and 474.6 g m^{-2} while under LMBL it was 733.3 g m^{-2} (Table 6.5). This was probably a result of the slower growth and development of LMBL than the other corn hybrids. However, this value was as high as 1277.3 g m^{-2} when plots were left free of corn (Table 6.5). The same pattern of differences was observed for the transplanted lamb's quarters and redroot pigweed at all site-years. In 1998 biomass produced by transplanted lamb's quarters were 27.8, 34.2, 52.9 g plant^{-1}; and redroot pigweed were 14.9, 19.7, 27.5 g plant^{-1} under the three corn hybrids (LRS, P3979 and LMBL), respectively (Table 6.5). It also seems that weed biomass production under LRS was low as opposed to the other two corn hybrids which was probably as a result of differences in their canopy architectures and faster early growth and ability to tolerate higher plant densities and weed pressure.

There was at least a 40 % reduction in biomass production by both transplanted and naturally occurring weeds due to an increase in corn plant population densities at the Macdonald site (Table 6.6). Tollenaar et al. (1994) also reported a greater reduction in weed biomass when corn was planted at higher plant populations. Greater yield reductions due to weed pressure have been previously reported for later maturing corn hybrids than for early maturing ones (Callaway, 1992). This could be one of the main reasons why yield reductions due to weeds for the LMBL are usually much higher than for the other two hybrids (data not shown). When weeds grew in the absence of competition from corn, biomass production by both transplanted and naturally occurring weeds was 70 to 85 % greater than in the presence of corn (Tables 6.3 and 6.5), thus we can see a benefit from the crops themselves (in particular competitive ones), plant population, and row spacing in reducing weed biomass production.

Light interception

Interactions between weed level and row spacing, and between weed level and hybrid for light interception by the plants as a whole existed at all site-years, while interactions between weed level and plant population existed only at the Macdonald site in 1998 (Table 6.2). Light interception was increased by high plant population and narrow row spacing more at the weedy than the plots with transplanted weeds for all hybrids (Tables 6.7 and 6.8).

There was at least a 3-5 % increase in light interception due to increased plant populations and decreased row spacing. However, light interception differences due to plant population densities and row spacings were more clear in the plots with transplanted weeds than in the weedy-plots. Several researchers (e.g. Ottman and Welch, 1989; Board and Haville, 1992; Tollenaar et al., 1994) reported increased light interception by crops such as corn and soybean due to higher plant densities and narrower row spacings. In the corn-free control plots where there were transplanted and naturally occurring weeds, light interception was lower than in the presence of corn plants (Table 6.8). Generally, in our study hybrids were not different in their light interception capability. This was probably because of the time of light interception measurement; which was only when LRS and P3979 were at the tasselling stage. Later measurements would probably have shown higher light interception for LMBL than the other hybrids, while very early light interception measurements would probably have shown highest values for LRS hybrids.

CONCLUSIONS

Biomass production by both transplanted and naturally occurring weeds were greatly affected by planting pattern, plant population and hybrid type. Reductions in biomass were more pronounced with the reduced row spacing than with increased plant population density for all hybrids. However, biomass produced by all types of weeds under all hybrids were 5-8 times less than biomass produced in the corn-free plots. A narrower row spacing favoured the LRS hybrids, probably as a result of differences in the canopy architectures, their faster early growth, and ability to tolerate higher plant densities and weed pressure. In particular, in plots where selected (lamb's quarters and redroot pigweed) weeds were transplanted, light interception increase due to decreasing row spacings and increasing plant populations was more obvious.

Biomass production by both transplanted and naturally occurring weeds under early maturing corn hybrids (LRS and P3979), and especially under LRS, because of their faster growth and development at early stages of growth, was more reduced due to decreased row spacings and increasing plant population than under LMBL corn hybrids.

Table 6.1. A summary of weed species observed during the three years and sites of the experiments.

Weed species	Ottawa 1996	Macdonald 1996	Macdonald 1997	Macdonald 1998
Barnyard grass (*Echinocula crusgali* L.)	H	I	H	H
Giant foxtail (*Setaria faberi* Herm.)	I	H	I	I
Yellow nutsedge (*Cyperus rotundus* L.)	L	H	L	L
Yellow foxtail (*Setaria glauca* L.)	I	H	I	I
Witch grass (*Panicum capillare* L.)	I	H	I	L
Quack grass (*Elytrigia repens* L.)	L	H	H	L
Smooth crabgrass (*Digitaria ischaemum* Schreb.)	I	I	I	I
Lamb's quarters (*Chenopodium album* L.)	H	I	H	H
Redroot pigweed (*Amaranths retroflexus* L.)	H	I	H	H
Canada thistile (*Cirsium arvense* L.)	L	H	H	L
Velvet leaf (*Abutilon theophrasti* Medic.)	L	I	L	L
Purslane (*Portulaca oleracea* L.)	L	H	H	I
Prostrate knotweed (*Polygonum aviculare* L.)	I	I	I	I
Field bindweed (*Convolvulus arvensis* L.)	L	L	H	H
Common ragweed (*Ambrosia artemisiifolia* L.)	L	L	L	L

Population ocurrance (H- high, I- intermidiate, L-low)

Table 6.2. Analysis of variance showing probabilities for the main and interaction effects on biomass production by transplanted lamb's quarters (LQ), redroot pigweed (RRPW), and naturally occurring (NO) weeds, and light interception by the plants as a whole at the Macdonald (S1), and the Ottawa site (S2) in 1996, 1997, and 1998.

		LQ and NO				RRPW and NO		Light interception		
		1996		1997	1998	1997	1998	1996	1996-1997	1998
		Site 1	Site 2	Site 1		Site 1		Site means	Year means	
source	df	P -value								
Block (B)	3	0.3614	0.6241	0.4482	0.6860	0.8549	0.4691	0.2904	0.2947	0.7531
Weed level (WL)	1	0.0002	0.0001	0.0001	0.0001	0.0001	0.0001	0.0004	0.0004	0.0014
Error (B x WL)	3									
Plant populations (PP)	1	0.0220	0.0006	0.0255	0.0001	0.025	0.0001	0.0280	0.0260	0.0620
WLx PP	1	0.6850	0.1517	0.7772	0.1291	0.8372	0.1157	0.097	0.098	0.01
Error Bx PP (WL)	6									
Row spacings (RS)	1	0.0010	0.0075	0.0001	0.0001	0.0001	0.0001	0.0012	0.0011	0.0014
WLx RS	1	0.308	0.8996	0.9867	0.1503	0.2999	0.8100	0.0264	0.0305	0.0035
PP x RS	1	0.2561	0.6864	0.057	0.8991	0.022	0.0440	0.3820	0.4366	0.5821
WLx PP x RS	1	0.6196	0.8096	0.8025	0.1455	0.7334	0.6409	0.6169	0.6120	0.6054
Error B x RS (WLx PP)	12									
Hybrids (H)	2	0.0001	0.063	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
WL x H	2	0.0001	0.3247	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
PP x H	2	0.2927	0.063	0.0820	0.0001	0.0333	0.0001	0.5609	0.5663	0.7139
WL x PP x H	2	0.5197	0.3247	0.5287	0.3938	0.3865	0.189	0.4413	0.4242	0.2139
RS x H	2	0.2570	0.09	0.0210	0.0001	0.0009	0.0001	0.3884	0.3942	0.2938
WL x RS x H	2	0.7901	0.3597	0.7912	0.601	0.4384	0.2942	0.7657	0.6975	0.5519
PP x RS x H	2	0.9834	0.5267	0.6481	0.8094	0.3907	0.2382	0.789	0.7631	0.9683
WL x PP x RS xH	2	0.9500	0.2484	0.3336	0.8298	0.5327	0.8828	0.9206	0.9205	0.8803
Error	48									
CV (%)		10.58	6.57	5.03	4.32	5.21	3.75	5.12	5.27	3.86

Table 6.3. Biomass production by transplanted lamb's quarter (LQ)and naturally occurring (NO) weeds as affected by main and interaction effects of weed level, corn hybrid, plant population, and row spacings at the Macdonald (S1) and the Ottawa (S2) sites in 1996.

		1996	
		LQ (g plant^{-1})	
Weed level	**Hybrid**	Site 1	Site 2
Transplanted	LRS	38.72e*	58.75e
	LMBL	50.41e	110.77e
	P3979	40.91e	88.82e
	None	341.70d	582.01d
		NO (g m^{-2})	
Naturrally occurring	LRS	719.48c	784.31c
	LMBL	1024.70b	1413.39b
	P3979	802.81c	957.99c
	None	2218.28a	3486.16a

	LQ and NO (g m^{-2})	
Plant population	Site 1	Site 2
Conventional	698.33a	1019.29a
High	610.92b	851.26b
Row spacings		
Narrow	591.76b	858.45b
Wide	717.76a	1021.10a

Abbreviations: LRS- Leafy-reduced stature, LMBL- Late maturing big leaf, Pioneer conventional 3979 (P3979), and None (corn-free plot). *Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Table 6.4. Biomass production by transplanted lamb's quarter (LQ), redroot pigweed (RRPW) and naturally occurring (NO) weeds as affected by main and interaction effects of plant population and row spacing at the Macdonald site in 1997, and 1998.

		Weed biomass (g m^{-2})	
		1997	1998
Plant population	**Row spacing**	RRPW and NO	RRPW and NO
Conventional	narrow	358.96bc*	269.42b
	wide	467.23a	386.17a
High	narrow	313.35c	192.90c
	wide	370.31b	269.27b

	LQ and NO
	1997
Plant population	Site1
Conventional	419.55a
High	349.07a

*Values, in the same column, followed by the same letter are not different ($p< 0.05$) based on an ANOVA protected LSD test.

Table 6.5. Biomass production by transplanted lamb's quarter (LQ), redroot pigweed (RRPW) and naturally occurring (NO) weeds as affected by interaction effects of weed level and corn hybrid at the Macdonald site in 1997 and 1998.

		1997		1998	
		LQ	RRPW	LQ	RRPW
Weed level	**Hybrid**	(g plant^{-1})			
Transplanted	LRS	13.82e*	10.12d	27.81f	14.86f
	LMBL	20.36e	15.03d	52.94f	27.45f
	P3979	14.91e	11.63d	34.24f	19.73f
	None	110.98d	69.97d	186.8d	116.76d
		NO (g m^{-2})			
Naturally occurring	LRS	433.47c	433.47c	296.99d	296.99d
	LMBL	731.33b	731.33b	502.47b	502.47b
	P3979	474.64c	474.64c	353.08c	353.08c
	None	1273.52a	1273.52a	904.21a	904.21a

Abbreviations: LRS- Leafy-reduced stature, LMBL- Late maturing big leaf, Pioneer conventional 3979 (P3979), and None (corn-free plot). *Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Table 6.6. Biomass production by transplanted lamb's quarter (LQ), redroot pigweed (RRPW) and naturally occurring (NO) weeds as affected by interaction effects of plant population, row spacing and hybrid at the Macdonald site in 1997 and 1998.

		Weed biomass (g m^{-2})			
		1997		1998	
Row Spacing	**Hybrid**	(LQ + NO)	(RRPW + NO)	(LQ + NO)	(RRPW + NO)
Narrow	LRS	166.19d	164.47d	107.03d	102.02e
	LMBL	325.78c	322.66c	197.36c	187.14d
	P3979	192.69d	191.08d	131.30d	125.25e
	None	684.52a	666.40a	545.54a	510.25a
Wide	LRS	281.09c	279.12c	217.77c	209.83d
	LMBL	425.91b	423.70b	358.04b	342.77b
	P3979	296.86c	295.19c	256.03b	247.56c
	None	699.98a	677.08a	545.46a	510.72a

		1997	1998	
Plant Population		(RRPW + NO)	(LQ + NO)	(RRPW +NO)
Conventional	LRS	256.04cd	210.87d	201.75c
	LMBL	453.56b	376.27b	360.24b
	P3979	269.05c	246.95c	238.48b
	None	673.72a	545.46a	510.72a
High	LRS	187.55d	113.93	110.10d
	LMBL	292.79c	179.14d	169.67c
	P3979	217.22cd	140.37	134.33d
	None	669.76a	545.54a	510.25a

Abbreviations: LRS- Leafy-reduced stature, LMBL- Late maturing big leaf, Pioneer conventional 3979 (P3979), and None (corn-free plot). [*]Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Table 6.7. Light interception by plants as a whole as affected by interaction and main effects of weed level and plant population at the Macdonald (S1) and the Ottawa (S2) sites in 1996 and 1997.

Plant population	1996 Means of sites	Site 1 Means of years (1996-1997)
	Light interception (%)	
Conventional	77.47b	75.86b
High	79.24a	77.63a

Weed level	**Plant population**	1998 Site 1
Transplanted	Conventional	66.98c
	High	70.07b
Naturally occurring	Conventional	82.77a
	High	81.91a

Abbreviations: *Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Table 6.8. Light interception by the plant as a whole as affected by interaction effects of weed level, row spacing and hybrid at the Macdonald (S1) and the Ottawa (S2) sites in 1996, 1997 and 1998.

		Light interception (%)		
		Means of sites	Means of years (1996-1997)	1998
Weed level	**Row spacing**	1996	Site 1	
Transplanted	Narrow	70.52b*	68.88b	69.98b
	Wide	67.12c	65.54c	67.07c
Naturally occurring	Narrow	88.32a	86.73a	82.44a
	Wide	87.47a	85.98a	82.25a
Weed level	**Hybrid**			
Transplanted	LRS	85.81c	84.18c	84.58b
	LMBL	86.54c	84.91c	81.13c
	P3979	88.61b	86.98a	82.95bc
	None	14.32e	12.75e	10.45e
Naturally occurring	LRS	95.91a	94.29a	94.01a
	LMBL	95.92a	94.30a	93.13a
	P3979	95.33a	93.71a	92.73a
	None	64.42d	62.85d	49.51d

Abbreviations: LRS- Leafy-reduced stature, LMBL- Late maturing big leaf, Pioneer conventional 3979 (P3979), and None (corn-free plot). *Values, in the same column, followed by the same letter are not different ($p < 0.05$) based on an ANOVA protected LSD test.

Table 6.9. Monthly temperature and accumulated rainfall during the four site-years and sites of the experiments.

Months	Mean temperature (^0C)				Rainfall (mm)			
	Ottawa	Macdonald			Ottawa	Macdonald		
	1996	1996	1997	1998	1996	1996	1997	1998
May	12.2	12.3	10.7	17.4	53.2	92	76	50.5
June	19.1	18.6	20.1	19.5	89.2	65.5	104.5	74.5
July	20.1	20.2	20.6	21.1	149.3	106	135	89.5
August	20.2	20.4	19	21	83	22.5	106.4	92.5
September	16.6	16.3	14.6	16.1	124.4	115.1	91.5	62
October	8.2	8.1	8	9.8	87.2	74.5	30.5	62.5

Preface to Chapter 7

This section will form a manuscript to be submitted in 1999 for publication in Planta. The format has been changed to be consistent within this thesis. All literature cited in this chapter are listed at the end of the thesis. Each table or figure is presented at the end of this chapter.

In chapter 6, I addressed the effects of light distribution caused by manipulation of planting patterns and choice of hybrids on biomass production by both transplanted (lamb's quarters and redroot pigweed) and naturally growing weeds. However, this was conducted under field conditions where plants would also compete for growth factors such as water and nutrients, in addition to light. In order to better understand low light level effects on morphology, growth and resource allocation of selected weeds, I carried out a greenhouse experiment to study the effects of light levels and sucrose injection (as carbon source) on C_3 (lamb's quarters and velvetleaf) and C_4 (redroot pigweed) weed species.

DECOUPLING OF LIGHT INTENSITY EFFECTS ON THE GROWTH (BIOMASS INCREASE) AND DEVELOPMENT (MORPHOLOGY) OF C_3 AND C_4 WEED SPECIES

ABSTRACT

Light is one of the most important resources that plants compete for. If no other resource is limiting, the growth of a plant is proportional to the amount of light it intercepts. Reduced light levels result in reduced carbon assimilation and this, in turn, results in reduced growth. Over the past ten years stem injection techniques have been developed for several crops. These allow injection of concentrated solutions of growth affecting materials, such as sucrose, in order to study their effects on the morphology and physiology of plants, including under varying light levels. However, no work has been done to expand this technique to non-crop species. A greenhouse experiment was carried out to test an injection technique developed for soybean plants on three weed species. The light levels were full sun and 75 % shade. The solutions injected were 150 g sucrose L^{-1} and distilled water. Uninjected plants were also included as a control on the injection process. Under both light levels all three weed species [redroot pigweed (*Amaranthus retroflexus* L.- C_4), lamb's quarters (*Chenopodium album* L.- C_3), and velvetleaf (*Abutilon theophrasti* Medic.- C_3)] took up greater volumes of distilled water than sucrose solution. The overall average total sucrose uptake was 7.6 and 5.9 g for the 0 and 75 % shading levels, respectively, which represented an average of 47 % of the total dry weight of the weed plants. For all species, plants injected with sucrose had higher total dry weights and greater shoot to root ratios under both light levels, but root dry weight and leaf area were unchanged by sucrose injection under the lower light level. Leaf area and leaf weight

ratio, particularly under the lower light level, were much lower for sucrose injected plants than distilled water injected or not injected plants. The reduction in dry matter in all species due to shading was more pronounced for below ground dry weight and reproductive parts than leaves and stems. Injected plants were larger than uninjected plants and this effect was slightly greater under shade than full sun. Plants injected with sucrose under 75 % shade achieved dry weights not different from uninjected or distilled water injected plants in full sun. Thus, it seems that, given an alternative source of sucrose, shade grown weed plants can produce as much dry matter as unshaded plants. However, in spite of the alternative source, shaded plants injected with sucrose underwent the same changes in allocation of dry matter among leaves, stems, roots and reproductive structures indicating that those effects are strictly due to light intensity and are not related to photosynthate availability.

INTRODUCTION

The basic resources that plants compete for are light, water, and nutrients. If water and nutrients are adequate then photosynthesis and growth rates of individual plants in a plant community will be roughly proportional to light interception (Melvin et al., 1993). Plants grown at high light intensities usually have greater photosynthesis rates per unit leaf area and become light-saturated at higher intensities than plants grown at lower light intensities. In general, plants grown in a reduced light environment are limited in carbon assimilation and this, in turn, results in changes (reductions) to growth and development. Shaded plants usually exhibit lower dry matter production and yields than unshaded plants. Several studies of weed species grown under light-limiting conditions have shown reduced growth, development, and seed production (e.g. Bello et al., 1995). For field grown velvetleaf Bello et al. (1995) found a greater leaf senescence rate, and more leaves for 0 or 30 % shaded plants than plants that were under 70% shade. The overall reduction in dry matter accumulation of shaded plants is mainly due to the inability to capture enough photosynthetically active radiation (PAR). A decrease in light intensity is the main reason for the reduction in photosynthesis by shaded plants.

Edward and Meyers (1989) reported that plants can adjust to low irradiance levels by decreasing light-saturated photosynthesis, leaf respiration rates, root:shoot ratios, and leaf density, while increasing leaf area ratio (LAR), which decreases the support tissue:leaf ratio and results in greater partitioning of plant material into leaf tissues that harvest the available PAR, with less biomass diverted to tissues that act as sinks for photosynthate. Decreasing leaf respiration rates, and increasing leaf area ratios are the commonly used positive adaptations to shading by many plant species regardless of their photosynthetic pathway. However, plant species that differ in their photosynthetic pathway (C_3 vs C_4) are likely to respond differently to light and CO_2 (Patterson, 1984). Biomass production patterns of C_3 and C_4 plants show large differences in response to CO_2 level at the high and low light levels. C_3 biomass increased with increasing CO_2 and C_4 biomass increased in the range from 300 ppm to 450 ppm but then declined from 450 ppm to 600 ppm (Zangerl and Bazzaz, 1984).

Several researchers (e.g. Reeves et al., 1994; Allen et al., 1991; Prior and Rogers, 1995) reported increases in total leaf area, dry weight, and seed number of soybean plants when grown under elevated carbon dioxide. Increases in leaf area and biomass accumulation by weeds and other plants due to elevated CO_2 have also been reported (Zangerl and Bazzaz, 1984; Tolley and Strain, 1985; Coleman and Bazzaz, 1992).

In the past, effector substances were supplied to plants through roots and leaves (Rending and Crawford, 1985; Tomar et al., 1988). However, during the last ten years several researchers (e.g. Grabau et al., 1986; Boyle et al., 1991a,b; Ma and Smith, 1992; Ma et al, 1994a,b; Zhou and Smith, 1996; Abdin et al., 1998) have succeeded in supplying exogenous solutions using techniques whereby solutions are injected into stems of crop plants. In general, sucrose injected plants accumulated more dry matter than uninjected or distilled water injected ones. Abdin (1996) found that deeply shaded (70%) soybean plants were taller, and senescenced earlier than unshaded or moderately (30%) shaded soybean plants. He also noted no response to injected sucrose by plants in 70% shaded, while the unshaded and 30% shaded plants weighed more when injected with sucrose. His data suggested that heavily shaded soybean plants had undergone a shift in both their architecture and physiology.

At the bottom of a plant canopy both light quantity and quality changes. The most profound result of this is a decrease in photosynthesis. However, there are changes in plant growth (e.g. morphology) which appear to relate directly to light intensity or quality rather than to photosynthetic rate. An injection system that can supply large amounts of sucrose to a plant could replace the reduced carbon that would have been supplied by photosynthesis and allow examination of other low light induced effects, in the absence of the reduced photosynthesis effect. In the absence of such effects an injected plant might be expected to achieve the same size and shape as an uninjected plant under greater light intensities. Kolb and Steiner (1990) reported seedling biomass reduction, but shoot:root and leaf area ratio increases in shaded northern red oak trees when compared to full sun grown trees. They also gave low light intensity as an explanation for the failure of seedling growth to respond favourably to increased moisture in shaded ferns and grasses. Abdin et al. (1998) found that up to 65% of the total plant dry weight of soybean could be supplied by a pressurised injection system. The objectives of this work were to determine: **1**. whether weed plants, which have evolved under conditions of intense competition for light, will respond in the way previously reported for soybean plants, **2**. whether, C_3 and C_4 weed species respond to the combination of injection and shading in the same way, and **3**. whether injecting shaded plants with large amounts of sucrose will overcome the effects of shading on plant size (weight) and shape.

MATERIALS AND METHODS

Seeds of lamb's quarters (*Chenopodium album* L) and redroot pigweed (*Amaranthus retroflexus* L.) were collected from a field site at the Emil A. Lods Agronomy Research Centre of the Macdonald Campus of McGill University in the fall of 1996. Seeds of velvetleaf (*Abutilon theophrasti* Medic.) included in the repetition of the experiment were also collected from the Emil A. Lods Agronomy Research Centre, but in the fall of 1997. Before their use seeds were placed in small bottles covered with water and left in a fridge for 48 hours (as a cold treatment) to break dormancy (Totterdell and Roberts, 1979). These seeds were planted in 11 X 21 cm trays divided into 32 small sections (5.5 cm deep cells) filled with a mixture of sand and Promix (Premier Horticulture L'tee, Rivier-du-Loup, Quebec, Canada) (1:3). Seedlings were left to grow until the 4 leaf stage and were watered as necessary during this time. At this stage, vigorous seedlings were selected from the trays of each species and four were transplanted into each 15.5 cm diameter and 15 cm deep plastic pot containing the same rooting medium as the trays. Approximately two weeks later the plants were thinned to one per pot and fertilized with

1.5 g L^{-1} pot^{-1} of NPK (20-20-20). Three days later the injection system modified from Zhou and Smith (1996) and used for soybean by Abdin et.al. (1996), was established.

In brief, the injection system was composed of a supporting stand syringe-tubing system that ended with a 25-guage 3/4 vacutainer needle (Vacutainer, Becton Dickinson Company, Rutherford, NJ). A hose clamp was tightened around each of two 40 cm long pipes at a distance of 30 cm above a wooden base, and a 23 cm X 13 cm wooden platform with two holes that rested on the hose clamps. At the mid distance between these two holes the wooden platform had a third hole that supported a 5 mL syringe. The injection tubing consisted of a 20 cm long flexible plastic tube (Tygon i.d 0.8 mm, o.d. 2.4 mm) that was connected at one end to a standard 18-guage 1½ needle (Becton Dickinson, Company, Franklin Lakes, NJ) and at the other end to a 25-guage 3/4 vacutainer needle (Vacutainer, Becton Dickinson, Company, Rutherford, NJ). The needles attached to each end of the tygon tubing were sealed in place with epoxy resin glue. The vacutainer needle was positioned at about 45^0 and inserted half way into the plant. The needles were sealed to the plant stems with latex (Vultex, General Latex Canada, QC, Canada). The latex was placed around the injection site in a cup formed by masking tape, and was allowed to set for 4 to 5 days. The injection systems were carefully tested for leakage and plants without leaks were then put under the various light level treatments for injection. The plants were injected for a period of 9 weeks.

The first experiment tested lamb's quarters and redroot pigweed using cages of 70 X 75 X 120 cm covered on all sides, except the bottom, with shading cloth (Tek Knit, Montreal, QC, Canada). The second experiment included one additional weed species velvetleaf. As a result bigger cages were required and the size was increased to 100 X 100 X 200 cm. One side of the cage had a small door that could be opened and closed to aid in data collection. The research was conducted at the greenhouse of the Plant Science Department of McGill University. A photoperiod of 16 hours was maintained, with high pressure sodium lamps to extend the day length. Daytime temperature was 25±3^0 C, night time temperature was 20±3^0 C, and the relative humidity was 60±5 %. The plants were injected with either distilled water or 150 g L^{-1} sucrose. Uninjected plants were also included as controls on injection effects. The injected solutions were forced into the plants using construction type ceramic bricks (approximately 2.7 kg each) with three holes, placed on top of the syringe plunger. One brick was added each day until reasonable flow rates were reached. In this experiment this did not require more than 2 ½ bricks.

The experiment was designed as a split-split-plot with three blocks, where shading level (0 and 75%) was the main plot and injected solutions (distilled water and sucrose) was the sub-plot. The three weed species were treated as sub-sub plot factors. The uptake of injected solutions were checked regularly and the syringe barrels were refilled as necessary. The injected plants were also checked regularly to make sure there were no leaks. Plants were harvested at complete senescence. Abscised leaves were collected, oven dried at 90^0 C to a constant weight and weighed. To determine the leaf area of the weeds a random collection of leaves of the plants at maturity for each treatments were measured using leaf area metre (Delta-T Devices Ltd., Burwell, Cambrige, England) and then dried and weighed. At final harvest plant height was measured from the soil level to the tip of the stem and the harvested plants were separated into leaf, stem, seed plus fruit and root material and oven dried for weight determination. Dry matter alocation patterns were assessed by calculating: dry weight of leaf, stem, seeds (including fruits), shoot (leaf, stem and seeds plus fruits) and total dry weight (shoot and root) (g), leaf weight ratio (leaf weight per total biomass), leaf area ratio (leaf area per total plant biomass, cm^2 g^{-1}).

shoot/root ratio (shoot biomass per root biomass). Total uptake (mL) of the injected solutions for the whole injection period was also calculated. All the above mentioned variables are given on a per plant basis.

Data from the two weed species included in both experiments (i.e. redroot pigweed and lamb's quarters) were pooled when the hypothesis of homogeneity of variance was tested and accepted by using Bartlett's test (Steel and Torrie, 1980) and afterward all data were subjected to analysis of variance with the PROC GLM Procedure of SAS (SAS Institute, 1994). Simple means comparisons for each multiple pairwaise were made with a GLM analysis protected LSD test at the 0.05 level probabilities.

RESULTS AND DISCUSSION

The tested factors affected most of the measured variables for all three weed species. For all variables except stem, seed and leaf dry weight, shading (light) level by injection interactions were detected, while shading by species interaction effects were found for all except seed and leaf dry weight, leaf area, and injected solution uptake (Table 7.1). Injection treatment by weed species interactions existed for seed dry weight, injection treatment uptake, and leaf area ratio. A three way interaction (shading level, injection treatment, and weed species) existed only for leaf dry weight (Table 7.1).

Injection treatments

The injected treatments were taken up most rapidly for the first two days, after which the uptake rate gradually slowed, probably as a result of callus tissue build up around the injection sites, in response to wounding. Ma et al. (1994b) also found that solution uptake by corn plants was limited by dead tissue resulting from the injection process. However, pulling the piston barrel forward and backward several times has been shown to overcome this problem in injected soybean plants (Abdin et al., 1998). This also worked in our case. Plant uptake of distilled water was more rapid than the 150 g L^{-1} sucrose solution for all species, both for shaded and unshaded plants (Table 7.2). This was probably due to the higher osmotic potential of the injected sucrose solution. Similar results have been reported in cereal crops (Ma et al., 1994a, Foroutan-pour et al., 1995), soybean (Abdin et al., 1998), and corn (Zhou and Smith, 1996).

The overall average total uptake of injected sucrose was 50.7 and 39.6 mL for 0 and 75 % shading levels, respectively; this represented 7.6 and 5.9 g of sucrose for the shaded and unshaded plants, respectively (Table 7.2). Greater total uptakes of injected sucrose have been reported [11.8 g in soybean (Abdin et al., 1998), 17.7 g in corn (Zhou and Smith, 1996), 15 g in corn (Boyle et al., 1991b)]. In our study the amount of injected sucrose, averaged over light levels and weed species, represented 47 % of the total plant dry weight. Abdin et al. (1998) reported injection of as much as 65 % of the plant dry weight as sucrose for soybean plants. The uptake of injected solutions averaged over shading levels was lower for lamb's quarters (8 %) and redroot pigweed (17 %) than velvetleaf (Table 7.4).

Biomass production

Biomass, in particular above ground (shoot) biomass, under both light levels was much greater for plants injected with sucrose than those injected with distilled water or not injected (Table 7.2). Several researchers have reported higher above and below ground biomass for unshaded than shaded plants (egs. Edward and Meyers, 1989; Kolb and Steiner, 1990; Reeves et al., 1994; Allen et al., 1991; Prior and Rogers, 1995). In our case shaded plants benefited more from the availability of an additional reduced carbon source than unshaded ones. With the availability of a large alternative source, sucrose injected shaded plants were as large as unshaded or distilled water injected uninjected plants. Thus, with a sufficient alternate (to photosynthesis) source of sucrose, deeply shaded plants can achieve the same levels of biomass production as those grown in full sun.

Morphology and resource allocation

Lamb's quarters and redroot pigweed plants were much taller under shade than full light regardless of the injected solutions. However, velvetleaf plants were taller under full light than under shade (Table 7.3). Although redroot pigweed plants were shorter than the lamb's quarters plants their response to reduced light intensity was greater (41 vs 20 % taller). Generally there were no differences amongst injection treatments (distilled water, sucrose, or not injected) for plant height (Table 7.2). This may be partially explained by a greater allocation of dry matter to leaves and seeds rather than to stems, when sucrose was injected (Tables 7.4 and 7.5). Under both light levels stem, leaf, seed (including fruits), shoot and total dry weight were greater for sucrose injected treatments, ($P<0.05$) (Tables 7.2, 7.3 and 7.4) while root dry weight was unchanged. Generally the values of these variables were higher for lamb's quarters than for redroot pigweed and velvetleaf. Like velvetleaf, lamb's quarters is a C_3 plant, however, lamb's quarters branched more and was taller than either velvetleaf or the C_4 redroot pigweed. Seed dry weight (including fruits) of both photosynthetic types (C_3 and C_4) whether they were injected with water, sucrose or not injected were affected by shading (Tables 7.4 and 7.5). Seed dry weight, averaged over weed species, was reduced by at least 53 % due to shading (Table 7.5). Bello et al.

(1995) found as much as 94 % reduction in seed production for velvetleaf grown under 76 % shade. Abdin (1996) reported a similar effect on the reduction of grain yield by shaded soybean plants.

Root dry weight generally responded to shading the same way as seed dry weight (Table 7.3). This may have been due to greater resource allocation to leaf and stem tissues than to below ground and reproductive parts of the plants under low light intensities. It seems reasonable for the plant to do so because this is the only way they are able to maintain reasonably levels of light interception and growth. Shoot to root ratios of redroot pigweed and lamb's quarters were higher for shaded than unshaded plants, but for velvetleaf this was unchanged (Table 7.3). However, the shoot to root ratio was higher for sucrose injected plants than for distilled water or not injected plants.

Generally leaf area was increased due to sucrose injection under both light levels. however, the increase due to sucrose supplementation was much higher for unshaded than shaded plants (25 vs 12 %) (Table 7.2). A higher leaf area was recorded for the C_3 species than the C_4 species, the highest being for velvetleaf (909.9 cm^2), followed by lamb's quarters (707.9 cm^2), and then redroot pigweed (565.3 cm^2). Even though the leaf area of lamb's quarters was higher than redroot pigweed, under both light levels, generally the leaf weight ratio and leaf area ratio of redroot pigweed were similar to lamb's quarters, whether or not they were supplied with sucrose (Tables 7.3 and 7.4). Several researchers (eg.s Bazzaz et al., 1989; Bello et al., 1995; Messier, 1992) have reported similar results for other species.

CONCLUSIONS

Even in the presence of substantial levels of exogenously added photosynthate, and regardless of photosynthetic pathway differences, light level plays a role in the development (shape) of the plants that is independent of the growth (increase in biomass). When plants were given sucrose as an additional source of reduced carbon, they weighed more than uninjected plants. When shaded plants were injected with sucrose, shading effects on growth were overcome, while those on development were not substantially affected. The reduction in dry matter due to shading was more pronounced for below ground dry matter and reproductive parts than leaf and stems. C_3 and C_4 weed species showed the same in response to shading and an alternative source. Thus, even though sucrose injection provided an alternative source of sucrose large enough to overcome the effects of deep shading on plant biomass accumulation it did not alter the low light intensity effects on plant shape (morphology) and allocation of dry matter. This was even true in the case of seed production, which was sharply decreased in shade, even for sucrose injected plants. This is the first report of successful decoupling of low light effects on photosynthesis and other light process that control plant responses to light level. The results show that photosynthate availability is not taken into account by weed plants in the degree of morphological responses to low light levels.

Table 7.1. Analysis of variance showing probabilities for the main and interaction effects of shading (SH), injection treatment (IT), and weed species (SP) on plant height, stem, leaf, seed, root, shoot, and total dry weight, leaf area, treatment uptake, shoot to root ratio, leaf area and leaf weight ratio.

	CV	SH	IT	SP	SH x IT	SH x SP	IT x SP	SH x IT x SP
	(%)	P-values						
Plant height	4.2	0.0081	0.0168	0.0001	0.0467	0.0001	0.9369	0.3860
Stem dry weight	7.8	0.0032	0.0001	0.0001	0.8109	0.0011	0.7290	0.6545
Leaf dry weight	8.7	0.0132	0.0012	0.0001	0.0114	0.2599	0.9630	0.0387
Seed dry weight	18	0.0019	0.0001	0.0001	0.1400	0.2065	0.0072	0.1205
Root dry weight	12	0.0001	0.0033	0.0001	0.0043	0.0091	0.8826	0.9230
Shoot dry weight	5.3	0.0044	0.0001	0.0001	0.0099	0.0016	0.2727	0.9889
Total dry weight	5.4	0.0034	0.0001	0.0001	0.0025	0.0069	0.3579	0.9928
Leaf area	8.9	0.0198	0.0012	0.0001	0.0264	0.3908	0.998	0.5095
Uptake	11	0.0878	0.0001	0.0001	0.0056	0.7132	0.0136	0.9609
Shoot to root ratio	14	0.0325	0.0001	0.0001	0.0029	0.0001	0.9061	0.3396
Leaf area ratio	11	0.0638	0.0030	0.0001	0.0295	0.0009	0.0122	0.7338
Leaf weight ratio	10	0.1132	0.0003	0.0001	0.0110	0.0001	0.0579	0.206

Table 7.2. Multiple pairwise comparisons for interaction effects between shading levels (SH) and injection treatment (IT) on plant height, root, shoot, and total dry weight, and leaf area, treatment uptake, shoo to root, leaf area, and leaf weight ratio of three weed species.

		Plant height	Root dry weight	Shoot dry weight	Total dry weight	Leaf area	Uptake	Shoot to root	Leaf area ratio	Leaf weight ratio
		(cm)		(g $plant^{-1}$)		(cm^2 $plant^{-1}$)	(mL)		(cm^2 g^{-1})	
Shading level (%)	**Injected treatment**									
0	None	122.6b[+]	2.09b	15.4b	17.5b	757.0b	0.0e	7.9c	48.8b	0.25b
	Sucrose	120.1b	2.51a	22.6a	25.1a	1003.1a	50.7c	9.6b	44.7c	0.23bc
	Distilled water	112.8c	2.04b	15.1b	17.2b	736.0b	87.4a	8.2c	48.1b	0.25b
75	None	137.0a	1.41c	10.1c	11.6c	594.3c	0.0e	9.0bc	59.5a	0.30a
	Sucrose	135.4a	1.42c	16.1b	17.5b	669.2bc	39.6d	13.5a	41.5c	0.20c
	Distilled water	135.6a	1.42c	10.3c	11.7c	606.5c	83.1b	9.0bc	59.7a	0.30a

[+]Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Table 7.3. Multiple pairwise comparisons for interaction effects between shading levels (SH) and weed species (SP) on plant height, stem, root, shoot, and total dry weight, and, shoot/root ratio, leaf weight ratio, and leaf area ratio of three weed species.

Shading levels (%)	Weed Species	Plant height (cm)	Stem dry weight	Root dry weight (g $plant^{-1}$)	Shoot dry weight	Total dry weight	Shoot/ root	Leaf weight ratio	Leaf area ratio (cm^2 g^{-1})
0	Redroot pigweed	91.0c*	9.0b	1.93c	15.4c	17.3b	8.8c	0.24c	43.8c
	Lamb's quarter	125.9b	11.6a	2.21b	19.5a	21.7a	9.7bc	0.23c	40.7c
	Velvetleaf	138.4a	9.6b	2.50a	18.3b	20.8a	7.3d	0.27b	57.1b
75	Redroot pigweed	129.0b	7.1c	1.28d	10.7f	12.0e	10.2b	0.22c	44.5c
	Lamb's quarter	151.2a	9.0b	1.12d	14.2d	15.3c	14.9a	0.23c	43.6c
	Velvetleaf	127.8b	5.8d	1.85c	11.6	13.4d	6.3d	0.34a	72.7a

*Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Table 7.4. Multiple pairwaise comparisons for interaction effects between shading levels (SH), injection treatment (IT), and weed species (SP) on plant height, seed dry weight, treatment uptake, and leaf area ratio of three weed species.

Shading levels (%)	**Injected treatment**	**Weed species**	Leaf dry weight (g)	**Injected treatment**	**Weed specie**	Seed dry weight (g)	Uptake (mL)	Leaf area ratio
0	None	Redroot pig weed	3.19gh	None	Redroot pig weed	1.75fg	0.0g	46.6cd
		Lamb's quarter	4.27d		Lamb's quarter	1.96de	0.0g	44.0de
		Velvetleaf	4.60bc		Velvetleaf	2.29cd	0.0g	72.0a
	Sucrose	Redroot pig weed	5.04ab	Sucrose	Redroot pig weed	2.33c	40.5f	38.7e
		Lamb's quarter	5.27a		Lamb's quarter	3.48b	44.7ef	38.9e
		Velvetleaf	5.58a		Velvetleaf	4.18a	50.1d	51.7b
	Distilled water	Redroot pig weed	3.09h	Distilled water	Redroot pig weed	1.73g	77.6c	47.1bc
		Lamb's quarter	4.15de		Lamb's quarter	1.88ef	85.5b	43.6de
		Velvetleaf	4.48cd		Velvetleaf	2.36c	92.7a	71.1a
75	None	Redroot pig weed	2.30i					
		Lamb's quarter	3.22g					
		Velvetleaf	3.58ef					
	Sucrose	Redroot pig weed	2.25i					
		Lamb's quarter	3.72ef					
		Velvetleaf	4.01de					
	Distilled water	Redroot pig weed	2.42i					
		Lamb's quarter	3.33fg					
		Velvetleaf	3.67ef					

†Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Table 7.5. Multiple pairwise comparisons of overall main effects of weed species, injection treatment, and shading levels on leaf area, stem and seed dry weight.

Weed species	Leaf area (cm^2)	**Injection treatment**	Stem dry weight (g)	**Shading level (%)**	Stem dry weight (g)	Seed dry weight (g)
Redroot pigweed	565.30c*	None	7.25b	0	10.11a	3.20a
Lamb's quarter	707.89b	Sucrose	11.68a	75	7.30b	1.68b
Velvetleaf	909.86a	Distilled water	7.19b			

*Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Preface to Chapter 8

This section will form a manuscript to be submitted in 1999 for publication in Plant Physiology. The format has been changed to be consistent within this thesis. All literature cited in this chapter are listed at the end of the thesis. Each table or figure is presented at the end of this chapter.

In chapter 7 I investigated the effects of light levels and sucrose injection (as carbon source) on C_3 (lamb's quarters and velvetleaf) and C_4 (redroot pigweed) weed species. In chapter 8, the reactions of photosynthetic activities and chlorophyll fluorescence of these weeds to low light levels or sucrose injection (as carbon source) are investigated

RESPONSES OF THREE WEED SPECIES TO SUCROSE SUPPLEMENTATION BY STEM INJECTION IN FULL SUN OR DEEP SHADE: Photosynthetic activity and Chlorophyll Fluorescence

ABSTRACT

Photosynthetic activity of plants, as individuals or in a plant community, is highly dependent on light intensity. Plants grown in a reduced light environment are limited in carbon assimilation leading to lower photosynthesis and this, in turn, results in changes (reductions) in growth and development. Over the past ten years stem injection techniques have been developed for several crops. These allow injection of concentrated solutions of growth affecting materials, such as sucrose, in order to study their effects on the morphology and physiology of plants, among other things, under varying light levels. However, no work has been done to expand this technique to non-crop species. A greenhouse experiment was carried out to test an injection technique developed for soybean plants on the photosynthetic activity and chlorophyll fluorescence of three weed species. The light levels were full sun and 75 % shade. The solutions injected were 150 g sucrose L^{-1} and distilled water. Uninjected plants were also included as a control on the injection process. Injected plants took up sucrose equivalent to 47 % of their dry weight. Photosynthetic activities were higher while chlorophyll fluorescence ratios (Fv/Fm) were lower under unshaded than shaded conditions for all weed species, but higher values were

recorded for distilled water injected and uninjected plants than plants injected with sucrose. Shade caused a reduction in photosynthesis, mostly through stomatal closures (up to 29 %), while the use of available light was improved both by allocation of more dry matter to leaves (higher leaf area and weight ratios) and thinner leaves, and by reduced fluorescence losses. Injection of large amounts of sucrose over time periods, long enough to have caused complete acclimation, into both C_3 and C_4 weeds photosynthesis was mainly by reducing CO_2 uptake, and also by causing reductions in stomatal aperture. The reduction in photosynthesis was greater when injection occurred in shade. In addition, chlorophyll fluorescence was increased. Interestingly, this did not affect overall patterns of dry matter allocation and their response to shade. Under full sun conditions redroot pigweed (*Amaranthus retroflexus* L.), a C_4 plant, had higher photosynthetic rates than either of the C_3 plants [lamb's quarters (*Chenopodium album* L) and velvetleaf (*Abutilon theophrasti* Medic.)], but under deep shade the weed species were not different in terms of their photosynthetic rate. However, the reduction in photosynthesis due to shading for C_4 weed species was greater than for C_3 weed species, probably indicating a better tolerance of shading by C_3 than C_4 weed species.

INTRODUCTION

The basic resources that plants compete for are light, water, and nutrients. If water and nutrients are adequate then photosynthesis and growth rates of individual plants in a plant community will be roughly proportional to light interception (Melvin et al., 1993, Lawlor, 1995). Plants grown under higher light intensities are usually capable of greater photosynthesis rates per unit leaf area and become light-saturated only at higher intensities. Plants grown in a reduced light environment are limited in carbon assimilation and this, in turn, results in reduced growth and changes in development. This is also, in part, as a result of limitations in the photosynthetic induction requirement that develops under low light intensity (Sassenrath-Cole and Pearcy, 1994). As a result, shaded plants exhibit lower dry matter production and yields than unshaded plants. Studies of weed species grown under light-limiting conditions have also shown reduced growth, development, and seed production (eg.s Bello et al., 1995; Zangerl and Bazzaz, 1984). The overall reduction in dry matter accumulation of shaded plants is mainly due to the inability to capture enough photosynthetically active radiation (PAR). Burky and Wells (1991) found a 50 to 75% reduction in photosynthesis for soybean plants transferred from sun to shade for a period of 40 days following that transition, however, maximum photosynthesis and chloroplast electron transport activity were stabilized or increased in response to increased light intensities.

Several researchers reported that plants can adjust to irradiance by decreasing light-saturated photosynthesis, leaf respiration rates, stomatal conductance, leaf thickness, root growth, root to shoot ratios, and leaf density, while increasing the leaf area ratio (LAR) which decreases the support tissue to leaf ratio and results in greater partitioning of plant material into leaf tissues that harvest the available PAR, with less biomass diverted to tissues that act as sinks for photosynthate (Edward and Meyers 1989; Kephart et al., 1992; Allard et al., 1991; Marler et al., 1994; Ghannoum et at., 1997; Bauer et al., 1997). Many of these physiological and morphological adaptation-to-shade strategies are shared by most plant species regardless of their photosynthetic pathway. However, plant species that differ in their photosynthetic pathway (C_3 vs C_4) are likely to respond at least somewhat differently to light and CO_2 (Patterson, 1984). Biomass production patterns of C_3 and C_4 plants show large differences in response to CO_2 level at the high and low light levels. C_3 biomass increased with increasing CO_2 up to 600 ppm while C_4 biomass increased in the range from 300 ppm to 450 ppm but then declined from 450 ppm to 600 ppm (Zangerl and Bazzaz, 1984).

Several researchers (egs. Reeves et al., 1994; Allen et al., 1991; Prior and Rogers, 1995) reported increases in total leaf area, dry weight, and seed number of soybean plants when grown under elevated CO_2 levels. Increases in leaf area and biomass accumulation by weeds and other plants due to elevated CO_2 have been also reported previously (Zangerl and Bazzaz, 1984; Tolley and Strain, 1985; Coleman and Bazzaz, 1992). Even though greenhouse grown plants have been enriched with carbon dioxide as an extra source of carbon, the plants often adjust to such an elevated carbon dioxide enrichment by decreasing the ribulose bisphosphate carboxylase (Rubisco) content (Sassenrath-Cole and Pearcy, 1994; Xu et al., 1994) and stomatal opening (Fay and Knapp, 1995) which can result in photosynthesis levels similar to plants growing without carbon dioxide enrichment.

Plants also exhibit numerous other physiological adaptations to low irradiance, including increased quantum yield and reduced dark respiration, light compensation and saturation points (Marler et al., 1994). These researchers also reported that trees under full sunlight had lower ratios of variable to maximum fluorescence (Fv/Fm) than those that were under 25 and 50 % full sun light. The shade plants and the slow-growing sun plants had higher efficiencies than the fast-growing-sun plants and this could be related to the presence of a higher electron transport capacity relative to carboxylation capacity in the former group, which seems to be associated with lower photosynthetic capacities (Ogren and Sundin, 1996). A higher light-induced reduction in photochemical capacity of photosystem II (Fv/Fm) for sun exposed plants were reported, while shaded plants showed only a slight alteration of photochemical capacity (Bolhar-Nordenkampf et al., 1991).

In the past, ways of supplying nutrients into plants involved addition through roots and leaves (Rending and Crawford, 1985; Tomar et al., 1988). However, during the last ten years several researchers (eg.s Grabau et al., 1986; Boyle et al., 1991a,b; Ma and Smith, 1992; Ma et al, 1994a, b; Zhou and Smith, 1996; Abdin et al., 1998) succeeded in supplying exogenous solutions using injection techniques whereby solutions are injected into the stems of crop plants. In general, sucrose injected plants accumulated more dry matter than uninjected or distilled water injected ones (Abdin et al., 1998). Abdin et al.

(1998) found that up to 65% of the total plant dry weight could be supplied as sucrose via a pressurised injection system. However, they also noted no response to injected sucrose by plants in 70% shaded, while the unshaded and 30% shaded plants weighed more when injected with sucrose. Their data suggest that heavily shaded soybean plants had undergone a shift in both their architecture and physiology.

At the bottom of a plant canopy both light quantity and quality are changed. The most profound result of this is a decrease in photosynthesis. There are changes in plant growth (e.g. morphology) which appear to relate directly to light intensity or quality which may or may not be influenced by the availability of photosynthate. The objective of this work was to determine the effect of shading and injected sucrose, or a combination of the two, on the photosynthetic physiologies of weed (C_3 and C_4) plants.

MATERIALS AND METHODS

Seeds of lamb's quarters (*Chenopodium album* L) and redroot pigweed (*Amaranthus retroflexus* L.) were collected from a field that had been used for corn at the Emil A. Lods Agronomy Research Centre of the Macdonald Campus of McGill University in the fall of 1996. Seeds of velvetleaf (*Abutilon theophrasti* Medic.) included in the repetition of the experiment, were also collected from the Emil A. Lods Agronomy Research Centre, but in the fall of 1997. Before their use seeds were placed in small bottles, covered with water, and left in a fridge for 48 hours (as a cold treatment) to break dormancy (Totterdell and Roberts, 1979). These seeds were planted in 11 X 21 cm trays divided into 32 small sections (5.5 cm deep cells) filled with a mixture of sand and Promix (Premier Horticulture Ltee, Rivier-du-Loup, Quebec, Canada) (1:3). Seedlings were left to grow until the 4 leaf stage and were watered as necessary during this time. At this stage, vigorous seedlings were selected from the trays for each species and four were transplanted into each 15.5 cm diameter and 15 cm deep plastic pot containing the same rooting medium as the trays. Approximately two weeks later the plants were thinned to one per pot and fertilized with 1.5 g L^{-1} of NPK (20-20-20). Three days later the injection system, modified from Zhou and Smith (1996) and used for soybean by Abdin et al. (1998), was established.

In brief, the injection system was composed of a supporting stand and an injection system that ended with a 25-guage 3/4 vacutainer needle (Vacutainer, Becton Dickinson Company, Rutherford, NJ). A hose clamp was tightened around each of two 40 cm long pipes at a distance of 30 cm above a wooden base, and a 23 cm X 13 cm wooden platform with two holes rested on the hose clamps. At the mid distance between these two holes the wooden platform had a third hole that supported a 5 mL syringe. The injection tubing consisted of a 20 cm long flexible plastic tube (Tygon i.d 0.8 mm, o.d. 2.4 mm) that was connected at one end to a standard 18-guage 1½ needle (Becton Dickinson, Company, Franklin Lakes, NJ) and at the other end to a 25-guage 3/4 vacutainer needle (Vacutainer, Becton Dickinson, Company, Rutherford, NJ). The needles attached to each end of the tygon tubing were sealed in place with epoxy resin glue. The vacutainer needle was positioned at about 45^0 and inserted half way into the plant. The needles were sealed to the plant stems with latex (Vultex, General Latex Canada, QC, Canada). The latex was placed around the injection site in a cup formed by masking tape, and was allowed to set for 4 to 5 days. The injection systems were carefully tested for leakage and plants without leaks were then put under the various light level treatments for injection.

The first experiment tested lamb's quarters and redroot pigweed using cages of 70 X 75 X 120 cm covered on all sides, except the bottom, with shading cloth (Tek Knit, Montreal, QC, Canada). The second experiment included one additional weed species, velvetleaf (*Abutilon theophrasti* Medic.). As a result of this bigger cages were required and the size was increased to 100 X 100 X 200 cm covered with shading cloth. One side of the cage had a small door that could be opened and closed to aid in data collection. The research was conducted at the greenhouse of the Plant Science Department of McGill University. A photoperiod of 16 hours was maintained, using lighting from high pressure sodium lamps to extend the day length. Daytime temperature was 25±3^0 C, nighttime temperature was 20±3^0 C, and relative humidity was 60±5 %. The plants were injected with either distilled water or 150 g L^{-1} sucrose. Uninjected plants were also included as controls on injection effects. The injected solutions were forced into the plants using construction type ceramic bricks (approximately 2.7 kg each) with three holes, placed on top of the syringe plunger. One brick was added each day until reasonable flow rates were reached. In this experiment this did not require more than 2 ½ bricks. The plants were injected for a period of 9weeks.

The experiment was designed as a split-split-plot with three blocks, where shading level (0 and 75%) was the main plot and injected solutions (distilled water and sucrose) was the sub-plot. The three weed species were treated as sub-sub plot factors. The uptake of injected solutions were checked regularly and the syringe barrels were refilled as necessary. The injected plants were also checked regularly to make sure there were no leaks.

Photosynthesis rate were measured with an Li-6400 Portable Photosynthesis System (Li-COR, Inc., Lincolin, NE) between 10:00 and 16:00h. Two readings per plant were recorded and the average of the two readings were considered as the photosynthetic rate of the plant. Chlorophyll fluorescence measurement was conducted with a Morgan CF-100 chlorophyll fluorescence measurement system (Morgan Scientific Inc., Andover. MA.). Two measurements from each plant were taken from each plant, two cuvettes per plant were placed on the upper most fully expanded leaf. The cuvettes were left for 5 to 10 minutes on each leaf in order to for the area of this leaf inside the cuvette acclimatize to darkness. After this an optical probe was inserted into the cuvette and a reading was taken and used to determine the Fo (non-variable fluorescence), the Fm (maximal fluorescence), the Fv (variable fluorescence), and the ratio of (Fv:Fm), which is a measure of the photochemical efficiency of photosystem II. The Fv/Fm ratios indicates the photochemical efficiency of leaves, with higher values indicating more photochemical efficiency and less fluorescence (Lichtenthaler, 1996). Plants were harvested at complete senescence. Abscised leaves were collected, oven dried at 90^0 to a constant weight and weighed. To determine the leaf area of the weeds a random collection of leaves for each treatments were measured using leaf area metre (Delta-T Devices Ltd., Burwell, Cambrige, England) and then dried and weighed. At final harvest plant parts were separated into leaf, stem, seeds plus fruit and root material and oven dried for determination of dry matter distribution. Allocation patterns were assessed by calculating: total dry weight (shoot and root) (g), leaf weight ratio (leaf weight per total biomass), leaf area ratio (leaf area per total plant biomass, cm^2 g^{-1}). All the above mentioned variables are given on a per plant basis.

All data were subjected to analysis of variance with the PROC GLM Procedure of SAS (SAS Institute, 1994). Simple means comparisons for each multiple pairwise were made with a GLM analysis protected LSD test at the 0.05 level probabilities.

RESULTS AND DISCUSSION

Photosynthetic activity and the ratio of variable to maximum fluorescence (Fv/Fm) were affected by all three factors (light levels, injected material and species), but interactions between shading and injected treatment, and between shading and weed species existed only for photosynthesis rate and intercellular CO_2 concentration (Table

8.1). Generally, recorded values of photosynthetic activities were higher, while chlorophyll fluorescence (Fv/Fm) were lower for unshaded than shaded plants. This was also clearly demonstrated through lower values of stomatal conductance, intercellular CO_2 concentration, and transpiration rates for shaded than unshaded plants. There were interactions between shading and injection treatments and between injection treatments and weed species for uptake of the injected solutions. The uptake of both distilled water and sucrose were higher for unshaded than shaded plants and under both light levels there was more uptake of distilled water than sucrose. Generally leaf area ratio and leaf weight ratio followed the same pattern as uptake of the injected treatment except that leaf area ratio was also affected by an interaction between shading and weed species (Table 8.1). In contrast to most of the photosynthetic activity values, leaf area and leaf weight ratios of plants were higher under shaded than unshaded conditions.

Injection treatment

The plants took up distilled water more rapidly than 150 g L^{-1} sucrose solution under both shaded and unshaded conditions. The overall average total uptake of injected sucrose was 50.7 mL (7.6 g sucrose) and 39.6 mL (5.9 g sucrose) for 0 and 75 % shading levels, respectively (Begna, Chapter 7). Greater total uptakes of injected sucrose have been reported 11.8 g in soybean (Abdin et al., 1998), 17.7 g in corn (Zhou and Smith, 1996), 15g in corn (Boyle et al., 1991b). In our study the amount of injected sucrose averaged over light levels and weed species represented 47 % of the total plant dry weight (Begna, Chapter 7). Under both light levels the uptake of injected solutions was much higher for velvetleaf than lamb's quarters and redroot pigweed.

Photosynthetic activities and chlorophyll fluorescence

In all weed species the photosynthetic rate was lower under shade than full sun. The reduction in photosynthetic rate due to shading averaged over all treatments was as high as 46 % (Table 8.2). Burky and Wells (1991) found that soybean plants transferred from sun tc shade had decreases in photosynthetic rates as great as 50 to 75% for a period of 40 days following the transition. Allard et al. (1991) reported a 20 % carbon exchange rate reduction for grass plants of tall fescue at low irradiance (30 % full sun) as compared to full sun grown plants. Under both greenhouse and field conditions shading reduced the carbon exchange rate of cotton plants to close to zero (Bauer et al., 1997). Under both light levels the photosynthetic rate of plants injected with sucrose was much lower than plants either injected with distilled water and not injected. Krapp et al. (1991) reported that mature spinach leaves supplied with glucose through the transpiration stream for several days had lower photosynthetic rate than water supplied leaves both at lower and higher irradiance, but the inhibition was less marked in limiting than saturating irradiance. In our case the reduction in photosynthetic rate due to sucrose injection was also higher for unshaded than shaded plants. Unshaded redroot pigweed plants had the highest photosynthetic rate (6.40 µmol $^{-2}$ s^{-1}) followed by velvetleaf (4.70 µmol $^{-2}$ s^{-1}), and then by lamb's quarters (3.90 µmol $^{-2}$ s^{-1}). However, when plants were shaded the photosynthetic rate was not different between the three weed species (Table 8.2). Thus, the reduction in photosynthesis due to shading for the C_4 redroot pigweed was higher, at 57 %, than C_3 lamb's quarters and velvetleaf at 31 % and 36 % , respectively (Table 8.2). This indicates a better tolerance of shading by the lamb's quarters and velvetleaf than redroot pigweed species.

Reduction in photosynthetic rates of plants due to shading, regardless of their photosynthetic pathway, was clearly demonstrated by a decrease both in stomatal conductance and transpiration rate for all tested weed species. Both stomatal conductance and transpiration rate of shaded plants were 29-37 % lower than the unshaded plants (Table 8.3). Intercellular CO_2, averaged over all other treatments, was lower by at least 25 % for shaded as compared to unshaded plants indicating that at least most of the photosynthesis reduction due to shading was due to stomatal closure. Several researchers have also reported a decrease in stomatal conductance, transpiration rate, and enzyme activities in response to reduced light conditions (Edward and Meyers 1989; Allard et al., 1991; Marler et al., 1994; Ghannoum, 1997). These are the main means of physiological adaptations by plants in response to lower light intensities.

Under both light conditions sucrose injection reduced stomatal conductance and transpiration rate while it increased intercellular CO_2 concentration in all weed species, resulting in lower photosynthetic rates for sucrose injected than distilled water injected or uninjected plants (Tables 8.3 and 8.5). Photosynthesis reduction as a result of sucrose injection would appear to be the result of both reductions in stomatal aperture and reductions in CO_2 uptake at the chloroplast, with the latter being most important. Krapp et al. (1991) reported accumulation of carbohydrates such as starch and soluble sugars in the leaf to be the main inhibitors of photosynthetic rate of spinach leaves supplied with glucose for several days as opposed to water supplied ones.

Unlike photosynthetic rate the chlorophyll fluorescence ratio (Fv/Fm) was increased for all weed species due to shading. Full sun light plants had a 13 % lower Fv/Fm values than shaded plants (Table 8.2). Marler et al. (1994) reported that trees under full sunlight had lower ratio of variable to maximum fluorescence (Fv/Fm) than those that were under 25 and 50 % full sun light. A lower value of Fv/Fm was also reported for full sun grown young Carambola trees than unshaded ones. Similar results have been reported for unshaded versus shaded cotton plants (Warner and Burke, 1993). The shade plants and the slow-growing sun plants had a higher efficiency than the fast-growing-sun plants and this could be related to the presence of a higher electron transport capacity relative to carboxylation capacity in the former group, which seems to be associated with lower photosynthetic capacities (Ogren and Sundin, 1996). The differences between shaded and unshaded plants in chlorophyll fluorescence was only 13 %, although their photosynthetic rate differences were by as much as 46 % (Table 8.2).

Of the two groups of weed species the C_4 redroot pigweed had greater reduction in Fv/Fm due to shading than the C_3 species.

Sucrose injected plants had lower Fv/Fm values than plants injected with distilled water or not injected plants. Krapp et al. (1991) also reported similar results whereby detached leaves of spinach supplied with glucose had less chlorophyll fluorescence than water supplied ones.

Leaf area, leaf area ratio and leaf weight ratio

Generally leaf area was increased due to sucrose injection under both light conditions, however, the proportional increase (25 vs 12 %) due to sucrose supplementation was much higher for unshaded than shaded plants (Table 8.4). In contrast to leaf area, leaf area ratio of sucrose injected plants both under shaded and unshaded conditions were lower than distilled water injected and not injected plants (Table 8.5). Similarly the leaf weight ratios of sucrose supplied plants were lower than distilled water or uninjected plants and this was so both for shaded and unshaded plants. This was probably due to more starch accumulation in chloroplast for sucrose injected than the other plants. Even though the leaf area of lamb's quarters was higher than redroot pigweed, under both light levels, the leaf weight ratio and leaf area ratio of redroot pigweed were similar to lamb's quarters, whether or not they were supplied with sucrose.

Several researchers have reported similar light level effects for other plant species (eg.s Bazzaz et al., 1989; Bello et al., 1995; Messier, 1992; Ghannoum et al., 1997).

CONCLUSIONS

Photosynthetic activities were reduced by shading while chlorophyll fluorescence values were increased for all weed species. The reduction in photosynthesis rate due to shading was much higher for C_4 (57 %) than the C_3 (34 %) weed species indicating better use of high light levels by the former than the latter weed species. Shading reduced photosynthetic rates largely by decreasing stomatal aperture, while CO_2 uptake at the chloroplast was less affected and the efficiency of use of available light increased. At both light levels plants injected with sucrose had lower photosynthesis rates and Fv/Fm chlorophyll fluorescence ratios than plants injected with distilled water and those not injected. Intercellular CO_2 concentrations of sucrose injected plants were higher while stomatal conductance was lower than distilled water injected and uninjected plants indicating slower entry of CO_2 into leaves and slower uptake at the chloroplasts, with the latter being more limiting than the former. Leaf area was higher for sucrose injected than distilled water or uninjected plants at both light levels, however, the ratio of leaf area and leaf weight of sucrose injected plants of all weed species was lower than uninjected or distilled water injected plants. This may have been as a result of more starch accumulation in chloroplasts for sucrose injected than other plants.

Table 8.1. Analysis of variance showing probabilities for the main and interaction effects of shading (SH), injected treatment (IT), and weed species (SP) on photosynthesis rate, chlorophyll fluorescence ratio (Fv/Fm), stomatal conductance, transpiration rate, intercellular CO_2 concentration, leaf area, leaf area ratio and leaf weight ratio.

	CV	**SH**	**IT**	**SP**	**SH x IT**	**SH x SP**	**IT x SP**	**SH x IT x SP**
	(%)	P-values						
Photosynthesis rate	14	0.0089	0.0001	0.0001	0.0065	0.0001	0.9855	0.7006
Fv/Fm	5.9	0.0143	0.0196	0.0124	0.9625	0.6066	0.9585	0.9722
Stomatal conductance	8.6	0.0346	0.0002	0.0038	0.2245	0.5638	0.068	0.4307
Transpiration rate	11.8	0.0036	0.0005	0.0113	0.853	0.9700	0.8528	0.7112
ICO_2 conc.*	9.5	0.0013	0.0003	0.0965	0.0346	0.0345	0.1741	0.2237
Leaf area	8.9	0.0198	0.0012	0.0001	0.0264	0.3908	0.998	0.5095
Leaf area ratio	11	0.0638	0.0030	0.0001	0.0295	0.0009	0.012	0.7338
Leaf weight ratio	10.3	0.113	0.0003	0.0001	0.0110	0.0001	0.058	0.206

* ICO_2 conc.- Intercellular CO_2 concentration

Table 8.2. Multiple pairwise comparisons for interaction effects between shading levels, injected treatment, and weed species on photosynthesis rate and chlorophyll fluorescence of three weed species.

		Photosynthesis rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)		Fv/Fm
Shading level (%)	**Injected treatment**		**Shading level (%)**	
0	None	5.54b[+]	0	0.657b
	Sucrose	3.64c	75	0.755a
	Distilled water	5.71a	**Injected treatment**	Fv/Fm
75	None	3.02d	None	0.740a
	Sucrose	2.09	Sucrose	0.665b
	Distilled water	2.91d	Distilled water	0.713a

				Fv/Fm
Shading level (%)	**Species**		**Species**	
0	Redroot pigweed	6.40a	Redroot pigweed	0.681b
	Lamb's quarter	3.79c	Lamb's quarter	0.723a
	Velvet leaf	4.70b	Velvet leaf	0.714a
75	Redroot pigweed	2.76d		
	Lamb's quarter	2.26d		
	Velvet leaf	3.02d		

[+]Values, in the same column, followed by the same letter are not different (P<0.05) based on an ANOVA protected LSD test.

Table 8.3. Multiple pairwise comparisons for interaction effects between shading levels, injected treatments, and weed species on stomatal conductance and transpiration of three weed species.

Shading level (%)	Stomatal conductance ($mol\ m^{-2}\ s^{-1}$)	Trans-piration ($mol\ m^{-2}\ s^{-1}$)	**Injected treatment**	Stomatal conductance ($mol\ m^{-2}\ s^{-1}$)	Trans-piration ($mol\ m^{-2}\ s^{-1}$)	**Species**	Stomatal conductance ($mol\ m^{-2}\ s^{-1}$)	Trans-piration ($mol\ m^{-2}\ s^{-1}$)
0	0.21a[+]	2.58a	None	0.20a	2.28a	Redroot pigweed	0.19a	2.24a
75	0.15b	1.62b	Sucrose	0.14b	1.78b	Lamb's quarter	0.17b	1.96b
			Distilled water	0.20a	2.25a	Velvet leaf	0.19a	2.10ab

[+]Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Table 8.4. Multiple pairwise comparisons for interaction effects between shading levels, injected treatment and weed species for intercellular CO_2 concentration, and leaf area of three weed species.

Shading level (%)	Injected treatment	Intercellular CO_2 concentration (ppm)	Leaf area ($cm^2 plant^{-1}$)	Shading level (%)	Species	Intercellular CO_2 concentration (ppm)
0	None	365.74b⁺	757.0b	0	Redroot pigweed	386.68a
	Sucrose	409.01a	1003.1a		Lamb's quarter	368.32a
	Distilled water	361.94b	736.0b		Velvetleaf	382.02a
75	None	275.17d	594.3c	75	Redroot pigweed	263.87c
	Sucrose	304.82b	669.2bc		Lamb's quarter	294.20b
	Distilled water	292.25c	606.5c		Velvetleaf	314.17b

⁺Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Table 8.5. Multiple pairwise comparisons for interaction effects between shading levels, injected treatment and weed species on leaf weight and leaf area ratio of three weed species.

Shading level (%)	Injected treatment	Leaf area ratio (cm^2 g^{-1})	Leaf weight ratio	Shading level (%)	Species	Leaf area ratio (cm^2 g^{-1})
0	None	48.8b*	0.25b	0	Redroot pigweed	43.8c
	Sucrose	44.7c	0.23bc		Lamb's quarter	40.7c
	Distilled water	48.1b	0.25b		Velvetleaf	57.1b
75	None	59.5a	0.30a	75	Redroot pigweed	44.5c
	Sucrose	41.5c	0.20c		Lamb's quarter	43.6c
	Distilled water	59.7a	0.30a		Velvetleaf	72.7a

*Values, in the same column, followed by the same letter are not different ($P<0.05$) based on an ANOVA protected LSD test.

Chapter 9

GENERAL DISCUSSION

In the absence of factors such as nutrient deficiencies, temperature extremes, or water stress, light is the major limitation to plant development and growth. Increasing plant populations and decreasing row spacings have been used as methods in improving interception of incoming solar radiation by corn canopies, leading to increased yield and better competition with weeds. This is true in any crop production area, but is of particular importance in an area such as Canada, where the growing season is short. Thus, manipulating plant population, row spacing and the use of corn hybrids with good canopy architectures should help the plants to make efficient use of the light that is available during the growing season.

Photosynthetic efficiency and growth are often related to canopy architecture, and canopy architecture is a function of leaf number, shape, distribution, and orientation, and of plant size, which collectively determine the vertical distribution of light within the corn canopy (Williams et al., 1968; Girardin and Tollenaar, 1994). In this study there were differences in canopy architectures among corn hybrids at all site-years. Generally, LRS hybrids were much shorter (at least 30 %) than both LMBL and P3979, both in the presence and absence of weed pressure, and had more leaf number and leaf area distribution above the ear than the other hybrids (Chapters 4, and 5). This would change the vertical light distribution in corn canopies whereby more light interception would be expected at ear level and above and less at the bottom of the canopies for LRS than both of the other hybrids, and this in turn should limit the growth and development of weeds under corn canopies. At both site-years biomass production by both transplanted (lamb' s quarters and redroot pigweed) and naturally growing weeds under early maturing LRS and P3979 (especially LRS) were much lower than under LMBL (Chapter 6). Increased plant populations and the reduced row spacing increased light interception by the plant as a whole and, as a result, under these planting patterns biomass of both transplanted and naturally growing weeds was reduced relative to under conventional plant populations and a wider row spacing.

Quicker dry matter accumulation and leaf area development at the early stages of plant development were achieved by LRS and P3979 (especially LRS) than LMBL both in the presence and absence of weed pressure (Chapter 3). This would lead to earlier canopy closure leading to better light interception and competitiveness against weeds. This was probably one of the reasons why the grain yield reduction of LRS was lower than the other hybrids under weed pressure, and the lower dry matter production by both transplanted and naturally growing weeds under the LRS canopy (Chapters 4, 5, and 6). Canopy light interception and photosynthesis are closely related to leaf area index and to crop yield (Pearce et al., 1965; Tollenaar and Bruuslema, 1988; Andrade et al., 1993; Cirilo et al., 1994). Callaway (1992) reported higher grain yield reductions due to weeds for late maturing than early maturing corn hybrids.

In spite of quick and early leaf development, leaves and other plant parts of LRS were not destroyed or damaged excessively by mechanical (rotary hoeing) weed control and, in addition, their morphology and grain yield response to mechanical and chemical methods of weed control were not different from that of P3979 (Chapter 5). Since LRS tassels at least a week earlier than P3979, the grain filling period of LRS is expected to be longer than both P3979 and LMBL (Modarres et al., 1997a,b; Modarres et al., 1998; Begna et al., 1999). Thus, LRS would seem to be well suited for use in a short growing season areas. Its earlier and faster leaf area development and lack of negative response to rotary hoeing would also help the plant to be more competitive with weeds than the other hybrids and may eventually help to reverse a trend of ever increasing herbicide use for weed control. Ghersa et al. (1994) suggested that manipulation of the radiation environment (total irradiation, and spectral composition) during the early stages of crop establishment may be a useful tool for weed control and for designing new agronomic practices that take full advantage of the differential responses of specific crop and weed species. The allocation of resources among competing plants will vary with resource levels, densities and spatial arrangements, environmental conditions which affect growth and development of the plants, and the plants' biological characteristics, such as emergence time and growth rate (Radosevitch, 1988).

In general, plants grown in a reduced light environment are limited in carbon assimilation and this, in turn, results in changes (reductions) to growth and development. A way to supplement the availability of photosynthate is injection of sucrose into plant stems. Both C_3 (lamb's quarters and velvet leaf) and C_4 (redroot pigweed) sucrose injected plants achieved higher dry matter than distilled water injected or uninjected plants both in full sun and deep shade conditions (Chapter 7). Increases in leaf area and biomass accumulation by weeds and other plants due to elevated CO_2 have also been reported (Zangerl and Bazzaz, 1984; Tolley and Strain,1985; Coleman and Bazzaz, 1992). Interestingly the dry weight of sucrose injected shaded plants were not different from full sun uninjected plants, indicating the possibility of overcoming shading effects on growth through sucrose injection. However, injection of sucrose did not alter shading effects on development (dry matter distribution among plant parts). When weeds were grown in deep shade without sucrose supplementation the reduction in biomass (dry weight) averaged over species was 34 % (Chapter 7). In the field, biomass production by both transplanted and naturally occurring weeds under a corn canopy was up to 85 % less than biomass production by both types of weeds in the absence of full competition from corn (Chapter 6). Some of the reduction in biomass differences between the greenhouse and field experiments could be related to differences in the percentage of light availability in the shade conditions whereby greenhouse shaded weeds were allowed to receive 25 % of full sun light while the light availability to the weeds under corn canopies ranged from 6 to 20 % at full canopy development, depending on the choice of plant population and row spacing as well as development stages and types of corn hybrids. Researchers have widely reported higher above and below ground biomass for full sun grown than for shaded plants (eg.s Edward and Meyers, 1989; Kolb and Steiner, 1990;   Reeves et al., 1994; Allen et al.,1995; Prior and Rogers, 1995). Of course the competition for light would have been much less intense during the early stages of canopy development under field conditions. The greenhouse grown plants were subjected to constant shade once the condition was imposed. However, in the field the corn crop and weed plants would also have competed for water and nutrients.

Under both controlled (greenhouse) and field shade conditions the pattern of resource allocation was similar: more resources were allocated to the vegetative than to the reproductive parts of the plants by both of the C_3 and C_4 species and, interestingly, the greenhouse work showed this to be independent of sucrose supplementation. Since the relative success of any plant species, both as an individual or in a plant community, strongly correlates with total biomass production, under shade conditions found at the bottom of corn canopies the population of both weed species would be greatly reduced. However, C_3 weed species could come to be more predominant over time mainly as a result of their better tolerance to shading and potential responsiveness to increasing CO_2 concentration in the atmosphere.

Since the beginning of the industrial revolution, the CO_2 concentration in the atmosphere has been increasing due to the rapid increase in global fossil fuel consumption and deforestation, particularly in the tropics. Results from several lines of research suggest that C_3 plants are much more sensitive to the changes in CO_2 concentration than C_4 plants (Zangerl and Bazzaz, 1984).They also reported that CO_2 elevation affected annual plant communities both in terms of productivity and species composition and suggested that the effect of increasing CO_2 on such systems may depend upon other resources such as light and nutrients. In our study, although shading was overcome through sucrose injection, both C_3 and C_4 weed plants injected with sucrose had much lower photosynthetic activities in deep shade than full sun light (Chapter 8). However, reductions in photosynthetic activities were much higher for the

C_4 redroot pigweed than the C_3 species (lamb's quarters and velvet leaf) indicating a possible increase in the occurrence of the latter relative to the former weed species in plant communities as CO_2 levels continue to increase. Under field conditions, the biomass of transplanted redroot pigweed (C_4) was more reduced by narrower rows, higher plant populations and more competitive than the C_3 lamb's quarters. Since the photosynthetic activities of C_3 plants are suggested to respond better to increased CO_2 concentration in the atmosphere and to be less affected by shading their presence under corn and other crop canopies may increase at the expense of C_4 weed species. Even though the occurrence of C_3 weeds is likely to increase under corn canopies their population under early maturing LRS and P3979 hybrids (especially LRS), principally as a result of early and quicker leaf area development, would be much lower than under LMBL hybrids.

Chapter 10

GENERAL CONCLUSIONS

The following conclusions may be drawn based on the research findings contained in this thesis:

1. Increased in plant population and decreased row spacing improved light interception and dry matter accumulation by all corn hybrids, resulted in less light reaching the bottom of the canopies and made the corn plants better able to compete with weeds.

2. Grain yields of all corn hybrids were reduced due to the presence of weeds, however the reduction in grain yield was much lower for early maturing LRS and P3979 (in particular LRS) than LMBL.

3. As a result of rapid leaf area development and other canopy architecture differences, at all site-years biomass production by both transplanted (lamb's quarters and redroot pigweed) and naturally growing weeds under early maturing LRS and P3979 hybrids (especially LRS) were much lower than under LMBL.

4. In spite of quick and early leaf area development, leaves and other plant parts of LRS hybrids were not damaged by rotary hoeing and their morphology and grain yield response to mechanical (rotary hoeing) and chemical methods of weed control was not different from P3979.

5. In the absence of competition from corn, biomass production by both transplanted and naturally occurring weeds was up to 85 % greater than biomass

produced by both weeds under corn canopies.

6. Of the transplanted weeds redroot pigweed seems to be more affected than lamb's quarters by choice of planting patterns and hybrids.

7. Both C_3 (lamb's quarters and velvetleaf) and C_4 (redroot pigweed) sucrose injected plants achieved higher final dry matters than those injected with distilled water or uninjected, both in full sun and in deep shade conditions.

8. Dry weight of sucrose injected shaded plants were the same as uninjected, full sun plants, indicating the possibility of overcoming some shading effects (those on growth) through sucrose injection.

9. Photosynthetic activities of both C_3 and C_4 weed plants were lower and were more reduced by sucrose injection in shade than full sun. However, reduction in photosynthetic activities was much higher for the C_4 redroot pigweed than C_3 (lamb's quarters and velvetleaf) weed species, suggesting increased population occurrence of the latter than the former weed species in the plant communities developing under higher CO_2 levels, as seems likely in the future.

10. The photosynthetic activities of shaded plants were mainly reduced due to reductions in stomatal aperture. The plants compensated somewhat for the lower light levels by reducing fluorescence losses. In contrast, the photosynthetic rates of sucrose injected plants decreased because of reduced stomatal aperture, reduced CO_2 uptake at the chloroplasts (the latter more than the former) and increases in light loss due to fluorescence.

11. The characteristic morphological responses plants make to shade (more dry

matter allocated to stems and leaves and less to seed and roots) were not affected by the amount of photosynthate present in the plant, even when sucrose was injected in amounts sufficient to allow dry matter accumulations not different from plants grown in full sun.

Chapter 11

ACCEPTANCE OR REJECTION OF HYPOTHESES

Hypothesis 1:

Because of their more rapid leaf generation and other canopy architecture differences, Leafy reduced-stature (LRS) corn hybrids will compete more strongly for light with weeds, will be better able to suppress weed plants, and will be less affected by the presence of weeds than conventional hybrids.

Early maturing hybrids, LRS and P3979, (and in particular LRS) were less affected by weeds than LMBL (Chapters 3, 4, and 5). In addition biomass produced by both species of transplanted weeds (lamb's quarters and redroot pigweed) and naturally growing weeds were lower under early maturing LRS and P3979 hybrids (especially LRS) than under LMBL (Chapter 6). Thus, I accept **hypothesis 1.**

Hypothesis 2:

Because of more rapid leaf area accumulation and canopy architecture differences, LRS hybrids will be more damaged by rotary hoeing than conventional hybrids.

Leaf area accumulation was quicker and leaf area distribution into above ear leaves was greater for LRS than for P3979, however their general morphological and grain yield responses to rotary hoeing and chemical weed control were not different from P3979 (Chapter 4). Thus, I **reject hypothesis 2.**

Hypothesis 3:

Because weed plants have evolved to compete for light, sucrose supplementation (injection) allow the weeds to overcome shading effects on growth and development.

Sucrose injected plants weighed more than plants injected with distilled water or uninjected ones both in full sun and deep shade. Sucrose injected shaded plants achieved the same dry weight as unshaded, uninjected plants indicating that sucrose supplementation can overcome shading effects on growth (Chapter 6). However, the morphological responses to shade were the same for both injected and uninjected plants. Thus I accept a part of **Hypothesis 3:** that sucrose supplementation will allow the weeds to overcome shading effects on growth However, I **reject** the remainder, that sucrose supplementation will allow the weeds to overcome shading effects on development (as indicated by biomass allocation)

Hypothesis 4:

Since C_3 and C_4 weed species are different in terms of photosynthetic pathways, their morphological and physiological responses to light levels and sucrose supplementation will be different.

Regardless of photosynthetic pathways differences, both C_3 and C_4 weed species took up substantial amounts of sucrose and showed similar patterns of resource allocations both in full sun and deep shade (Chapter 7 and 8), but photosynthetic activities were more reduced due to deep shade (75 % of sun light) for C_4 redroot pigweed than for C_3 (lamb's quarters and velvetleaf) weed species. Thus with this result

I **accept** the first part (that morphological differences will be the same)of **hypothesis 4,** but **reject** the second part (that physiological differences will be the same).

Chapter 12

CONTRIBUTIONS TO KNOWLEDGE

1. This was the first evaluation of the combination of corn plant population and row spacing in combination with corn hybrids very different in canopy architectures on the ability of corn plants to compete with weeds.

2. Early maturing LRS and P3979 hybrids (especially LRS) competed better with weeds and allowed less light to reach into the bottoms of their canopies and were less affected by weed pressure. This is the first such demonstration with regard to the LRS hybrid.

3. Regardless of quicker leaf area development and differences in canopy architecture, the responses of LRS hybrids to mechanical (rotary hoeing) and chemical methods of weed control were not different from a conventional hybrid (P3979) indicating the possible use of rotary hoeing at early stages of plant development in weed control systems for LRS corn. This has not been demonstrated before now.

4. Biomass produced by both transplanted (lamb's quarters and redroot pigweed) and naturally growing weeds was greatly reduced by all hybrids, however weed biomass production under early maturing LRS and P3979 hybrids (especially LRS) were much lower than under the LMBL hybrid. This is the first such demonstration for LRS corn.

5. This thesis contains the first detailed report on the way in which the photosynthetic physiologies of C_3 and C_4 weed plants react to long term sucrose injection both in full sun and deep shade.

6. This is the first work to show that the effects of shade on photosynthate availability

was overcome by sucrose injection, and that sucrose injection could overcome shading effects on growth (leading to increased biomass) but not effects of development (partitioning of dry matter among plant parts). Thus, this work provides the first demonstration that shade induced changes in growth and development are independent of each other.

Chapter 13

SUGGESTIONS FOR FUTURE RESEARCH

The following work would extend the findings of this thesis.

1. In order to better understand the effects of canopy architecture and time to maturity on corn use of light and competitiveness an experiment using conventional and LRS types with a wide range of maturities should be conducted.

2. Various combinations of rotary hoeing and strip application of herbicide should be tested to establish an effective low herbicide weed management program for LRS.

3. The relevance of the injected sucrose work to future high CO_2 atmospheric conditions should be verified by conducting the greenhouse work described in this thesis again, but with elevated CO_2 levels, instead of sucrose injection.

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