Water Relations of Different Height Sunflower (*Helianthus annuus* L.) Cultivars

BY

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A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

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THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES
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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree

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DEDICATION

This thesis is dedicated to my late father **Shri. Virupakshappa Gurubasappa Angadi**
for his many sacrifices for the sake of my education
and
to my living father-in-law, **Shri. Puttanagouda Mallanagouda Patil** for his support
and constant encouragement for the academic endeavor.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. Martin H. Entz for his guidance during the course of this study and the preparation of this manuscript. The moral support from Martin and Jereleen and the friendship from Connor and Meghan to our family is greatly appreciated. I also take this opportunity to thank my committee members Drs. C.F. Shaykewich, P.B.E. McVetty, W. Woodbury and P.R. Bullock for their support, critical assessment of the project and creative suggestions to the manuscript. Thanks also go to Dr. A.A. Schneiter for serving as an external examiner.

Research is not done without the assistance and input from many people. I thank Drs. J. F. Miller, USDA, Fargo and W.Dedio, AAFC, Morden for their keen interest in the project and for providing seed material for the project. I acknowledge the help of staff at Morden research centre, especially Dr. K.Y Rashid. My gratitude is also extended to Dr. J. K. Vessey for allowing me to use the hydroponic setup for hydraulic conductivity studies. I thank Keith Bamford for the expert technical help and moral support. The support of scientists at the Semiarid Prairie Agricultural Research Centre, Swift Current, namely Drs. H.W. Cutforth, B.G. McConkey, R.P. Zentner, P.G. Jefferson, F. Selles, Y. Gan and P. Basnyat is greatly acknowledged.

The financial support from the Canadian Commonwealth Committee during this study is acknowledged. I also thank my parent institute, The University of Agricultural Sciences, Dharwad for providing an opportunity to pursue my doctoral studies. The effort

of the International Center for Students in arranging a host family on arrival and in creating a friendly atmosphere for easy acclimatization is cherished.

The support of all friends, who made our stay in Canada more enjoyable is appreciated. I would like to especially mention the names of Rohini and Shivu Halli, Vatsala and Ratnakumarasamy, Jayashree and Raj Hulasure, Vinaya and Raj Yadwad, and Msafiri and Gloria Mbaga in this regard. The affection of Jack and Nadia Hamian, our host family, is highly acknowledged. I thank all technicians, graduate students and friends who directly or indirectly helped me in completing this project.

Finally I would like to thank my wife Lalita Angadi, who in spite of agonies she had to put up with, patiently supported me through out this long sojourn. I also thank my sons, Pavan and Rohan for enduring the long days and weeks at home in my absence. I am also grateful to my brother, Dr. Vivekanand G. Angadi for his encouragement.

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List of Symbols and Abbreviations

Ψ_l	-Water potential
Ψ_p	-Turgor potential
Ψ_π	-Osmotic potential
Ψ_g	-Gravitational potential
Ψ_m	-Matric potential
$\Psi_{\pi 100}$	-Osmotic potential at full turgor
WUE_{DM}	-Water use efficiency for dry matter production
WUE_{Seed}	-Water use efficiency for seed production
SW-103	-Sunwheat-103
SW-101	-Sunwheat-101
Aurora	-AC-Aurora
Sierra	-AC-Sierra
Head:Veg ratio	-Head Dry Matter to Vegetative Dry Matter Ratio
Seed:Head ratio	-Seed Dry Matter to Head Dry Matter Ratio
PPFD	-Photosynthetic Photon Flux Density

ABSTRACT

Angadi, Sangamesh Virupakshappa, Ph.D., The University of Manitoba,
February, 2001. Water Relations of Different Height Sunflower Cultivars.
Major Professor; Martin H. Entz.

Recently developed dwarf sunflower cultivars have the potential of increasing sunflower acreage in the Canadian prairie. However, no information is available on the adaptability of dwarf sunflowers to different agro-climatic situations. In addition, dwarf cultivars differ in plant architecture. Therefore, information on variations within dwarf cultivars is equally important. Field and green house experiments were conducted during 1993 to 1996 to understand the effect of reduced plant stature on the water extraction ability, drought tolerance and productivity of sunflower cultivars. Dwarf open pollinated cultivars (sunola; cv. Aurora and Sierra), and dwarf hybrids (sunwheats; cv. SW-103 and SW-101) were compared to standard height hybrids (cv. IS-6111 and SF-187).

The ability to extract soil water decreased with reduction in plant stature. The dwarf cultivars had a smaller tap root diameter compared to the standard height cv. IS-6111. Rooting depth, extraction front velocity and root distribution were higher in IS-6111 compared to SW-103, although they were similar between IS-6111 and Aurora. Thus, the dwarfing gene and/or the genetic background of the cultivar played a role in determining the root system of sunflower cultivars. Greater water extraction ability of taller cultivars than dwarf cultivars was attributed to differences in growth duration, and a deeper root system. Tall cultivars were particularly efficient in extracting water below 110 cm soil depth.

The dwarf hybrid, SW-103, consistently had higher leaf water potential, which was frequently higher than that for IS-6111. However, Aurora had leaf water potentials lower, or at best, similar to IS-6111. The strategy adopted to overcome water stress differed between height classes. The standard height cv. IS-6111, under stress, allowed leaf water potential to drop lower and depended more on the root system to extract more soil water. In contrast, the dwarf cultivars sensed water stress early and initiated osmotic and stomatal regulation and depended less on their root system. Genotypic differences in osmotic adjustment per unit of water stress were observed. Under the moderate water stress conditions encountered in the present study, which represented the long term weather trends of the region, all height classes of sunflower maintained positive turgor. However, the standard height cv. IS-6111 maintained higher stomatal conductivity and photosynthesis than the dwarf cultivars.

The lower plant height of dwarf cultivars did not consistently translate to an increased harvest index. Only one out of four cultivars had a higher harvest index than both standard height hybrids. Seed yield was more dependent on cultivar than on stature. Aurora and IS-6111 produced similar yields. The photosynthates conserved by dwarf cultivars were retained by the complex head in some cultivars. These results suggest that more breeding work is needed to develop an ideotype with water extraction ability of IS-6111, stress responses of dwarf cultivars, small head and thin stem of Aurora and better retranslocation of photosynthates to seed of SW-103.

Thus, short stature sunflower cultivars have lower water extraction ability but higher drought tolerance compared to standard height sunflower cultivars. However, productivity under moderate stress conditions depends more on cultivar than on plant stature.

FOREWORD

This thesis is written in manuscript format. The journal format of Crop Science is used for the format. The section on 'Water Relations of Different Height Sunflower Cultivars' (chapter 5) has been submitted to the Crop Science Journal. The section on 'Agronomic Performance of Different Height Sunflower Cultivars' (chapter 3) has been reformatted for Canadian Journal of Plant Science and will be submitted for publication soon. Similarly, the section on 'Root System and Water Use Patterns of Different Height Sunflower Cultivars' (chapter 4) has been modified for Agronomy Journal and will be submitted soon.

1.0 INTRODUCTION

Water is one of the most important factors limiting crop productivity in the Canadian prairies, where precipitation is unevenly distributed and is lower than the potential evapotranspiration (De Jong and Cameron, 1980). Therefore, crops depend, in part, on stored soil moisture for their water requirements (Ash et al., 1992). In spite of this, a significant amount of water is left behind in the soil by small grain crops (Hurd, 1974) due to their limited root system (O'Toole and Bland, 1987). Therefore, a crop that maximizes both water recovery efficiency and water use efficiency is essential for yield stability in the prairies.

Sunflower (*Helianthus annuus* L.) is a highly adaptive crop, which has been recognized in the prairie region for some time (Green and Read, 1983). Consistent yields of sunflower under dryland conditions are attributed to the efficient water extraction compared to other annual crops (Cabelguenne and Dabaeke, 1998; Dardanelli et al., 1997; Hattendorf et al., 1988) and due to their deep and explorative root system (Bremner et al., 1986; Dardanelli et al., 1997). Since sunflower withstands short periods of water stress without serious yield penalty, sunflower acreage is spreading in dry regions of the world. In Canada, the short growing season is limiting sunflower acreage in the prairie to southern Manitoba. With climate change, the area suited to sunflower could increase substantially.

The success of short stature cereals has encouraged development of reduced height cultivars in other crops including sunflower. The advantages realised with the semidwarf cereals like improved harvest index, reduced crop lodging, improved kernel to dry matter ratio, and higher crop productivity are also expected in sunflower. In addition, shorter growth duration and possibility of managing with conventional equipments have renewed interest of non-traditional producers in dwarf sunflowers (Beckie and Brandt, 1996; Johnston et al., 1995; Schneiter, 1992).

The short stature sunflower cultivars are classified into semidwarf and dwarf cultivars (Schneiter, 1992). Although, semidwarf sunflower cultivars were developed in mid 1980`s, the adoption of short stature cultivars started in Canada with the development of dwarf cultivars in the early 1990`s. Different genetic sources have been used to reduce the plant height in sunflower (Miller and Hammond, 1991; Miller, 1992). Sunola cultivars were developed in western Canada and are unique with thin stem, small leaves, and small heads (Beckie and Brandt, 1996; Johnston et al., 1995).

Effect of short stature on the root system, plant water relations and productivity determine the adaptability of dwarf sunflowers. However, the above information is absent in sunflower. Even in cereals, where isogenic lines for plant height are available for more precise studies, clear understanding of the effect of dwarfing genes on morphology and physiology is lacking. Although, some research on semidwarf sunflower has been initiated (Schneiter 1992; Sadras et al., 1991a and b), information on dwarf sunflower, which is more important in a shorter growing season of western Canada, is urgently needed (Schneiter, 1992). Therefore, the objectives of this study were to:

1. Compare the genetic and agronomic potential of different stature sunflower cultivars grown under field conditions in the Canadian prairie.
2. Study the root systems and water use patterns of different stature sunflower cultivars.
3. Generate information on water relations of different stature sunflower cultivars.

This information will increase our understanding of the role of sunflower in cropping systems and will help to assess how breeding strategies could be improved for dryland sunflower cultivar development.

2.0 LITERATURE REVIEW

2.1 Origin and Development of Sunflower

Sunflower (*Helianthus annuus* L.) is one of the important crops domesticated in North America (Seiler and Rieseberg, 1997). Archeological evidence indicates that sunflower was domesticated before 3000 BC; native Indians used it as a food crop. Over 50 wild species of sunflower, both annual and perennial, have been reported. Sunflower habitat ranges from natural plains, cultivated fields, swamps, to sand dunes (Seiler, 1992; Seiler and Rieseberg, 1997). In North America, wild sunflower is distributed from the temperate Canadian prairie to tropical Mexico. Early European settlers introduced sunflower into Europe as a garden crop. Breeding efforts in the former USSR identified high oil sunflower cultivars and from there it spread to the rest of the world as an oilseed crop. Sunflower was reintroduced into North America in the early 18th century. The major areas of sunflower production in North America are in North Dakota, South Dakota and Texas in the United States and in Manitoba in Canada. Sunflower seed (achene) contains more than 40% oil, which is rich in unsaturated fatty acids (oleic, linoleic acid, etc) and hence nutritionally desirable.

Sunflower is currently one of the four most important oil crops in the world (Putt, 1997). The world sunflower acreage is increasing mainly in arid and semiarid regions, where water is the major yield limiting factor for annual crops. Sunflower is a drought tolerant crop and it tolerates warmer and drier environments than canola (*Brassica napus* L. and *B. rapa.* L.). Due to this high adaptability, significant sunflower production is occurring on every crop producing continent.

The adaptability of sunflower has been recognized in the Canadian prairie for some time (Green and Read, 1983), where crop development strongly depends on seasonal temperature (Shaykewich, 1994). However, the short growing season in western regions of the prairie has limited sunflower acreage to southern Manitoba. Crop lodging due to wind storms is another factor restricting sunflower acreage in the prairie. Although, sunflower cultivation in Canada started earlier than in the USA (Putt, 1997), the acreage is only 0.2 M ha compared to about 1.4 M ha in the USA. However, sunflower acreage in Canada increased by 60 per cent from 1989 to 1999 (Saskatchewan Agriculture and Food, 2000). This was mainly due to early maturing short sunflower cultivars extending the acreage in Saskatchewan (> 300 % increase). Thus, the introduction of dwarf sunflower genotypes should increase sunflower production in non-traditional areas.

2.2 Development of Short Stature Sunflower

The advantage of reducing investment of photosynthates into stem in increasing the harvest index in cereals was realised in the 1960's (Evans, 1994). As a result, genes responsible for reducing plant height were introduced into several cereal crops including wheat (*Triticum aestivum* L.) (Vogel et al., 1963), sorghum (*Sorghum bicolor* L. Moench) (Stickler and Younis, 1966), rice (*Oriza sativa* L.) (Dat et al., 1978) and barley (*Hordeum vulgare* L.) (Ali et al., 1978). In addition to improved dry matter partitioning, reduced crop lodging has contributed to the better recovery of grain in dwarf cereals. The success of short stature cereals has created interest in incorporating dwarfism genes in many other crops including sunflower.

In sunflower, wide genetic variation for plant height (50 to 400 cm) has been observed (Fick, 1978) and typically a plant height of 150 to 200 cm has been used in sunflower production. Breeding efforts in sunflower have identified several genetic sources for reducing plant height (Miller, 1992; Miller and Hammond, 1991). The incorporation of these genes have developed two distinct phenotypes, semidwarf (1.2-1.5 m) and dwarf (0.8-1.2 m) (Schneiter, 1992). Semidwarf sunflower cultivars were developed in the mid 1980's, while dwarf sunflower cultivars were developed in the late 1980's. The semidwarf phenotypes were developed by the compression of internodal length, while the dwarf phenotypes resulted from the reduction in the number of leaves (or internodes) (Schneiter, 1992). Some new cultivars may have both genes. These early maturing short stature sunflower genotypes are suited for the Canadian prairie, where a short growing season has restricted sunflower acreage.

2.3 Sunflower Productivity

Traditionally, sunflower is a tall, robust crop, that accumulates more dry matter per unit area than many other annual crops. Sunflower has a high photosynthetic rate and radiation use efficiency among C_3 crops (Connor and Sadras, 1992). In fact, the CO_2 exchange rate in sunflower is 90 to 140 per cent that of corn (*Zea mays* L.) (Kiniry et al., 1992). Similar, exceptionally high photosynthesis by a C_3 species was observed in Moricandia species (*Moricandia arvensis* L.) (McVetty et al., 1989). Though the canopy structure in sunflower is not conducive for high productivity (Connor and Sadras, 1992), higher specific Rubisco activity, efficient chloroplast electron transport and higher stomatal conductance have resulted in higher photosynthesis (Connor and Sadras, 1992; Merrien, 1992). The saturation light intensity for sunflower is 1500 μmol m^{-2} s^{-1} (sometimes >2000 μmol m^{-2} s^{-1}; English et al., 1979), which is higher than the average value for most C_3 species (Connor and Sadras, 1992). As a result, the lack of full sunlight often limits sunflower productivity (Bange et al., 1997; Robinson, 1978). Ontogenic variation in sunflower productivity has been reported. Merrien (1992) and Connor and Sadras (1992) suggested that the maintenance of active post-anthesis leaf area in sunflower will be beneficial for better seed development. Genotypic variation in photosynthetic rate per unit leaf area has also been reported in sunflower (Gimenez et al., 1992) and this variation was attributed to the smaller cell size which concentrates higher RuBP per unit leaf area. Lloyd and Canvin (1977) observed that the mean photosynthetic rate for cultivated and wild sunflower genotypes ranged between 24 and 52 mg CO_2 dm^{-2} h^{-1}, respectively, indicating the availability of genetic potential to further improve sunflower photosynthesis rate.

Radiation use efficiency is the ratio of above ground dry matter to intercepted solar radiation and it differs from the net photosynthesis rate, because it accounts for the differences in biomass partitioning into root and shoot, and biochemical composition of the biomass. Sunflower is reported to intercept 10 to 23 per cent more radiation due to its heliotropic leaf architecture than a fixed leaf architecture (Robinson, 1978). Quantum yield of sunflower, 0.06 mol CO_2 mol^{-1}, is comparable with those of C_3 species (0.047-0.056 mol CO_2 mol^{-1}) (Connor and Sadras, 1992). The leaf heliotropism is significant in young plants and the proportion of heliotropic leaves in the canopy decreases with age (Connor and Sadras, 1992). The light extinction co-efficient, a measure of canopy efficiency in intercepting radiation per unit leaf area index, also decreases with ontogeny until about anthesis and then increases up to maturity (Sadras et al., 1991a). Similarly, radiation use efficiency varies with ontogeny (Trapani et al., 1992) and water stress (Joel et al., 1997). The first stage of the crop, establishment (emergence to head visible), had smaller radiation use efficiency (1.0 g MJ^{-1}), which was attributed to greater investment into below ground parts. The radiation use efficiency increased to 2.4 g MJ^{-1} in the second stage of rapid growth (head visible to anthesis) and finally decreased to 1.3 g MJ^{-1} in the third post-anthesis stage (anthesis to physiological maturity). The higher synthesis cost of oil and protein as well as the reduction in photosynthetic efficiency of leaves are responsible for the reduced radiation use efficiency in the post-anthesis stage (Trapani et al., 1992; Whitfield et al., 1989). The radiation use efficiency is also related to leaf nitrogen levels (Bange et al., 1997; Joel et al., 1997) and the reduction in leaf N with ontogeny may also contribute to the reduction in radiation use efficiency after anthesis (Hall et al., 1995). Genotypic variations in radiation use efficiency have been reported (Bange et al., 1997; Sadras et al., 1991b). The radiation use efficiency declines in response to plant water stress (Joel et al., 1997; Whitfield et al., 1989). The radiation use efficiency of sunflower is higher than many C_3 plants and it can be as high as that of corn (Kiniry et al., 1992). Thus, sunflower makes use of available radiation efficiently compared to other crops.

Another important input, that poses the greatest limitation to crop productivity is water. The water use efficiency for biomass production in sunflower ranges from 11 to 25 kg ha^{-1} mm^{-1}, while that for seed production ranges from 1 to 10 kg ha^{-1} mm^{-1} (Kiniry et al., 1992). Transpiration efficiency of individual plants is similar to other C_3 plants like wheat, cotton (*Gossypium hirsutum* L.) and soybean (*Glycine max* L. Merr) (Connor and Sadras, 1992). However, lower water use efficiency for seed production compared to corn or grain sorghum is reported (Hattendorf et al., 1988). The differences in water use efficiency for dry matter production between sorghum and sunflower widened with ontogeny, which was mainly attributed to the higher energy content of sunflower seed at the later stages (Bremner and Preston, 1990). Water use efficiency for seed production is a product of water use efficiency for biomass production and harvest index. Therefore, more variation due to environment, water stress and management practices has been reported (Kiniry et al., 1992). In general, higher levels of available water result in lower water use efficiency values in sunflower.

The ultimate efficiency of a plant in using CO_2, sunlight and water depends on the biomass partitioning into economic products. Before floral initiation the biomass is partitioned among stem, leaf and root, while, after floral initiation, inflorescence and vegetative organs grow simultaneously. Therefore, traits reducing demand by vegetative organs (e.g. short stem) would build a stronger sink within the reproductive organs (Connor, 1992). However, the harvest index of sunflower ranges from 0.29 to 0.33, relatively low and narrow range among seed crops (Kiniry et al., 1992). In sunflower, the photosynthate produced before anthesis and intermediate storage organs play a major role in the yield formation compared to cereals. The period of seed filling is characterized by decreasing photosynthetic capacity, higher respiratory load and retranslocation of reserve from vegetative tissue to seed (Connor and Sadras, 1992).

Genotypic variation in stem reserve remobilization has been reported for sunflower (Sadras et al., 1993a). However, excessive levels of stem reserve remobilization cannot sustain the weight of the head (Schneiter et al., 1987) due to pith autolysis (Carr and Jeffe, 1995). The head size depends on the genotype and is affected by growing environment (Connor and Sadras, 1992). However, genotypic variation in harvest index in sunflower is observed (Kiniry et al., 1992) and the possibility of improving harvest index exists (Zaffaroni and Schneiter, 1991).

2.3.1 Plant Stature and Productivity

In general, reducing plant stature was predicted to increase plant productivity by diverting assimilates saved from reducing stem height to yield formation. Bush and Evans (1980) did not observe any difference in water-soluble stem reserves in isogenic tall and dwarf lines of wheat, and suggested that the assimilate saving might have been invested into development of a larger ear or higher grain number in dwarf lines. In some studies with dwarf isogenic lines of wheat and barley, the saving from stem growth was not converted into additional grain (Ali et al., 1978; Rebetzke and Richards, 2000). Short statured wheat genotypes are reported to perform better than tall cultivars only under favourable conditions (Entz and Fowler, 1990b), which was also observed in sorghum (Blum et al., 1997a). Working on different height classes of wheat genotypes, Nizam Uddin and Marshal (1989) reported that the effect of drought stress on productivity was severe on dwarf lines, moderate on semidwarf lines and mild on tall genotypes indicating the role of stem reserve in yield stability. However, dwarfing genes are often reported to interact differently in different genetic backgrounds (Ehdaie and Waines, 1996; McCaig and Morgan, 1993). Thus, it can be inferred from the above information that unless a breeding effort is made to identify suitable genotypes, assimilate saved from reduced stem growth may not be directly converted into grain yield (Ali et al., 1978; Evans, 1994; Sadras et al., 1993a).

Dwarfing in sunflower reduces internode length and/or leaf number (Schneiter, 1992). Sadras et al., (1991a) reported that reduction in internode length below the fourth internode was 50 per cent, while that above the fourth node was only 26 per cent. It is also believed that dwarfing genes in sunflower are associated with erect and semi-erect head angle, which makes these short genotypes more susceptible to schlerotinia head rot, sunscald damage and bird damage (Sadras and Villalobos, 1994). The complexity of sunflower heads lead to greater respiration and energy consumption (Whitfield et al., 1989). Therefore, there is an urgent need to generate physiological information on short stature sunflower cultivars to assist in breeding and adoption of newer cultivars in the cropping system.

It has been suggested that the advantages realised with semidwarf cereals may not be transferred completely to short stature sunflower cultivars (Connor, 1992; Sadras and Villalobos, 1994). Agronomic advantages like reduced crop lodging, early maturity and ease of cultivation have been realised with reduced height sunflower cultivars, resulting in wide spread acceptance of these reduced height sunflower cultivars in the Canadian prairie (Johnston et al., 1995). However, the reduced stature will possibly affect canopy structure, root system, seed number and stem reserve in sunflower (Connor, 1992; Sadras and Villalobos, 1994). The altered canopy structure of short stature sunflower is believed to affect the interception of radiation and aerodynamic conductance of the canopy (Sadras et al., 1991a), thus reducing photosynthesis and transpiration per unit area (Connor, 1992). A limited number of studies have observed no yield advantage with reduced plant stature in sunflower (Feoli et al., 1993; Schneiter, 1992).

2.4 Water Stress and Plant Adaptation

The full expression of genetic yield potential by field crops is rarely achieved due to ever prevailing biotic and abiotic stresses. Plants, being rooted in one place, have to face environmental stresses through adaptation. Hence, the yields of most crops under field conditions are only 12 to 30 % of record yields (Boyer, 1982). On a global scale, water stress is the most important limitation to crop production. Water stress or drought can be defined as any combination of restricted water supply, either resulting from low rainfall or from limited water holding capacity of the soil, and/or enhanced rate of water loss due to high evaporative demand that tends to reduce crop productivity (Jones, 1992). Most annual crops can tolerate variation in water supply, at the cost of production, but to achieve full production they must be supplied with full water requirement throughout their life cycle. In any water stressed environment, timing and intensity of water stress, drought susceptibility and potential yield influence productivity.

The genotypic variation for drought tolerance is quite vast. Drought tolerance in crops can be defined both in terms of survival and productivity. Extremely drought tolerant plants (e.g. Resurrection plants; Scott, 2000) can survive desiccation at the cost of productivity. In the modern commercial agriculture, interest is in traits which contribute to yield in water limiting conditions. The importance of different putative traits depends on whether the stress is terminal or intermittent (Ludlow and Muchow, 1990).

Table 2.1 Drought tolerance mechanisms in crops.

- Drought Escape or Avoidance
  - a. Rapid phenological development
  - b. Developmental plasticity
- Drought Tolerance at High Plant Water Status
  - a. Avoidance of water loss
    - i. Increased stomatal and cuticular resistance
    - ii. Reduced interception of radiation
    - iii. Reduced leaf area
  - b. Maintenance of water uptake
    - i. Increased rooting depth and density
    - ii. Increased root hydraulic conductance
- Drought Tolerance at Low Plant Water Status
  - a. Maintenance of turgor
    - i. Osmotic adjustment
    - ii. Increased elasticity
    - iii. Decreased cell size
  - b. Tolerance of dehydration or desiccation
    - i. Protoplasmic tolerance
    - ii. Cell wall properties

Adapted from Turner (1986)

Strategies for drought tolerance have been classified into a number of categories (Table 2.1). Plants may adopt one or several of these traits to overcome drought. Each of these traits have some advantages as well as some costs associated with them (Ludlow and Muchow, 1990). For example, drought avoidance may be good in dry regions with low rainfall, while, in a year of above normal precipitation, this strategy may limit yield potential. Maintaining water uptake under prolonged dry period may exhaust the soil moisture reserve resulting in moisture stress during the grain filling stage. The suitability of a trait depends on the location and/or nature of drought. For example, deep rooting is beneficial only if water is available at depth and there are no limitations for utilising that water. In addition, a plant exhibiting a drought tolerance strategy at a particular stage may not confer better yield, because yield is an integral of growth over the entire season (Ludlow and Muchow, 1990).

In the Canadian prairie, a precipitation deficit during the growing season is common in all agronomic regions, although the magnitude varies from region to region (Ash et al., 1992). Therefore, crops have to rely on soil moisture reserves to meet their moisture requirement. However, lower soil temperatures (Entz et al., 1992) and limited rooting capacity of small grain crops (Hurd, 1974) can restrict soil moisture use. Therefore, to ensure yield stability under prairie conditions a crop should have an efficient root system to utilise the soil moisture, a regulatory mechanism to reduce water loss from plants and, finally, mechanisms that help in tolerating water stress.

2.5 Soil Water Extraction

2.5.1 Root System

Root systems of plants, in addition to functions like anchorage, production of some chemicals and storage of food materials, play an important role in the acquisition of water and mineral nutrients (O'Toole and Bland, 1987). The rooting pattern may affect the amount and timing of water availability. Roots may have a direct effect, by changing the supply of water available to the crop, or an indirect effect, by changing the rate at which the supply becomes available (Ludlow and Muchow, 1990). A well-distributed root system or a deeper root system, if capable of delaying or avoiding the water stress at a critical stage, could increase the crop productivity.

The size of the root system needed to efficiently utilize the soil moisture has been debated. While some studies have suggested that a suboptimal root system limits soil moisture utilization (Hurd, 1974; O'Toole and Bland, 1987; Jamieson and Ewert, 1999), others have cautioned against the use of excessive root systems in crops (Passioura, 1986). In general, annual crops increase root dry matter under drought. Deep roots will be beneficial only when this increased exploration alleviates or delays water deficit at critical growth stages. The success of deeper roots also depends on the assumption that there is water in the soil profile, and that the present root system is not able to extract that water (Ludlow and Muchow, 1990). If it is not true, then the diversion of photosynthates to root may reduce above ground biomass and harvest index. Better root proliferation may also reduce loss of water by deep percolation.

While some have attributed the major differences in drought tolerance between species or genotypes to deep rooting (Boyer, 1996), others felt that the assimilate cost of deeper root systems or higher root length density are sometimes found to offset the benefits of extra water gained with deeper roots (Passioura, 1986). A root length density of 0.5 cm root cm^{-3} is often found sufficient for the complete extraction of available water but many crops have 4 to 6 times that value, at least in the surface soil layers (Ludlow and Muchow, 1990). However, compared to the above ground dry matter, biomass associated with increased root growth is negligible. Further, the benefit of a bigger root system will be more pronounced when the root system is more uniformly distributed and the root length density is just sufficient to extract maximum water (O'Toole and Bland, 1987). It has been observed that an explorative root system with a combination of thick and thin roots and low root density is more cost effective than an exploitative root system dominated by fine roots and large root length density (Fitter, 1996).

Sunflower has an explorative root system to explore a large volume of soil with a combination of thick and thin roots, low specific root length and low root length density (Connor and Sadras, 1992). Due to the vast adaptability of sunflower, benefits of root traits depend on the local pattern of water availability. Sunflower roots start growing earlier than the shoot and at a faster rate than shoot growth (Merrien, 1992). Compared with other annual crops, root penetration of sunflower, as measured by extraction front velocity, was faster (Dardanelli et al., 1997). Sunflower tap roots and laterals maintain more or less steady growth over time. The lateral roots follow an acropetal succession and length decreases with depth. Sunflower roots continue to grow up to physiological maturity (Jaafer et al., 1993), extracting water from deeper layers during seed filling. Deeper roots are also considered more efficient in water extraction because they are younger, less crowded and are in a wetter soil profile (Taylor and Klepper, 1978). Rooting depths of 2 m or beyond is often reported in sunflower (Bremner et al., 1986; Jaafer et al., 1993 and Sadras et al., 1989). Root length density, both vertical as well as horizontal, changes with ontogeny (Sadras et al., 1989).

Genotypic variations among different crop plants for root traits have been reported. These include rooting depth, root distribution, rate of elongation, xylem vessel diameter and root hydraulic resistance (O'Toole and Bland, 1987). However, environmental conditions also influence root characteristics. The relative sink strength of roots increases under drought (Eghball and Maranville, 1993; Passioura, 1994). The root proliferation under stress is an adaptive mechanism and it depends on severity of stress. The root response to drought also depends on developmental stage of the crop (Meisner et al., 1992). Different species may have different temperature optimums, although, warmer temperature usually favours root growth (Bland, 1993). Low spring soil temperatures have been reported to limit root growth of crops (Entz et al., 1992; McMichael and Burke, 1996) including sunflower (Aguirrezabal and Tardieu, 1996, Seiler, 1998). Thus, although the root system is under genetic control, the environment modifies it significantly.

2.5.2 Root Hydraulic Conductance

The ability of the root system to absorb and transport water is known as root hydraulic conductance (Huang and Nobel, 1994; Steudle, 2000). Hydraulic conductance can override the differences in rooting depth or root length density to decide the water extraction ability of crops (Gallardo et al., 1996), unless soil hydraulic conductance is more limiting (Huang and Nobel, 1994). The active regulation of water extraction by hydraulic conductance was presented in the work of Everard and Drew (1989), who observed a many fold increase in hydraulic conductance after the death of root systems. It was also supported by the observation of faster recovery of wilted tomato plants placed in water if the roots were cut out (Markhart and Smit, 1990). The root hydraulic resistance (inverse of conductance) restricts the amount of water absorbed by the plant and may help in its survival by saving water for later development stages (Passioura, 1986). An attempt by R.A. Richards to increase yield of spring wheat grown on stored soil moisture under south Australian conditions by increasing root hydraulic resistance has increased yield by 5-10 per cent (Passioura, 1986). On the other hand, higher root hydraulic conductance is beneficial especially in extracting water from deeper layers in sunflower (Bremner et al., 1986). This information on sunflower root hydraulic activity indicates that, in addition to acting as a water pump to replenish lavishly spent water from the canopy, the root system of sunflower actively regulates water use.

2.5.3 Water Extraction

Water uptake by plants is governed by traits associated with roots like depth, density, hydraulic resistance and soil characteristics (Robertson et al., 1993) and by demand parameters such as leaf area index and potential evapotranspiration (Ehlers et al., 1991; Steudle, 2000). Genotypic variations among sunflower cultivars in water extraction have been observed by many workers (Giminez and Fererez, 1986; Majid and Schneiter, 1988; Sadras et al.,1991a; Schneiter, 1992; Zaffaroni and Schneiter, 1989). Effect of growing season on the water extraction by sunflower has been observed (D'Andria et al., 1995). Sunflower is cultivated world wide and the patterns of water availability in those diverse environments vary. The root system of sunflower, during the course of evolution, has adapted morphologically as well as anatomically to different environmental conditions. Variations in habitat of wild sunflowers from clay plains to sand dunes to swamps add to the genetic diversity of sunflower crops (Seiler and Rieseberg, 1997). Under Mediterranean conditions, where the spring sown crop relies on stored soil moisture, longer season cultivars had deeper root systems than shorter season cultivars (Gimenez and Fereres, 1986). The deeper root system along with longer duration of water extraction generated a larger soil moisture gradient and thus more water from deeper wet layers was extracted. Short season cultivars extracted water to 1.80 m while longer season cultivars showed substantial extraction up to 2.70 m in south western Spain (Gimenez and Fererez, 1986). However, when a crop depends on intermittent rainfall for its water requirement deeper rooting has no advantage. Thus, in Argentina, rooting density beyond 2 m did not benefit spring sown sunflower crops (Sadras and Hall, 1989).

In general, a deep root system ensures stability in yield under water stress and sunflower possesses that deep root system. Many workers have reported better extraction of water by sunflowers compared to other crops (Bremner et al., 1986; Bremner and Preston, 1990; Cox and Jolliff, 1986; Dardanelli et al., 1997). Cox and Jolliff (1986), from their study on a silt loam soil in Oregon, attributed superiority of sunflower under a water deficit over soybean to its ability to extract more water from soil, especially between 0.9 to 1.8 m. The additional water allowed sunflower plants to avoid severe drought during bud formation to early seed fill (the most sensitive period). In a similar study in Kansas, Hattendorf et al. (1988) confirmed superior soil water extraction of sunflower over corn, grain sorghum, pearl millet (*Pennisetum americanum* L. Leeke) and soybean. They observed more water depletion by sunflower between 0.99 and 1.60 m depth of soil than other crops. Mean daily water use for sunflower was 22% greater than for the other five crops.

Complete exhaustion of the soil moisture by sunflower compared to other crops (Bremner et al., 1986; Cabelguenne and Debaeke, 1998) has implications for the cropping system. For example, exhaustion of water from deeper layers may not affect the following shallow rooted crops such as wheat but, thorough depletion of the top 1 m layer necessitates recharging of the profile. Bremner et al. (1986) suggested that sunflower should be included as an opportunity crop on perfectly recharged soil rather than a regular crop in the rotation, which concurs with the practice of using sunflower in western parts of Manitoba and western

North Dakota. Thus, sunflower is highly adapted to areas with a high probability of annual soil water replenishment, but should be used as an opportunity crop where soil water replenishment is infrequent.

2.5.4 Sunflower Stature and Water Extraction

Research on the water extraction by short stature sunflower genotypes is limited. Majid and Schneiter (1988) found no difference between the water extraction patterns of semi-dwarf and standard height cultivars in the northern Great Plains. However, in another study in the same region, Zaffaroni and Schneiter (1989) observed higher soil moisture extraction by standard height cultivars compared to semidwarf cultivars in some years. Contradictory observations on effects of plant stature have also been reported in other crops like wheat. For example, while, some studies reported a smaller root system with reduced plant height (Ehdiae and Waines, 1996), others observed either no effect (Entz et al., 1992; Richards, 1992) or increased biomass allocation to roots (Miralles et al., 1997). However, in wheat, drought increased root dry matter in tall cultivars (7%), while it decreased root dry matter in semidwarf (by 2%) and dwarf (by 20%) cultivars (Ehdaie, 1995).

Shallow rooting by dwarf sunflower genotypes has been attributed to a shorter life cycle of dwarf genotypes (Schneiter, 1992). In southern Australia, Sadras et al. (1991a) did not observe any difference in root activity between different stature sunflower hybrids with the same growth duration. These studies suggest that reported differences in water extraction in different stature sunflower are mainly related to crop duration. However, similar to wheat, the genetic background of different height classes of sunflower genotypes may have an effect on water extraction.

Limited information is available on root growth and water extraction by sunflower on the Canadian prairie, where cooler soil temperatures may limit root growth and soil water extraction. Therefore, information on the water extraction pattern of sunflower with special emphasis on newer dwarf genotypes is important from a cropping system perspective.

2.6 Plant Water Relations

Plant water relations is the oldest area of plant physiology to be studied (Kramer and Boyer, 1995). Though the importance of plant water status in growth, function and productivity was realised in the early era of scientific investigation, progress was slow. Prior to the middle of the 20th century, plant water status was measured using parameters such as water content of the tissue, suction, water absorbing power and osmotic pressure. A new concept, which includes both water content of the tissue and the energy content of the water was introduced in the 1950s and was termed water potential (Slatyer and Taylor, 1960). Since then water potential is the most common water relations measurement. The cohesion theory, which uses the water potential differential, in spite of recent controversy, is the most commonly used theory for water extraction and movements in plants (Wei et al., 1999).

2.6.1 Leaf Water Potential

Water potential (Ψ_l) can be defined as the free energy of water available to do work relative to that of free water at the same temperature, pressure and elevation. Water potential has strong roots in thermodynamic principles. Though the direct relationship between Ψ_l and plant metabolic processes is not established (Sinclair and Ludlow, 1985), Ψ_l gradients are considered to be responsible for water absorption. Total Ψ_l can be partitioned into its components:

$$\Psi_l=\Psi_p+\Psi_\pi+\Psi_m+\Psi_g \quad \ldots\ldots \quad (1)$$

Where, leaf turgor potential (Ψ_p) represents the hydrostatic pressure inside the cell, and leaf osmotic potential (Ψ_π) results from dissolved solutes in the cell and vacuole. By definition Ψ_π of pure water is zero. The presence of solutes lowers free energy of the solution, therefore Ψ_π is always negative. Gravitational potential (Ψ_g) is small and is often ignored except in tall trees. Matrix potential (Ψ_m) develops from the adhesive forces of the cell matrix and in the cell it usually merges with osmotic potential or turgor potential (Turner, 1981). Hence, it is not measured separately. Therefore, the total Ψ_l in a tissue is the algebraic sum of turgor potential and osmotic potential. Lockhart (1965) proposed that cell expansion is linearly related to hydrostatic pressure (Ψ_p) above a threshold level. Therefore, stress tolerance in cell expansion in plants involves maintaining positive Ψ_p by altering Ψ_l and Ψ_π.

The difference between leaf Ψ_l and soil Ψ_l is the driving force for soil moisture extraction. As the soil moisture around the roots decreases, the extraction of water to replenish the transpiration loss becomes more difficult and the leaf water potential drops. The leaf water potential regulates extraction of water, stomatal conductance and plant productivity (Kramer and Boyer, 1995). A lower Ψ_l increases soil moisture extraction (Giminez and Fereres, 1986) and decreases stomatal conductance (Entz and Fowler, 1990a). A diurnal decrease of Ψ_l by -1.5 MPa in sunflower decreased photosynthesis by 50% (Wise et al., 1990). The process continues until very low soil moisture reduces Ψ_l to lethal levels, which may affect the metabolic activity of the plant. The lower Ψ_l also initiates other drought tolerance mechanisms like osmotic adjustment, leaf senescence, and wilting to reduce the impact of increasing moisture stress.

Sunflower maintains a higher Ψ_l to continue metabolic activity during a stress period compared to a crop like sorghum (Bremner and Preston, 1990). Although, increasing the rooting depth to increase water supply is the main strategy adopted by sunflower, it may have to senesce some leaves to economise water use. Generally a Ψ_l range of -1 to -2 MPa is often reported in sunflower (Bremner and Preston, 1990; Martin et al, 1992), although less than -3 MPa was observed under extreme stress (Connor and Jones, 1985; Giminez and Fereres, 1986). Genotypic variation for Ψ_l has been reported within cultivated genotypes (Giminez and Fereres, 1986; Prasad et al., 1985) and between cultivated and wild species (Seiler, 1988). Genotypes extracting water from greater depth usually recorded lower Ψ_l (more negative) than shallow rooted sunflower genotypes (Giminez and Fereres, 1986).

The role of reduced plant stature on Ψ_l in sunflower has not been studied. A limited number of studies have been conducted recently in wheat. Contrary to the traditional notion of greater susceptibility of dwarf genotypes to water stress, dwarf wheat genotypes maintained higher Ψ_l than tall genotypes (Blum and Sullivan, 1997; Kirkham and Smith, 1978). In another study on the Canadian prairie, Entz and Fowler (1989) observed a similar trend, although the difference was not significant. However, the sunflower plant is totally different from cereal plants and information on stress experienced by shorter stature sunflower genotypes is needed for the adoption of newer cultivars.

2.6.2 Leaf Osmotic Response

Some plants accumulate solutes (sugars, amino acids, organic acids, inorganic salts, etc.) under water limited conditions, which is known as osmotic adjustment (Morgan, 1983; Losch, 1995). Ions of these small molecular weight compounds decrease the solute potential (Ψ_π) of the cell sap, resulting in increased water content and turgidity of the cell. The osmotic adjustment can occur by active solute accumulation or passive solute concentration (Entz et al., 1990a; Hsio, 1973 and Girma and Krieg, 1992). Being an inducible trait, plants use osmotic adjustment when water is scarce, at a very small cost. If water is plentiful, then osmotic adjustment is not used at no cost to the plant (Boyer, 1996). The benefits of osmotic adjustment include maintenance of stomatal conductance and photosynthesis (although at a lower rate) at low water potential, delayed leaf senescence, floret survival, increased root penetration and extraction of more water (Ludlow and Muchow, 1990; Turner, 1997). The yield benefits of osmotic adjustment in wheat were presented by Morgan (1983) by using genotypes from the same genetic background. Blum et al. (1999) used diverse genotypes including two lines from Morgan to reconfirm the variability and the relationship between osmotic adjustment and crop yield. The yield benefits of osmotic adjustment were higher in drier conditions or where the lighter soils limit the water supply (Morgan, 2000). However, comparing osmotic adjustment of sugarbeet (*Beta vulgaris* L.) with stomatal regulation of cowpea (*Vigna unguiculata* L. Walp.), McCree and Richardson (1987) concluded that carbon gain by osmotic adjustment or stomatal regulation were similar.

A number of crop species, including sunflower, use osmotic adjustment to counter water stress (Ludlow and Muchow, 1990). Genetic variability for osmotic adjustment has been observed in many crops (Ludlow and Muchow, 1990; Morgan, 1984; Turner, 1997). Limited information for intraspecific variation for osmotic adjustment in sunflower is available (Chimenti and Hall, 1993). Although, factors like crop stage, rate of stress development and pre-conditioning affect the osmotic adjustment (Morgan, 1984), it is possible to assess the variability of osmotic adjustment in sunflower genotypes by measuring osmotic adjustment at a single stage (Chimenti and Hall, 1993). Therefore, information on genetic variability for osmotic adjustment is needed in sunflower for using osmotic adjustment in a breeding program.

Similar to Ψ_l, few studies have compared the effect of plant stature on osmotic adjustment in cereals. In wheat, higher osmotic adjustment was observed in tall compared to semidwarf cultivars (Kirkham and Smith, 1978; Entz and Fowler, 1990a). However, Blum and Sullivan (1997) observed no difference in Ψ_π among different isogenic wheat lines in a hydroponic study. Information on effect of stature on osmotic adjustment in sunflower, which is needed for the adoption of newer dwarf genotypes, is lacking.

2.6.3 Regulation of Water Loss by Plants

A major portion of water absorbed by the root system of a plant (more than 95 %) is lost to the atmosphere by transpiration (Kramer and Boyer, 1995). Transpiration is responsible for the death of the largest number of plants in the world. However, transpiration is essential for efficient supply of water, and nutrients, CO_2 gas exchange, buffering leaf temperature and avoiding xylem cavitation (Woodward, 1998). Thus, transpiration is an unavoidable evil and plants have to adapt to differences in availability of water without sacrificing transpiration completely.

The loss of water from plants is regulated in the long term by changes in leaf area, stomatal characters, leaf hairiness, leaf waxiness, osmotic adjustment, root traits and in the short term by stomatal sensitivity, and interception of radiation (wilting) (Ludlow and Muchow, 1990; Schulz, 1993). Cultivated crop species have also co-evolved to adjust to the water availability in the region where they are grown. Sadras and Milroy (1996) reviewed soil water thresholds for leaf expansion and gas exchange and concluded that tissue expansion was more sensitive to water stress than gas exchange in crop plants. The reduction in leaf expansion was related to severity of the water stress (Flenet et al., 1996). However, the stress response also depended on other factors like phenology, plant type, genotype, soil type and drought acclimation.

Physiologists and ecologists believe that stomata have evolved to provide a means of controlling water loss from plants while allowing photosynthesis (Jones, 1998; Losch, 1995). Stomatal apertures reduce in response to water stress. But sensitivity of the stomata varies among crop species. Intraspecific variation for stomatal regulation is also reported in some crops (Ludlow and Muchow, 1990) including sunflower (Hernandez and Orioli, 1985). A crop with a high stomatal conductance takes advantage of abundant water supply (Kramer and Boyer, 1995), while a crop adapted to lower water supply with lower stomatal conductance has limited productivity regardless of water supply.

Sunflower uses water lavishly (Merrien, 1992) and the more available water, the higher the stomatal conductance rate. However, water stress triggers various water saving measures in plants (Connor and Sadras, 1992). Phenological, morphological and physiological traits help sunflower in regulating water loss (Robinson, 1978).

In sunflower, reduced water loss in drying cycles by reduced leaf area and stomatal conductance was observed only late in the season (Cox and Jolliff, 1987). Soybean, on the other hand, regulated its water by reducing leaf area and closing its stomata early in the drying cycle. Bremner and Preston (1990) reported that sunflower, in order to reduce water loss, senesced its older leaves and maintained a smaller leaf area at higher water potential. By contrast, sorghum maintained a larger leaf area at lower leaf water potential. Further, stomata of sunflower opened early and closed late, thus increasing photosynthesis potential relative to sorghum. Higher transpiration in sunflower had a higher cooling effect, especially in irrigated sunflower.

The relative importance of mechanisms of regulating water loss in sunflower differ with developmental stage of the plant (Connor and Sadras, 1992). During pre-anthesis stress, reduced leaf expansion had the most negative effect on transpiration followed by leaf senescence and wilting. Sensitivity of sunflower leaf expansion to pre-anthesis moisture stress has been well documented (Cox and Jolliff, 1986; Sadras and Milroy, 1996). Stomatal regulation had a smaller role in reducing transpiration than leaf expansion during the pre-anthesis period (Sadras et al., 1993c). However, during the post-anthesis period, water stress had little effect on leaf expansion (Connor and Jones, 1985). At this point, accelerated leaf senescence was more effective in reducing transpiration than leaf wilting (Sadras et al., 1991a). However, crop productivity is usually related to quantity of water transpired after anthesis (Ludlow and Muchow, 1990). Therefore, leaf senescence may be more detrimental, if stress is relieved at later stages.

Genotypic variation for stomatal traits has been observed in sunflower (Prasad et al., 1985). Comparing changes in stomatal conductance to unit change in Ψ_l, Hernandez and Orioli (1985) concluded that some sunflower genotypes actively regulate stomatal conductance, while some do not. Stomata in sunflower respond to osmotic adjustment (Turner et al., 1978). Since genotypic variation in osmotic adjustment has been reported, greater variability in stomatal regulation is predicted (Connor and Sadras, 1992). Stomata provide a coarse control over dehydration, but can not buffer diurnal variation in Ψ_l completely (Tardieu and Simonneau, 1998). Sadras et al. (1991a) partitioned transpiration per unit area into transpiration per unit radiation interception and radiation interception per unit leaf area and concluded that sunflower genotypes of different plant height differed in transpiration per unit leaf area due to differences in radiation interception.

2.7 Summary

Sunflower has been used in the past as a model crop to understand productivity and water relations of crop plants. Sunflower can adapt to diverse environmental conditions. A deep explorative root system for efficient water extraction, higher photosynthetic rates, and radiation use efficiencies enable sunflower to produce large amounts of biomass. Genotypic variation for water extraction, stress responses and productivity have been observed. Strategies used by sunflowers experiencing water stress and their water stress response is different from many other annual crops. In spite of this, gaps in the knowledge on sunflower physiology exist. The effects of reducing plant stature on sunflower drought tolerance and environmental adaptability are not known. Therefore, those aspects of sunflower physiology form the basis for this research.

3.0 AGRONOMIC PERFORMANCE OF DIFFERENT STATURE SUNFLOWER CULTIVARS

ABSTRACT

Early maturing, short stature sunflower (*Helianthus annuus* L.) cultivars improve the adaptability of sunflower to the short growing season of western Canada. However, the agronomic potential of the recently developed dwarf cultivars in comparison to standard height sunflower is yet to be characterized. A multi-environment field study, consisting of space planted trials with minimal interplant competition, and agronomy trials where plants were grown at commercial population densities, were conducted in southern Manitoba to compare yield potential of dwarf hybrids (sunwheats; SW-101 and SW-103), and dwarf open pollinated cultivars (sunola; Aurora and Sierra) with standard height cultivars (IS-6111 and SF-187).

As plant height decreased, the genetic potential for dry matter accumulation and water use efficiency for dry matter production (WUE_{DM}) also decreased. When compared at optimum (commercial) population densities, differences in dry matter accumulation and WUE_{DM} among the different height classes were masked. The diversion of assimilate from stem to head depended on the genetic background, while the efficiency of utilising assimilate in the head for seed production was lower in dwarf cultivars. Only one of the four dwarf cultivars (SW-103) displayed a higher harvest index than IS-6111. Both higher dry matter production and improved dry matter partitioning were contributors to the higher yield observed in the standard height cultivar, IS-6111, and the dwarf open pollinated cultivar, Aurora, compared to other cultivars. Environmental influence on the dry matter partitioning was significant. However, variations observed among the dwarf cultivars for dry matter accumulation and partitioning revealed that the dwarfing gene was not a limiting factor for

breeding a dwarf sunflower cultivar with better partitioning of dry matter along with better yield potential.

3.1 INTRODUCTION

On the Canadian prairie, accumulated precipitation falls behind potential evapotranspiration throughout the growing season (De Jong and Cameron, 1980), and crops depend on stored soil moisture for much of their water requirements (Ash et al.,1992). Adaptability of sunflower in this region has been recognised for some time (Green and Read, 1983). However, the short growing season in most regions of Saskatchewan and Alberta has limited the inclusion of the standard height sunflower in cropping systems. Therefore, the production of standard height hybrids has been centred in southern Manitoba. Another environmental factor that limits productivity of standard height hybrids is wind, which often causes crop lodging.

The recent development of early maturing dwarf sunflower cultivars has renewed interest in sunflower production among producers in areas that are marginal for standard height sunflower hybrids. Short stature cultivars in sunflower are classified as semidwarf (1.20 m to 1.50 m typical height) and dwarf (0.80 m to 1.20 m typical height) types (Schneiter, 1992). Dwarf cultivars are more recent in development and include dwarf hybrids and dwarf open pollinated cultivars. Dwarf open pollinated sunola cultivars, developed in western Canada, have gained popularity due to their ease of management (i.e. solid seeding), lodging resistance, and reduced growth duration (Beckie and Brandt, 1996; Johnston et al., 1995).

Development of short stature sunflower follows that in cereals, where genetic reduction in plant height has resulted in improved harvest index, reduced crop lodging, improved kernel to dry matter ratio, and higher crop productivity (Blum and Sullivan, 1997; Ehdaie and Waines, 1996; Entz and Fowler, 1990b; Ludlow and Muchow, 1990; Passioura, 1986). The shorter stem of semidwarf and dwarf sunflower was believed to conserve extra photosynthate for the development of extra florets, which at later stages, will demand extra photosynthate leading to more seed yield per plant (Connor, 1992). However, few studies conducted on sunflower stature have supported this hypothesis (Feoli, et al., 1993; Schneiter, 1992; Sadras and Villalobos, 1994).

Agronomic performance of a short stature cereal depends on the nature of the dwarfing gene and genetic background of the cultivar (Ehdaie and Waines, 1996; Blum et al.,1997b). Different genetic sources have been used to reduce plant height in sunflower (Miller and Hammond, 1991; Miller, 1992; Schneiter, 1992). While variation in agronomic performance of different stature sunflower has been predicted, very little agronomic information is available for within and between height class variation in sunflower. Therefore, a field study was conducted to evaluate the effect of reducing plant height on biomass production, biomass distribution, and yield formation in sunflower. The role of plant height on the water use and water use efficiency was also determined.

3.2 MATERIALS AND METHODS

3.2.1 Plant Material and Growing Conditions

Field experiments were conducted at three locations in Manitoba, representing different agroclimatic conditions and soil types. The Winnipeg (49.8°N, 97.2°W) experiments were conducted at the Department of Plant Science Field Research Facility. The soil at Winnipeg was clay (Riverdale series, Entisol, Cumulic Regosol) characterised by a gradual release of water and slow development of stress. The Carman (49.5°N, 98.0°W) trials were conducted at the Carman Research Station and the soil was sandy clay loam (Denham and Eigenhof series, Udic Boroll, Orthic Black Chernozem) with a characteristic quick release of water and rapid development of stress. The third location was at the Agriculture Agri-Food Canada Research Centre at Morden (49.1°N 98.1°W). The soil at this site was a coarse textured Hochfeld fine sandy loam (Udic Boroll, Orthic Black Chernozem). The typical relative water deficit for long season crops like corn (*Zea mays* L.) at Carman and Morden averages 50 mm more than at Winnipeg (Ash et al., 1992).

In the present study, sunflower cultivars from three height classes were compared for agronomic performance (Table 3.1). The first class was dwarf open pollinated cultivars (two Sunola cultivars: AC-Aurora and AC-Sierra; referred to as Aurora and Sierra). The second class was dwarf hybrids (two Sunwheat hybrids: Sunwheat-101 and Sunwheat-103; referred to as SW-101 and SW-103). The third class was standard height hybrids (IS-6111 and SF-187).

Two types of field experiments, space planted trials and agronomy trials, were used to assess the performance of sunflower cultivars. All trials were fertilized based on soil test results (Norwest lab, Winnipeg) (Appendix 1). The preceding crop at each location was a cereal grain (wheat or barley). Minimum tillage (one or two passes using a cultivator) before

Table. 3.1. Details of sunflower cultivars used in the present investigation.

Cultivar	Year†	Height (cm)	Days to Flower	Days to Maturity	Oil (%)	Breeder Information
AC-Aurora	1992	83	-	98	44.0	Western Grower Seed Corp., Canada
AC-Sierra	1992	94	-	101	47.2	Western Grower Seed Corp., Canada
Sunwheat-101	1989	100	62	109	43.3	Seedtech International, Woodland, CA, USA
Sunwheat-103	1992	95	56	106	46.2	Seedtech International, Woodland, CA, USA
IS-6111	1992	145	75	117	47.5	Interstate Seed Co., Fargo, ND, USA
SF-187	1989	127	71	118	46.4	Cargill Hybrid Seeds, Pontiac, IL, USA

Source: Description of Variety, Agriculture Canada, Food Production and Inspection Branch.
† Year of release in Canada.

seeding was used except for the space planted trial at Carman in 1994, where neither fall nor spring tillage was used. Wherever necessary, pre-seeding glyphosate was used to control weeds, followed with hand hoeing and hand weeding to keep the plots weed free. Sunflower beetles were controlled by periodic spraying of systemic insecticides, except at Morden in 1993, where no insecticides were sprayed.

Space Planted Trials. The space planted trials were like big pot experiments in the field, where cultivars were grown with minimal interplant competition. These trials were used to study different height classes under the same population density without the confounding effects of plant population and row spacing. The space planted trials were conducted during 1994 and 1995 at Carman and Winnipeg, respectively. In these trials, cultivars representing three sunflower height classes (Aurora, SW-103 and IS-6111) were hand seeded in 5 m x 8 m plots at 1 m x 1 m spacing. The experiments were over seeded with 3-4 seeds at each spot and at V_2 to V_4 stages (Schneiter and Miller, 1981; Appendix 2) extra seedlings were removed. The over seeding ensured 38 to 40 (95-100 % of desired) plants per plot. These trials were seeded between May 23 and June 2 (Appendix 3). In 1994, additional cultivars, SW-101 and Sierra, were included in the trial to compare the within dwarf height class variation.

Agronomy Trials. The major management difference in the cultivation of standard height and dwarf sunflower cultivars is the solid seeding of dwarf cultivars. Therefore, agronomy trials concentrated on evaluating agronomic traits under recommended row spacings and plant populations. In the agronomy trial, two commercial cultivars from each of the three height classes were assessed for within and between height class variations. Three different plant populations of 55 000 (for standard height hybrids), 100 000 (for dwarf hybrids) and 170 000 per ha (for dwarf open pollinated cultivars), and two row spacings, 0.75 m (for standard height hybrids) and 0.30 m (for dwarf cultivars) were used. These are the agronomic practices recommended for producers on the Canadian prairie (Dr. W. Dedio, AAFC, Morden Research Centre, personnel communication). Plots were 8 m long and either 3.6 (for dwarf cultivars) or 5.4 m (for standard height hybrids) wide. Experimental plots were seeded using a Fabro small plot seeder (Swift Manufacturing Co., Swift Current, SK). The experiments were over seeded between May 13 and May 30 (Appendix 3) and hand thinned to the recommended plant population at V_4 to V_6 stage (Schneiter and Miller, 1981). Agronomy trials were conducted at Morden in 1993, at Carman in 1995, and at Winnipeg in 1993 and 1994 growing seasons.

3.2.2 Observations

Weather conditions in all field trials were monitored between May to September with meteorological stations located less than 500 m away from the research plots. Daily values of minimum and maximum air temperatures recorded from the weather stations were used to calculate sunflower growing degree-days, using a base temperature of 6.7 °C (Kandel, 1995). In 1994, the rain-gauge at the Department of Plant Science Field Research Facility did not function properly. Therefore, rainfall data from the nearby Glenlea Research Station (about 15 km away from plots) was used.

In the 1994 and 1995 agronomy trials, development stages were assessed on five randomly selected plants using the scale developed by Schneiter and Miller (1981) (Appendix 2). Plant heights to the base of the head of five randomly selected plants were measured in space planted trials after anthesis, when the plant height was maximum.

The total above ground dry matter accumulation was measured in all field trials. In the space planted trials, this observation was made at the end of the season on five randomly selected plants. In the agronomy trials, 25 plants (15 plants in 1993 trials) were used for assessing seed yield and final dry matter. All plants were oven dried for 3 to 5 days at 65 °C before recording dry weight. Five hundred seeds from randomly drawn seed samples were counted on an automatic seed counter for assessing thousand seed weight. Seed number per square meter was calculated from thousand seed weight and seed yield data. The harvest index was calculated in agronomy trials as the ratio of seed yield to the above ground dry matter yield. In space planted trials, plants harvested for dry matter were separated into vegetative (leaf and stem) and reproductive (capitulum/head) parts before drying. The dry matter in vegetative, reproductive structures and seed yield were used to assess reproductive to vegetative dry matter (Head:Veg) and seed to reproductive dry matter (Seed:Head) ratios.

Soil moisture was measured with a pre-calibrated neutron probe (Model 4330, Troxler Labs, Triangle Park, North Carolina, USA). Aluminium access tubes were installed to a depth of 2.1 m in all field trials. In agronomy trials the tubes were within a row, while in space planted trial the neutron tubes were 0.15 m from the nearest plant. Growing season water use was calculated as the sum of water extraction from the whole profile (1.90 m deep) between spring and fall soil moisture readings and the precipitation received during this interval. Downward and upward water movement across the 1.90 m depth and runoff were assumed to be negligible. The data from agronomy trials at Morden and Winnipeg in 1993 were not used for water use calculation due to probable deep percolation and runoff resulting from very high summer precipitation amounts. Water use efficiency for above ground dry matter production (WUE_{DM}) was assessed in all field trials except the 1993 trials, while water use efficiency for seed yield (WUE_{Seed}) was assessed only in the 1994 and 1995 agronomy trials. WUE_{DM} is the ratio of dry matter produced per unit of water used, while, WUE_{Seed} is the seed yield produced per unit of water used.

Analysis of variance was conducted by using a GLM procedure (SAS Institute Inc., Cary, NC, 1985). The statistical design adopted for all trials was a randomised complete block (RCB) with four replicates. The data from space planted trials and agronomy trials were analysed separately. Locations and years were combined and termed as environments. Error variances from the separate analysis of total dry matter, seed yield, thousand seed weight, seeds per square meter, harvest index, total water use, and water use efficiencies from each environment were tested for homogeneity of variance by using Bartlett's test and then pooled to assess the effect of cultivar, environment and cultivar x environment interaction. SW-101 and Sierra, which were used in only two space planted trials, were excluded from the pooled analysis of space planted trials.

3.3 RESULTS

3.3.1 Weather Parameters

The long-term average growing season (May-September) precipitation is similar for all three locations (Table 3.2). Growing season precipitation varied among the years of the experiments. In 1993, Morden and Winnipeg received 65% and 127% more rainfall than the long-term average, respectively. At Carman, precipitation was 20 % below the long-term mean in 1994, while it was similar to the long-term average in 1995. However, several long dry spells, periods of high daily temperatures and lower fraction of seasonal rainfall during the active growing period of the season were experienced at Carman in 1995 (Figure 4.1). Above-normal precipitation and below-normal air temperatures were experienced at Winnipeg in 1994, and this was followed by lower than average rainfall, intermittent dry spells and high temperatures in 1995. The growing season in 1995 was warmer than in 1993 and 1994, and it accumulated more growing degree days between April and September (Table 3.2). Overall, all the growing seasons were favourable for good sunflower crops without any serious soil moisture or high temperature limitations.

3.3.2 Space Planted Trial

Sunflower cultivars differed significantly in plant height and dry matter production (Tables 3.3 and 3.4). Pooled over environments, sunwheat and sunola cultivars were 38%

Table 3.2. Long term average precipitation, growing season precipitation and heat accumulation at Morden, Carman and Winnipeg during field trials.

Month	Precipitation †									Growing Degree Days§					
	Morden		Carman			Winnipeg				Morden	Carman		Winnipeg		
	1993	Mean‡	1994	1995	Mean	1993	1994	1995	Mean	1993	1994	1995	1993	1994	1995
May	64	60	41	62	60	44	150	41	58	207	251	195	212	227	200
June	170	80	27	41	74	112	95	26	84	267	354	421	292	336	441
July	196	70	66	84	79	308	97	33	72	331	379	419	379	355	433
August	86	64	70	83	61	266	101	129	75	364	345	411	385	307	437
September	18	49	63	40	52	40	83	39	51	167	270	232	163	244	231
Total	534	323	267	310	334	770	526	267	340	1336	1599	1677	1431	1469	1742

† Data were collected from the weather station set up on the research station except in 1994 at Winnipeg, where rainfall data from Glenlea research station was used due to failure of raingauge.

‡ Long term average data from 1925 to 1990 from Environment Canada for Graysville (Carman), Morden, and Winnipeg International Airport.

§ Growing degree days were calculated from [(Daily Max. Temp + Daily Min. Temp)/2]-6.7 °C. If daily Max or Min. Temp. was less than 6.7 °C, then it is set to 6.7 °C (Kandel, 1995).

Table 3.3. Plant height (cm) of different sunflower cultivars in space planted trials.

	Carman		Winnipeg		
Cultivars	1994	1995	1994	1995	Mean
Aurora	74.7 c†	91.7 b	83.5 c	99.3 b	87.3 b
Sierra	78.6 c	-	93 b	-	-
SW-101	91.4 b	-	84.3 c	-	-
SW-103	73.1 c	84.3 b	78.3 c	87.9 b	80.9 c
IS-6111	134.4 a	136.4 a	144.2 a	138.1 a	138.3 a
Mean††	94.1 C	104.1 AB	102.0 B	108.4 A	

† Values within a column followed by the same small letter and mean values followed by same capital letters are not significantly different at $P<0.05$.

†† Mean of common three cultivars.

LSD for cultivar x environment interaction was 9.8 ($P<0.05$).

shorter than the standard height cultivar, IS-6111 (Table 3.3). Similarly, dry matter production by SW-103 and Aurora was 56 and 64 % lower than IS-6111, respectively (Table 3.4). However, plant height was not the only factor affecting dry matter production. SW-101 accumulated higher dry matter among dwarf cultivars. The dwarf hybrid, SW-103, which was the shortest of all cultivars, had higher mean dry matter compared to Aurora. Thus, in addition to plant height, genetic background of the cultivar determined dry matter accumulation. Literature on comparing sunflower cultivars in the absence of interplant competition is not available. However, differences in biomass accumulation by different height sunflower cultivars grown under the same population density have been reported (Majid and Schneiter, 1988; Zaffaroni and Schneiter, 1991; Sadras et al., 1993a). Higher dry matter accumulation by IS-6111 and SW-101 compared to other cultivars also suggests the role of longer growth duration in biomass accumulation (Giminez and Fereres, 1986).

Table 3.4. Dry matter production and partitioning into head and seed, consumptive water use and water use efficiency in dry matter ($\mathrm{WUE_{DM}}$) production in the field by space planted sunflower cultivars.

Cultivars	Carman 1994	Carman 1995	Winnipeg 1994	Winnipeg 1995	Mean
			Head:Veg Ratio		
Aurora	1.06 a†	1.53 a	1.70 a	0.71 a	1.25 a
SW-103	0.97 a	0.67 a	0.87 c	0.43 b	0.74 c
IS-6111	0.80 a	1.53 a	1.06 b	0.47 b	0.93 b
Mean††	0.94 B	1.21 A	1.21 A	0.54 C	
			Seed:Head Ratio		
Aurora	0.36 b	0.28 b	0.50 b	-	0.38 c
SW-103	0.50 a	0.39 a	0.47 b	-	0.45 b
IS-6111	0.45 a	0.43 a	0.57 a	-	0.49 a
Mean	0.44 B	0.36 C	0.52 A		
			Dry Matter (kg ha^{-1})		
Aurora	2636 c	2404 c	3532 c	2126 c	2674 c
Sierra	2483 c	-	3707 c	-	-
SW-101	4153 b	-	5049 b	-	-
SW-103	2633 c	2988 b	3763 c	3663 b	3262 b
IS-6111	7270 a	6491 a	7976 a	7654 a	7407 a
Mean	4179 BC	3735 C	5090 A	4481 B	
			Consumptive Water Use (mm)		
Aurora	238 a	234 b	443 a	242 ab	298 ab
Sierra	244 a	-	-	-	-
SW-101	250 a	-	-	-	-
SW-103	238 a	230 b	429 a	231 b	286 b
IS-6111	289 a	289 a	456 a	263 a	327 a
Mean	257 B	251 B	443 A	246 B	
			$\mathrm{WUE_{DM}}$ (kg ha^{-1} mm^{-1})		
Aurora	11.2 c	10.6 b	8.0 b	8.9 b	9.3 c
Sierra	11.1 c	-	-	-	-
SW-101	17.2 b	-	-	-	-
SW-103	11.4 c	13.1 b	8.8 b	15.8 b	12.3 b
IS-6111	26.0 a	21.4 a	17.5 a	29.1 a	23.3 a
Mean	16.8 AB	15.0 B	11.4 C	17.9 A	

† Values within a column followed by the same small letter and mean values followed by same capital letters are not significantly different at $P<0.05$.

†† Mean of common three cultivars.

LSD for cultivar x environment interactions for Head:Veg ratio, Seed:Head ratio, dry matter, consumptive water use, $\mathrm{WUE_{DM}}$ were 0.36, 0.06, 1126, ns and 4.2, respectively ($P<0.05$).

While the dry matter production was mainly influenced by cultivar, dry matter partitioning into reproductive parts was dependent on both environment and cultivar (Table 3.4). Significant influence of environment and cultivar x environment interaction on the dry matter fraction in reproductive parts (Head:Veg Ratio) and in seed (Seed:Head Ratio) indicated that the biomass distribution, rather than the dry matter production, was responsible for the environment or cultivar x environment interaction. Reducing the plant height did not increase the Head:Veg ratio of all dwarf sunflower cultivars (Table 3.4). On the contrary, dwarf cultivars had lower mean Seed:Head ratio than IS-6111. However, the highest Head:Veg ratio in Aurora, and the significant variation in mean Seed:Head ratios between dwarf cultivars, indicate the effect of genetic background of the cultivar on the dry matter partitioning. The thin stem and smaller leaf reported for sunola (Beckie and Brandt, 1996; Johnston et al., 1995) was supported by the observation of the highest Head:Veg ratio in Aurora.

The consumptive water use and WUE_{DM} varied among sunflower cultivars. However, the influence of environment on water use was greater than that of cultivar. The greater available water, the greater is the amount of water sunflower uses for evapotranspiration (Connor and Sadras, 1992; d`Andria et al., 1995). Therefore, differences in availability of water were responsible for the effect of environment. Pooled over three common cultivars, consumptive water use at Winnipeg in 1994 was 72, 76 and 80% higher than at Carman in 1994, Carman in 1995 and Winnipeg in 1995, respectively ($P<0.01$). Mean consumptive water use by IS-6111 was 9 and 13% higher than Aurora and SW-103, respectively. The longer growth duration of IS-6111 might be partly responsible for the extra water used by IS-

6111 (Schneiter 1992). Contrary to water use trends, the WUE_{DM} was more dependent on cultivar than on environment. For example, mean WUE_{DM} for IS-6111 was 150 and 89% more than Aurora and SW-103, respectively. Sadras et al., (1991b) reported similar, higher WUE_{DM} for the standard height sunflower cultivar compared to the semidwarf sunflower cultivars under Australian conditions. Thus, the standard height sunflower was more efficient in using limited water for dry matter production compared to dwarf cultivars.

3.3.3 Agronomy Trial

The most important benefit expected from dwarf sunflower cultivars is the ease of management. Solid seeding and higher population densities enable managing dwarf sunflower cultivars with conventional small grain equipment. Therefore, comparing agronomic performance of the different height sunflower under their optimum row spacing and population density has practical significance. The agronomy trial is similar to a crop adaptation trial involving more than one crop. However, differences in management practices have significant influence on the performance of different height sunflower cultivars (Feoli et al., 1993; Schneiter, 1992; Zaffaroni and Schneiter, 1989). Therefore, the results of agronomy trial should be interpreted for broader comparison of standard height and dwarf sunflower crops.

The comparison of development stages revealed that the dwarf cultivars developed more quickly than the standard height cultivars (Table 3.5). Development stages of the dwarf cultivars, with the exception of SW-101, were 10 to 15 days more advanced than the standard height cultivars. Early maturity of dwarf sunflower cultivars has also been reported (Table 3.1; Dedio, 1993; Schneiter, 1992). Variations in the developmental stages among cultivars

Table 3.5. Seasonal development of divergent sunflower cultivars grown in agronomy trials in the field.

Cultivar/Location	Days After Seeding				
Winnipeg 1994	37	50	68	77	111
Aurora	$V_{16}R_{1.7}$†	$V_{19}R_{3.3}$	$V_{19}R_{6.9}$	$V_{19}R_{7.8}$	$V_{19}R_{9.0}$
Sierra	$V_{17}R_{1.4}$	$V_{20}R_{2.9}$	$V_{20}R_{6.1}$	$V_{20}R_{7.3}$	$V_{20}R_{9.0}$
SW-101	$V_{18}R_{1.2}$	$V_{23}R_{2.6}$	$V_{23}R_{5.6}$	$V_{23}R_{6.6}$	$V_{23}R_{8.5}$
SW-103	$V_{15}R_{1.9}$	$V_{15}R_{3.3}$	$V_{15}R_{7.1}$	$V_{15}R_{7.8}$	$V_{15}R_{8.9}$
IS-6111	$V_{17}R_{1.0}$	$V_{22}R_{2.3}$	$V_{22}R_{5.4}$	$V_{22}R_{6.8}$	$V_{22}R_{8.7}$
SF-187	$V_{15}R_{1.0}$	$V_{21}R_{1.2}$	$V_{23}R_{3.7}$	$V_{23}R_{5.5}$	$V_{23}R_{8.3}$
Carman 1995		51	65	97	103
Aurora		$V_{21}R_{2.8}$	$V_{22}R_{5.5}$	$V_{22}R_{8.7}$	$V_{22}R_{8.9}$
Sierra		$V_{22}R_{2.6}$	$V_{22}R_{5.0}$	$V_{22}R_{8.8}$	$V_{22}R_{9.0}$
SW-101		$V_{23}R_{2.3}$	$V_{24}R_{4.3}$	$V_{24}R_{8.1}$	$V_{24}R_{8.2}$
SW-103		$V_{17}R_{2.7}$	$V_{17}R_{5.7}$	$V_{17}R_{8.5}$	$V_{17}R_{8.8}$
IS-6111		$V_{23}R_{1.9}$	$V_{24}R_{4.1}$	$V_{24}R_{7.4}$	$V_{24}R_{8.3}$
SF-187		$V_{21}R_{1.0}$	$V_{26}R_{2.9}$	$V_{26}R_{7.1}$	$V_{26}R_{7.6}$

† Growth stages are detailed in Appendix 2 (Schneiter and Miller, 1981).

of the same height class were also observed. For example, development stages of SW-101 were behind other dwarf cultivars, while those of IS-6111 were more advanced than SF-187 on most observation dates. All cultivars developed maximum number of leaves by 65 to 68 days after seeding. These observations agree with observations reported in the literature, that the leaf area in sunflower gradually increases up to anthesis due to increase in leaf number and leaf expansion, and after anthesis leaf number decreases due to leaf shedding (Conner and Sadras, 1992; Whitefield et al., 1989).

Table 3.6. Dry matter accumulation and seed yield by field grown sunflower cultivars in agronomy trials.

Cultivar	Morden 1993	Winnipeg 1993	Winnipeg 1994	Carman 1995	Mean
			Dry Matter (kg ha^{-1})		
Aurora	6278 b†	10887 a	11360 c	12821 a	10337 b
Sierra	6802 b	9936 ab	11281 c	13406 a	10356 b
SW-101	6287 b	8832 bc	10642 c	9922 b	8921 c
SW-103	5947 b	8178 c	10623 c	8161 c	8379 c
IS-6111	7053 b	7861 c	16034 a	12569 a	10879 b
SF-187	9559 a	10986 a	14298 b	13476 a	12080 a
Mean††	7033 C	9447 B	12373 A	11726 A	
			Seed Yield (kg ha^{-1})		
Aurora	1240 c	3905 a	2733 bc	3218 a	2774 ab
Sierra	1197 c	3359 b	2401 c	3007 ab	2491 c
SW-101	1401 abc	2882 bc	2950 bc	2541 bc	2444 c
SW-103	1756 ab	3253 b	3184 b	2377 c	2643 bc
IS-6111	1374 bc	2368 c	4649 a	3382 a	2943 a
SF-187	1819 a	2465 c	3270 b	2447 c	2500 c
Mean	1487 C	3038 A	3198 A	2828 B	

† Values within a column followed by the same small letter and the means followed by the same capital letter are not significantly different at $P<0.05$.

†† LSD for cultivar x environment interactions for dry matter and seed yield were 1734 and 483, respectively ($P<0.05$).

The final dry matter accumulation and seed yield varied among sunflower cultivars (Table 3.6). However, an effect of plant stature was not consistently observed. The variations in populations and row spacings might have masked the plant height effect on dry matter accumulation, which was observed in the space planted trials. Pooled over locations, the standard height hybrids were either similar or better than sunola cultivars in dry matter accumulation, while sunwheat hybrids accumulated the lowest dry matter among three height classes. Seed yield depended more on the genetic background of the cultivar than on the height class.

The high seed yields observed in the present study reflect the good growing conditions that prevailed during the study. On average, the standard height hybrid, IS-6111, produced higher seed yield than all other cultivars except Aurora. However, one of the lowest seed yields was observed with the other standard height hybrid, SF-187. Differences in weather conditions and soil characteristics resulted in a significant effect of environment on dry matter and seed yield. The cool and wet conditions of 1993 might have delayed maturity of standard height hybrids leading to poor yield formation. The severe infestation of sunflower beetles may be partly responsible for the lowest dry matter and seed yield observed in 1993 at Morden. Both changes in cultivar ranking and magnitude of differences led to the cultivar by environment interactions for dry matter and seed yield.

Seed number and seed weight are the two major yield components in sunflower. Cultivar differences in both thousand seed weight and seeds per meter square were observed (Table 3.7). However, variations in both yield components depended on genetic background of the cultivar and not on the plant height. Similar to our observations, Sadras et al. (1993a) reported lack of relationship between seed number and plant stature in semidwarf and standard height sunflower cultivars, while, seed number was dependent on genetic background in wheat (Ehdiae and Waines, 1996). Sunola cultivars, which had the highest number of seeds per square meter, recorded one of the lowest thousand seed weights. In contrast, SW-103 and IS-6111, which had the lowest number of seeds per square meter, had

Table 3.7. Thousand seed weight, kernel number and harvest index of different height classes of sunflower in agronomy trials.

Cultivar	Morden 1993	Winnipeg 1993	Winnipeg 1994	Carman 1995	Mean
			Thousand Seed Weight (g)		
Aurora	39.7 b†	48.7 c	43.2 d	58.4 bc	47.5 b
Sierra	34.4 b	46.2 cd	38.4 e	52.1 cd	42.8 d
SW-101	38.4 b	47.8 c	48.3 c	50.8 d	46.3 bc
SW-103	50.7 a	60.8 a	66.5 a	61.5 ab	59.9 a
IS-6111	51.0 a	56.5 b	62.0 b	66.9 a	59.1 a
SF-187	39.9 b	43.2 d	45.6 cd	48.7 d	44.4 cd
Mean††	42.4 C	50.5 B	50.7 B	56.4 A	
			Kernel Number (m^{-2})		
Aurora	3494 bc	8037 a	6317 bc	5578 a	6014a
Sierra	3643 b	7302 a	6261 bc	5841 a	5903a
SW-101	3655 b	6016 b	6052 c	5005 a	5182bc
SW-103	3455 bc	5342 b	4788 d	3898 b	4371d
IS-6111	2684 c	4190 c	7504 a	5054 a	4858cd
SF-187	4544 a	5708 b	7137 ab	5037 a	5606ab
Mean	3580 C	6099A	6343 A	5069 B	
			Harvest Index		
Aurora	0.20 bc	0.36 b	0.24 c	0.25 b	0.27 b
Sierra	0.18 c	0.34 bc	0.21 d	0.23 c	0.24 c
SW-101	0.23 b	0.33 cd	0.28 b	0.26 b	0.27 b
SW-103	0.31 a	0.40 a	0.30 a	0.29 a	0.32 a
IS-6111	0.19 bc	0.30 d	0.29 ab	0.27 b	0.27 b
SF-187	0.19 bc	0.22 e	0.23 cd	0.18 d	0.21 d
Mean	0.21 D	0.32 A	0.26 B	0.25 C	

† Values within a column followed by the same small letter and mean values followed by the same capital letter are not significantly different at $P<0.05$.

†† LSD for cultivar x environment interactions for thousand seed weight, kernel number per square meter and harvest index were 5.5, 957 and 0.03, respectively ($P<0.05$).

the heaviest seed. Thus, the results support the presence of a complex compensatory mechanism between seed number and seed weight in sunflower (Connor and Hall, 1997).

The success of increasing seed yield by reducing plant height in cereals was achieved by increasing the harvest index (Entz and Fowler, 1990b; Ehdiae and Waines, 1996; Rebetzke and Richards, 2000). Similar results were expected in sunflower (Connor, 1992). However, the results of the present study did not indicate any plant stature effect on the harvest index, although cultivar differences were observed (Table 3.7). Harvest index of dwarf cultivars were either higher, similar or lower than those of standard height cultivars. Other tests with standard height and semidwarf sunflower cultivars have reported no difference in harvest index (Schneiter, 1992; Zaffaroni and Schneiter, 1991). SW-103 had significantly higher harvest index than IS-6111 in three of four trials, indicating the superior conversion of dry matter to grain by one of the dwarf hybrids. These results suggest that it is possible to improve harvest index in dwarf sunflower. Harvest index is the summary of relative allocation of growth to the production of yield during the entire growing season. Therefore, variations in growing seasons were evident from the significant environment and environment by cultivar effects on the harvest index.

Since water is important for crop productivity, consumptive water use and water use efficiencies should account for much of the cultivar differences in dry matter and seed yield. Cultivar differences for consumptive water use, WUE_{DM} and WUE_{Seed} were significant in our study (Table 3.8). Pooled over two locations, standard height hybrids used up to 93 mm more water than dwarf cultivars. Genetic variations for water use were also observed within standard height and dwarf cultivars. Mean water use by SW-101 and SF-187 were significantly higher than SW-103 and IS-6111, respectively. Water use differences were not reflected in the WUE_{DM} and WUE_{Seed}. Majid and Schneiter (1988) reported WUE_{Seed} values

Table 3.8. Water use efficiency for dry matter production (WUE_{DM}) and seed yield (WUE_{Seed}) of different height sunflower cultivars in agronomy trials.

Cultivar	Winnipeg 1994	Carman 1995	Mean
	Consumptive Water Use (mm)		
Aurora	428.7 bc†	271.9 c	350.3 d
Sierra	418.6 c	295.6 c	348.3 d
SW-101	429.1 bc	339.6 b	384.3 c
SW-103	418.6 c	299.8 c	350.7 d
IS-6111	437.1 b	402.3 a	419.7 b
SF-187	476.4 a	406.7 a	441.5 a
Mean††	436.2 A	336.0 B	
	WUE_{DM} (kg $ha^{-1}mm^{-1}$)		
Aurora	26.6 b	47.4 a	37.0 a
Sierra	26.2 b	45.2 a	37.1 a
SW-101	24.9 b	29.4 b	27.1 c
SW-103	25.8 b	27.3 b	26.6 c
IS-6111	36.7 a	31.3 b	34.0 ab
SF-187	30.0 b	33.4 b	31.7 b
Mean	28.6 B	35.6 A	
	WUE_{Seed} (kg $ha^{-1}mm^{-1}$)		
Aurora	6.4 bc	11.9 a	9.1 a
Sierra	5.4 c	10.1 b	8.1 b
SW-101	6.9 bc	7.5 c	7.2 bc
SW-103	7.7 b	7.9 c	7.8 b
IS-6111	10.6 a	8.4 c	9.5 a
SF-187	6.9 bc	6.1 d	6.5 c
Mean	7.4 B	8.7 A	

† Values within a column followed by the same small letter and mean values followed by the same capital letter are not significantly different at $P<0.05$.

†† LSD for cultivar x environment interactions for consumptive water use, water use efficiencies for dry matter and seed formation were 27.0, 5.7 and 1.4, respectively ($P<0.05$).

similar to our results among semidwarf and standard height sunflower cultivars, and they also failed to observe a plant stature effect. Differences in weather conditions at both locations and variations in responses of different cultivars to environmental conditions lead to the significant environment and environment by cultivar interactions for water use, WUE_{DM} and WUE_{Seed}. The variations in development stages of different cultivars might have contributed to environment by cultivar interaction.

3.4 DISCUSSION

3.4.1 Space Planted Trial

In the present study, dwarfing genes reduced plant height of all short stature cultivars by about 38% compared to standard height cultivars ($P<0.001$) (Table 3.3). However, variations among dwarf cultivars for plant height signify the role of the genetic background of the cultivar, source and/or level of expression of dwarfing genes in regulating plant height (Blum et al., 1997b; Ehdaie and Waines, 1996; Morgan et al., 1990). This indicates that a range of genetic material differing in plant height has been used in the present study.

In the present investigation, reduced plant height of sunflower cultivars was accompanied by a substantial reduction in dry matter production. Similar differences in dry matter production by container grown sunflower plants of different height cultivars have been reported (Sadras et al., 1993a). In cereals, dwarfing genes usually do not result in a reduced dry matter production (Bush and Evans, 1980). Sunflower plants in the space planted trials had abundant water and nutrient supply, and radiation levels were near saturation. Therefore, the sunflower cultivars should have expressed their full genetic potential in these trials. However, the dry matter production by dwarf cultivars was less than half of IS-6111, indicating a large variation in the genetic potential between standard height and dwarf sunflower cultivars. IS-6111 had higher water use and WUE_{DM} than dwarf cultivars. In a crop like sunflower, one role of a longer stem is to expose leaf area to sunlight. Therefore, standard height cultivars are reported to have less leaf overlap and intercept more radiation than dwarf cultivars (Sadras et al., 1991a). Crop growth duration also has a significant influence on dry matter accumulation in sunflower (Connor and Hall, 1997). Therefore, the differences observed in dry matter accumulation might have resulted from differences in water use and water use efficiency, radiation interception and growth duration of cultivars. Consistent differences in all environments (i.e., standard height cultivars consistently had greater productivity) suggest that the genetic influence of dwarfing genes on the dry matter production was stronger than the environmental effect.

The major yield improvement in cultivated cereals is attributed to improved dry matter partitioning, which was also expected in sunflower (Connor, 1992). Accordingly, reduced plant height, due to reduced competition from the stem, was expected to increase biomass partitioning into reproductive parts (head). Larger heads have been observed in the semidwarf sunflower compared to the standard height sunflower (Zaffaroni and Schneiter, 1991). However, our results indicated both lower and higher Head:Veg ratios in dwarf sunflower cultivars compared to the standard height hybrid. This suggests that genetic variation for biomass partitioning into reproductive parts exists in cultivated sunflower.

Heavier panicle generally increases seed yield in cereals due to greater assimilate partitioning to reproductive plant parts (Miralles et al., 1997). Therefore, the heavier head or capitulum in sunflower was predicted to increase seed yield. Sadras et al., (1993a) observed higher concentration of labile carbohydrate in the semidwarf cultivar compared to the standard height cultivar, indicating greater availability of assimilate for seed filling in short cultivars. In spite of this, seed:head ratio in the present study was lower in dwarf sunflower cultivars than in the standard height cultivars. The receptacle and seed are the biological components of the head in sunflower. The receptacle, unlike the rachis in cereals, is a massive structure and utilises nearly half of the head dry matter for construction. Therefore, the assimilate conserved by reducing plant height was diverted to the receptacle in some dwarf cultivars (only observed in sunolas in the present study). However, retranslocation of assimilate from receptacle to seed generally was lower in dwarf sunflower cultivars, similar to the observation in semidwarf cultivars (Zaffaroni and Schneiter, 1991). Capitular growth is an important yield limiting factor in sunflower (Steer and Hocking, 1987). Therefore, dwarf cultivars seem to utilize the extra photosynthates for capitular growth. Thus, contrary to the prediction based on observations from cereals, the heavier heads did not increase seed dry matter in dwarf sunflower cultivars.

Results of the present study indicate that the dwarf sunflower cultivars currently available for cultivation do not have the superior productivity or efficient biomass conversion capability compared to conventional standard height cultivars. However, the presence of genetic diversity for biomass partitioning is encouraging for further breeding work. Future studies should focus on the physiological reasons and genetic variability for seed:head ratio.

3.4.2 Agronomy Trial

Inefficiencies of dwarf cultivars in resource utilization can be compensated by management practices. In sunflower, plant population and row spacing have strong effects on plant growth and yield formation (Gubbels and Dedio, 1990; Feoli et al, 1993; Schneiter, 1992). Efficiency of light interception by short stature sunflower cultivars increases with solid seeding (30 cm vs 60 or 75 cm row spacing) (Gubbels and Dedio, 1990; Zaffaroni and Schneiter, 1989). In general, plants sustain grain filling with remobilised assimilate when subjected to stress (Blum et al., 1997a). Therefore, interplant competition should improve remobilisation of photosynthates in sunflower. Thus, results of agronomy trials provided another perspective for comparing different height classes of sunflower.

Averaged across environments, dry matter and seed yield of different height sunflower cultivars depended on the genetic background and not on the plant stature alone. Row spacings and populations were different for each height class in the present study, making this study unique compared to the published literature. Recommended, but different, row spacings and population densities were used for each cultivar to permit maximum expression of their respective potential yields (Dedio, personal communication). Therefore, similar mean yield between IS-6111 and Aurora suggests that the solid seeding of Aurora might have improved seasonal radiation interception by early canopy closure, increased water (Table 3.8) and nutrient acquisition, and used limited water more efficiently (Table 3.8). In spite of this, the results support the general observation that seed yields were not related to plant height alone (Feoli et al., 1993; Gubbels and Dedio, 1990; Schneiter, 1992; Zaffaroni and Schneiter, 1991).

Dry matter production and partitioning into seed are the two major factors determining the seed yield in sunflower. However, neither the cultivar with maximum dry matter production nor the cultivar with the highest harvest index produced the highest seed yield in the present study. Plant height effects observed in space planted trials for dry matter production were masked by population differences in the agronomy trial. Similarly, harvest indices of different height sunflower cultivars did not show any trend. This contrasts what has been reported for cereals, where the major yield increase in semidwarf cultivars was achieved through increases in the harvest index (Ehdaie and Waines, 1996; Entz and Fowler, 1990b; Rebetzke and Richards, 2000). In wheat, reduced plant height reduced the competition between stem and panicle growth, which led to a greater fraction of fertile florets (Miralles, et al, 1997). In contrast, assimilate supply does not limit floret number in the unstressed semidwarf and standard height sunflower (Sadras et al., 1993a). Further, remobilisation of assimilate from the stem, which is more important for yield formation in sunflower than in cereals, was more dependent on cultivar and not on plant stature (Sadras et al., 1993a). In general, the increase in seed number in the present study was compensated by a decrease in seed weight or a decrease in seed number was compensated by increase in seed weight in sunflower. This suggests that yield formation in sunflower is more complex than for cereals, with plant stature having a smaller effect on yield formation in sunflower compared to cereals.

Yield formation was more influenced by environment and environment x cultivar interaction than by the cultivar alone (Table 3.5). This suggests that the different cultivars responded differently to environments. A similar observation was reported by Zaffaroni and Schneiter (1991). Significance for WUE_{Seed} between cultivars (Table 3.8) indicates that availability of moisture at critical growth periods might have influenced seed yield. Differences in development stage and water extraction abilities may be responsible for the different cultivar responses. This study was conducted when growing season precipitation was above or near normal. A similar study conducted under more arid or restricted water supply conditions (rainout shelter) would provide better insight into the responses of different height sunflower cultivars as suggested by Miller et al. (1998).

3.5 CONCLUSIONS

Reducing the plant height in sunflower reduced the genetic potential to accumulate dry matter and water use efficiency. The extent to which photosynthate was diverted to the head varied with cultivar and not with plant stature. However, the efficiency of using assimilate present in the head for seed production was lower in the dwarf cultivars compared to standard height cultivars in this study. The genetic background of the cultivar and source of dwarfing genes contributed to the variation in performance among dwarf cultivars.

Management aspects like optimum plant population masked the stature effect on dry matter production, seed yield and water use efficiency. Seed yield was poorly correlated with harvest index or seeds per square meter. The yield formation depended on both efficient biomass production and distribution, which was again not related to plant stature. Thus, the effect of dwarfing genes in sunflower was substantially different from the observed effects in cereals. Dwarf sunflower cultivars tested in this study did not appear to have assimilate partitioning advantage that would provide a yield advantage over standard height cultivars. However, shorter stature cultivars do have agronomic advantages like ease of management, rotational benefits and less crop lodging.

4.0 Root System And Water Use Patterns of Different Height Sunflower Cultivars

ABSTRACT

Recently developed dwarf sunflower (*Helianthus annuus* L.) cultivars have been accepted for cultivation in the Canadian prairie due to management benefits. A variety of short stature cultivars from different breeding programs, exhibiting different plant architecture, are available for cultivation in the Canadian prairie. However, the effects of reduced plant stature on root systems and water extraction characteristics are not known. Therefore, field and greenhouse trials were conducted in western Canada during 1994 to 96 to compare root system characteristics and water extraction patterns of Sunwheat-103 (SW-103), a dwarf hybrid, and AC-Aurora (Aurora), an open pollinated dwarf cultivar, with IS-6111, a standard height hybrid.

Reducing plant height reduced rooting depth, root length density and root distribution in SW-103 compared to IS-6111, while there was no difference between IS-6111 and Aurora. This indicated that the genetic background of the cultivar modified the effects of dwarfing genes on root parameters. The soil water extraction front velocities, indirect measure of rate of root penetration, of sunflower cultivars were influenced by accumulated heat units, suggesting a strong temperature effect on the rooting characteristics. IS-6111 and Aurora had significantly higher extraction front velocities compared to SW-103. The standard height hybrid depleted significantly more water than the dwarf cultivars, especially on lighter textured soils. Although the role of growth duration of sunflower cultivars could not be ascertained in this study, the differences in soil moisture depletion are significant for commercial sunflower production. Thus, evaluation of presently available dwarf cultivars

indicated the loss of soil moisture extraction ability with the adoption of dwarf sunflower cultivars under Canadian Prairie conditions.

4.1 Introduction

The increasing demand for food world wide, especially in water limited regions, means that rainfall use efficiency should be a high priority in crop production. In water limited areas, the efficiency of water use can be increased in two ways, either by increasing water recovery efficiency or by increasing water use efficiency (Pierce and Rice, 1988). The purpose of this research is to study the soil water use (i.e., water recovery efficiency) differences among sunflower (*Helianthus annuus* L.) cultivars grown in western Canada.

Most of the world crop production is rainfed and a suboptimal root system of crop plants restricts the use of limited soil resources (O' Toole and Bland, 1987). Literature on the intra-specific variations in root system of crop plants is limited (O' Toole and Bland, 1987). Boyer (1996) showed that rice (*Oryza sativa* L.) and soybean (*Glycine max* L. Merr) cultivars adapted to a drier growing conditions are reported to be more drought tolerant than cultivars from humid regions. Similarly, Fereres et al. (1986) observed that sunflower cultivars adapted to a more arid climate were less sensitive to water stress than the cultivars developed for a humid climate. Genotypic variation in rooting depth has been observed in sunflower and greater rooting depth is usually associated with longer growth duration (Fereres et al., 1986; Schneiter, 1992). Therefore, it is desirable to compare the rooting habits of phenotypically diverse sunflower cultivars.

Sunflower is a drought tolerant crop with a deep explorative root system (Connor and Sadras, 1992). The superior performance of sunflower under dryland conditions is attributed to its ability to extract a significant proportion of water from the deeper soil layers (Bremner et al., 1986; Cox and Jolliff, 1986; Hattendorf et al., 1988). Deep rooting has been beneficial in other crops as well. For example, in wheat (*Triticum aestivum* L.) and sorghum (*Sorghum bicolor* L.Moench), deep rooted cultivars have shown a 20 to 50% yield advantage over shallow rooted cultivars in low rainfall years (Turner and Passioura, 1986). Many studies have reported rooting depth in sunflower beyond 2.0 m, which is deeper than many annual crops like corn (*Zea mays* L.), sorghum, soybean and wheat (Bremner et al., 1986; Dardanelli et al., 1997). The deeper root system in sunflower is coupled with low hydraulic resistance for extraction of more water from the soil profile (Passioura, 1986).

On the Canadian Prairie, precipitation falls behind potential evapotranspiration throughout the growing season (Ash et al., 1992; De Jong and Cameron, 1980) and the crop depends on stored soil moisture for its water requirements. Even in the driest part of Canada, water from deeper layers is left unused (Hurd, 1974). Therefore, a crop like the standard height sunflower, capable of extracting water from deeper layers will have a distinctive advantage over shallow water extracting annual crops like canola and wheat. However, adoption of the standard height sunflower in the Canadian Prairie is limited by the short growing season.

Recent dwarf sunflower cultivars are gaining popularity with farmers due to ease of cultivation and the reduced growth period (Johnston et al., 1995). The development of dwarf sunflower follows that in cereals. In cereals, the influence of dwarfing genes on rooting characters have been observed (Ehdaie and Waines, 1996; Entz et al., 1992; Grant et al., 1991). In wheat (*Triticum aestivum* L.), the changes are host specific (Blum and Sullivan, 1997; Ehdaie and Waines, 1996). Information on root systems of different stature sunflower cultivars is lacking. A limited number of studies conducted on water extraction in relation to sunflower plant height have produced contradictory results (Sadras et al., 1991a; Schneiter, 1992; Zaffaroni and Schneiter, 1989). Therefore, information on the root system characteristics and water use pattern of dwarf sunflower cultivars in comparison to standard height cultivars, especially under western Canadian conditions, is urgently needed to evaluate their suitability for the Prairie cropping system.

This study was conducted to study the effect of reducing plant height on the rooting characters like rooting depth, root length density and root hydraulic conductivity in sunflower. Further, the role of plant stature on water use and water use pattern was evaluated.

4.2 Materials and Methods

4.2.1 Plant Material and Growing Conditions

Field experiments were conducted in 1994 and 1995 at two locations in Manitoba, representing different agroclimatic conditions and soil types. The Winnipeg (49.8°N, 97.2°W) experiments were conducted at the Department of Plant Science Field Research Facility. The soil at Winnipeg was a clay (Riverdale series, Entisol, Cumulic Regosol) with gradual release of water and slow development of stress. The Carman (49.5°N, 98.0°W) trials were conducted at the Carman Research Station and the soil was a sandy clay loam (Denham and Eigenhof series, Udic Boroll, Orthic Black Chernozem) with characteristic quick release of water and rapid development of stress. The typical relative water deficit for a long duration crop like corn at Carman averages 50 mm more than at Winnipeg (Ash et al., 1992). Data from two field trials conducted at Winnipeg and Morden during 1993 were not used for soil-plant-water relation studies due to excessive rainfall.

In the present study, sunflower cultivars from dwarf open pollinated, dwarf hybrid and standard height hybrid classes were used. Sunola cultivars (AC-Aurora and AC-Sierra; Western Grain Seed Corporation, Canada; referred to as Aurora and Sierra) belong to dwarf open pollinated class and they were developed on the Canadian Prairie. Sunola cultivars are characterised by thin stem, small leaves and long internode (Beckie and Brandt, 1996). The second class of dwarf hybrid was represented by two sunwheat hybrids, Sunwheat-101 and Sunwheat-103 (SeedTec International Inc, California, USA; referred to as SW-101 and SW-103). Two standard height hybrids, IS-6111 (Inter State Hybrid Seed Company, Fargo, North Dakota) and SF-187 (Cargill Inc. USA) were used as checks (Table 3.1).

Two types of field experiments, space planted trials and agronomy trials, were used to assess the performance of sunflower cultivars. All trials were fertilized based on soil test results (Norwest lab, Winnipeg) (Appendix 2). The preceding crop at each location was a cereal grain (wheat or barley). Minimum tillage (one or two passes using a cultivator) before seeding was used except for space planted trial at Carman in 1994, where neither fall nor spring tillage was used. Wherever necessary, pre-seeding glyphosate was used to control weeds, followed with hand hoeing and hand weeding to keep the plots weed free. Sunflower beetles were controlled by periodic spraying of systemic insecticides.

Agronomy Trials. In agronomy trials, commercial crops of two cultivars from each of the three height classes were assessed for within and between height class variations. Plant populations were 55 000, 100 000 and 170 000 per ha for standard height hybrids, dwarf hybrids and dwarf open pollinated cultivars, respectively. Row spacings were 0.75 m for standard height hybrids and 0.30 m for dwarf cultivars. These are the agronomic practices recommended for the respective class of cultivars on the Canadian Prairie (Dr. W. Dedio, AAFC, Morden Research Centre, personal communication). Plots were 8 m long and either 3.6 (for dwarf cultivars) or 5.4 m (for standard height hybrids) wide. Experimental plots were seeded using a Fabro small plot seeder (Swift Manufacturing Co., Swift Current, SK). The experiments were over seeded and hand thinned to the recommended plant population at the V_4 to V_6 stage (Appendix 2). Agronomy trials were conducted at Winnipeg in 1994 and at Carman in 1995 and were seeded on May 30th and May 13th, respectively (Appendix 3).

Space Planted Trials. In space planted trials, individual plants of different height cultivars were grown with minimal interplant competition. These trials were used to study genetic differences among different height classes under the same population density, without the confounding effects of plant populations and row spacings. The space planted trials were conducted during 1994 and 1995 at Carman and Winnipeg, respectively. In these trials, cultivars representing three sunflower height classes (Aurora, SW-103 and IS-6111) were hand seeded in 5 m X 8 m plots at 1 m X 1 m spacing between May 23 and June 2 (Appendix 3). The experiments were over seeded with 3-4 seeds at each spot and at the V_2 to V_4 stage extra seedlings were removed. The over seeding ensured 38 to 40 (95-100% of desired) plants per plot. In 1994, additional dwarf cultivars, SW-101 and Sierra, were included in the trial to compare the variations within the dwarf height classes. An additional space planted study was conducted in 1994 at Carman to study the root systems of three height classes of sunflower under field conditions (Appendix 3).

Greenhouse Trials. A greenhouse trial was used to study the root hydraulic conductance of different height sunflower cultivars. The trial was conducted in 1996 in small 2.0 L pots (0.10 m in diameter and 0.25 m height) filled with 2.4 kg of sieved Almisippi fine sandy loam soil (Appendix 3). One seedling was grown in each pot and the pots were watered from the surface. The plants were maintained for 30 days without moisture stress. At that stage, soil from the pot was carefully washed and the plants were transferred to a continuous flow hydroponic unit (PPFD 400-600 μmol/m^2/sec, temperature 24 °C, daylight 18hrs) (Vessey et al., 1988). Sand culture solution providing all major and minor nutrients was used in the chamber and plants were left in the hydroponics for 48 hours to habituate to the new environment. After 48 hours, the root system was cut from the plant, placed into the same sand culture solution in a Scholander type pressure bomb (PMS Instruments, Corvallis, Oregon) with the root stump protruding out of the lid. The root system was gradually pressurised with N_2 gas. The sap coming out of the root stump at each pressure level (0.1 to 0.8 MPa range) was collected into a pipette fitted to the root stump with a Tygon rubber tube for 1 min and measured. The hydraulic conductance was calculated as the slope of linear relation between sap flux and the pressure.

4.2.2 Observations

In general, space planted trials were used to assess the water extraction and root system of cultivars representing each of the three height classes of sunflower cultivars. Agronomy trials were used to assess the inter- and intra-height class variations in root system and water use patterns.

The weather conditions in all field trials were monitored between May to September with weather stations located less than 500 m away from the research plots. Daily values of minimum and maximum air temperatures recorded from the weather stations were used to calculate sunflower growing degree-days, using a base temperature of 6.7 °C (Kandel, 1995). In 1994 the rain-gauge at the Department of Plant Science field research facility did not function properly. Therefore, rainfall data from the nearby Glenlea research station (about 15 km away from plots) was used.

The root architecture of divergent sunflower cultivars was studied in the field. The profile wall method (Bohm, 1979) was used to expose four root systems of each of Aurora, SW-103 and IS-6111 at 90 days after seeding. Two vertical trenches, 2.50 m deep and 0.15 m from the row, were dug using a back hoe. The face of the trench was trimmed with shovels and trowels to get a perfect vertical face (checked using a plumb line), 1.0 cm away from the tap root. The final 1.0 cm soil was washed using water under pressure (0.25 MPa) (Entz, 1988). A handgun with a teejet nozzle was used to wash the root system. Care was taken to wash all root systems in the same way (i.e., using the same spatial washing pattern and total washing time). The exposed root system was traced on a clear plastic sheet and the root length density was determined by using the line intercept method (Tennant, 1975). In addition to the total root length density, vertical and horizontal distribution of roots in 0.20 m increments were also determined.

The tap root is the main channel for movement of water from deep in the profile to the shoot. Therefore, the root diameters of all three height classes of sunflower were measured in 0.05 m increments between 0.05 and 0.25 m depths at 100 days after seeding in the space planted trial at Winnipeg in 1994.

Soil moisture was measured with the neutron attenuation technique. In all field trials aluminium neutron access tubes were installed in the centre of each plot to a depth of 2.10 m. In the space planted trials, the access tubes were 0.15 m from the nearest plant in the centre of the plot. In the agronomy trials, the access tube was placed in between two plants in the central portion of the middle row. The tubes were installed one week after seeding in the space planted trials and at the V_2 to V_6 crop development stage in the agronomy trials. Soil moisture contents between 0.10 and 2.10 m were measured in 0.20 m increments using a field calibrated neutron probe (Model 4330, Troxler labs, Research Triangle Park, NC). Soil moisture monitoring was initiated 10 to 20 days after seeding and repeated every 15 to 20 days (Appendix 4). Surface (0-0.10 m) soil moisture content was determined using the neutron probe in combination with a surface shield as described by Chanasyk and Naeth (1988). In the present study, the surface shield was made up of thick plastic sheets and was covered by a lead sheet (Appendix 5). Regression equations, developed separately for 0.10 to 2.10 m and the surface 0.10 m (Bullied, 1997), were used to convert probe readings into volumetric soil moisture (cm^3 cm^{-3}) content.

The net water depletion on any observation date was calculated by subtracting water content in each 0.20 m layer between 0.10 to 1.90 m from the water content at the same depth at the beginning of the season (the initial soil moisture reading). An effort to compare net water extraction from different soil depths of different height sunflower cultivars was made by using precipitation and soil moisture release characters (field capacity and wilting point). Frequent rainfall events between soil moisture readings confounded the results. Therefore, only the net water depletion was used for cultivar comparison. Similarly, it was not possible to assess the maximum extractable water for each cultivar due to lack of long dry period. The deepest 0.20 m layer showing statistical significance ($P<0.05$), as ascertained by a significant LSD between the water content during the initial reading and on the observation date, was considered the effective rooting depth. This technique was used by Entz et al. (1992) and others.The observation date on which the roots penetrated a particular layer for the first time in field studies, expressed as days after seeding, was regressed against the rooting depth to determine the extraction front velocity. Deep percolation, upward soil moisture flux and runoff were assumed to be negligible.

4.2.3 Statistical Analysis

Analysis of variance was conducted by using GLM procedure (SAS Institute Inc., Cary, NC, 1985) and a Fisher protected LSD test was used for mean comparison. The experimental design for all field trials was a randomised complete block design with four replications. Unless specifically mentioned, 5% significance was used for all statistical analysis. Soil moisture data for all field trials were analysed separately to assess the effect of cultivars and time on the water extraction at various depths. The root depth was regressed against accumulated growing degree days to obtain a relationship between rooting depth and thermal time for different height sunflower cultivars. Slopes of regression equations were tested for statistical significance using JMP software (Sall and Lehman, 1996).

4.3 Results

4.3.1 Environmental Conditions

Details of weather parameters prevailing during 1994 and 1995 are presented in Fig. 4.1 and Table 3.2. In general, 1994 growing season was cooler and received either above normal (Winnipeg) or slightly below normal (Carman) rainfall compared to 1995 season, which was warmer with intermittent dry spells. In addition, a greater portion of seasonal rainfall in 1995 was received late in the season, which, sunflower cultivars could not utilise for active growth and development.

4.3.2 Root System Analysis

Root observations were taken just after anthesis, when the root length density was reported to be at its peak in sunflower (Sadras et al., 1989). The root length density in the top 1 m^2 of soil for SW-103 and Aurora was 10.19 ± 1.87 and 14.21 ± 1.99 m m^{-2} ± SE, respectively, compared with 16.79 ± 4.48 m m^{-2} for standard height hybrid, IS-6111 (Fig. 4.2). The difference between IS-6111 and SW-103 for root length density in the top 1.00 m was significant at $P=0.10$, while no difference between IS-6111 and Aurora or between SW-103 and Aurora was observed.

The data on the vertical and the lateral spread supports the visual observation of a more spread out root system for IS-6111 (Fig. 4.2 a and b). The vertical distribution data (Fig 4.2 a) revealed that about 90 % of root length density was present in the top 0.40 m soil layers in sunflower. Similarly, Sadras et al. (1989) observed more than 90 % of root length density in the top 0.20 m soil layer in standard height sunflower cultivars in Argentina. The decrease in root length density with depth was more gradual with IS-6111 than with SW-103.

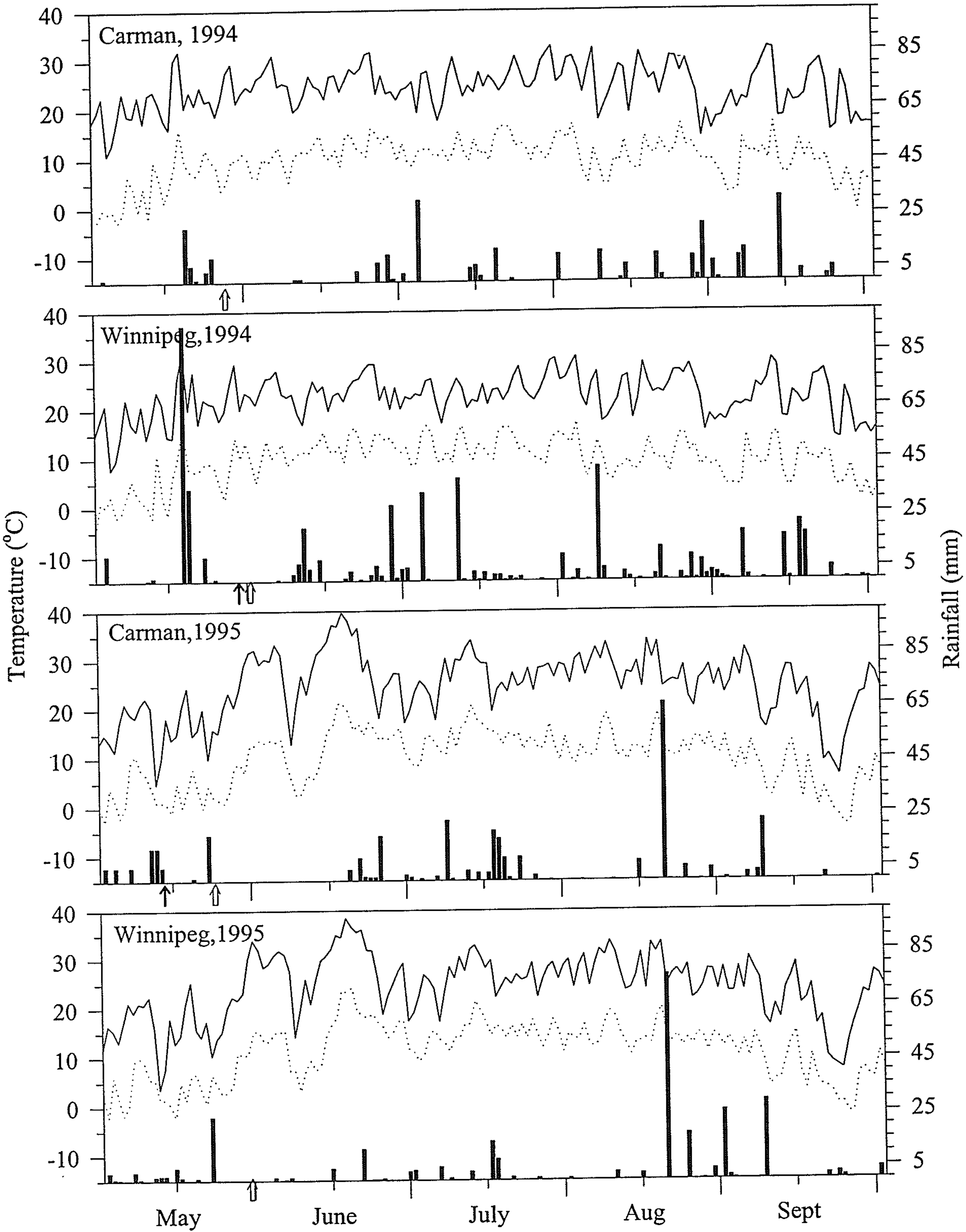

Figure 4.1. Weather parameters at Carman and Winnipeg during 1994 and 1995 growing seasons. Solid lines and perforated lines represent maximum and minimum temperature, respectively. The precipitation is represented by vertical solid bars. Seeding dates of space planted trials and agronomy trials are shown with open and solid arrows, respectively.

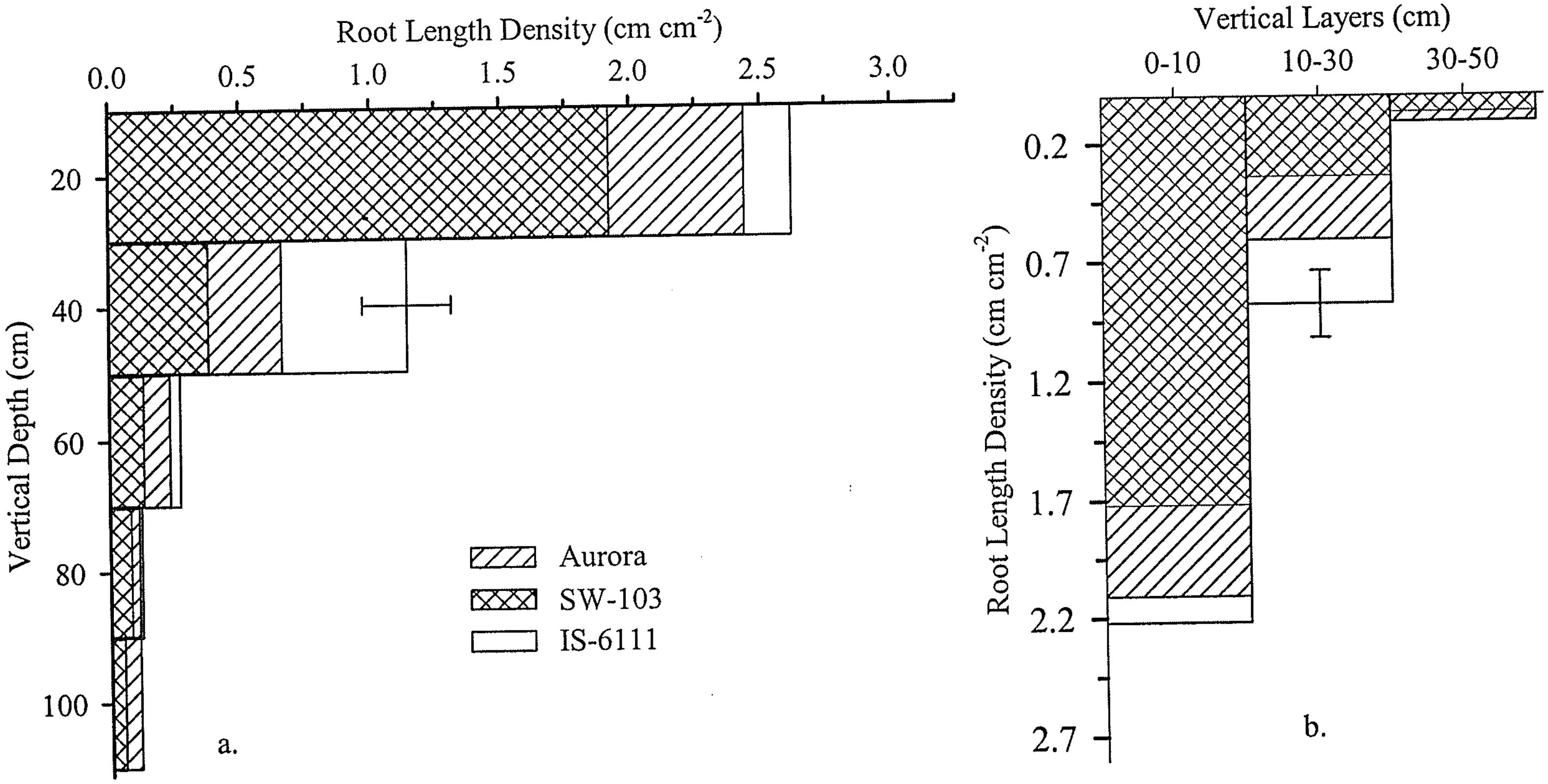

Figure 4.2. Vertical (a) and horizontal (b) distribution of root length density of space planted sunflower cultivars in the top one square meter of soil profile under field conditions at Carman in 1994. The error bars are LSD values at P=0.10. The horizontal distribution was obtained by dividing square meter sample area into five 20 cm vertical layers. The tap root was in the centre of the middle layer. Values of 10-30 and 30-50 cm are means of layers on both sides of the tap root.

The horizontal distribution data (Fig 4.2 b) indicated that most of the roots of SW-103 were concentrated in the central 0.20 m along the tap root, while roots of IS-6111 were distributed to the next 0.20 m vertical layer on both sides of the tap root. These differences in root distribution explain the better water extraction observed from the inter-row space by standard height hybrid compared to a dwarf open pollinated cultivar (Schneiter, 1992). The relationship between plant height and root length density was weak ($r^2=0.49$; $P=0.07$). The direct observation of effect of plant height on the root system of sunflower is lacking. However, similar to these results, the effects of dwarfing genes on the root system of isogenic lines in wheat were small and dependent on the genetic base (Ehdaie and Waines, 1996).

4.3.3 Tap Root Diameter and Root Hydraulic Conductance

The ability of plants to transport water from the soil to the shoot is an important characteristic in water limited environments. In the present study, both root diameter and root hydraulic conductance were tested to determine possible genotypic variations.

In sunflower, the tap root is the major channel conducting water from deep in the soil to its foliage. The diameter of the tap root is an indicator of water transportation ability of the root system (O' Toole and Bland, 1987). At 0.05 m depth under field conditions, the tap root diameters of all cultivars were similar (Fig. 4.3). However, as seen from the significant differences at lower soil depths, the tap root of dwarf cultivars tapered more rapidly than that of the standard height hybrid. Thus, IS-6111 appears to have a bigger channel to transport water.

The root hydraulic conductance is an important root trait that regulates water extraction by plants (Gallardo et al., 1996; Lopez and Nobel, 1991). Genotypic variation for

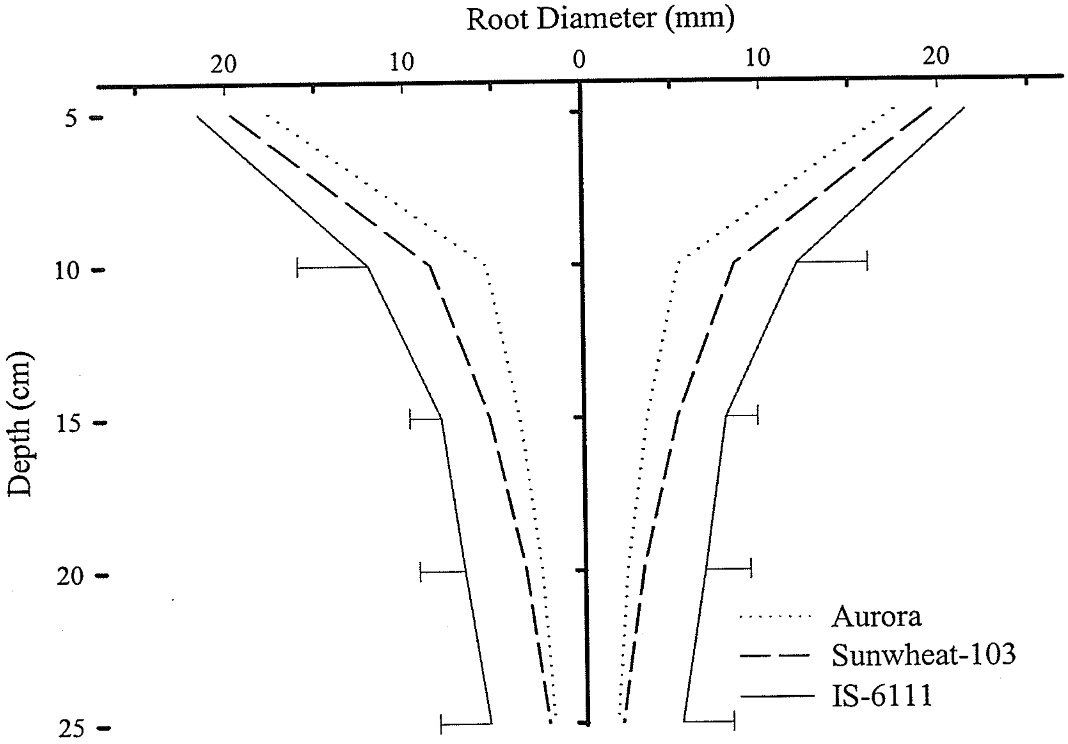

Figure 4.3. Tap root diameter of different height classes of sunflower cultivars between 5 and 25 cm depth at 100 days after seeding in space planted trial at Winnipeg in 1994. Error bars are LSD values at 0.05P.

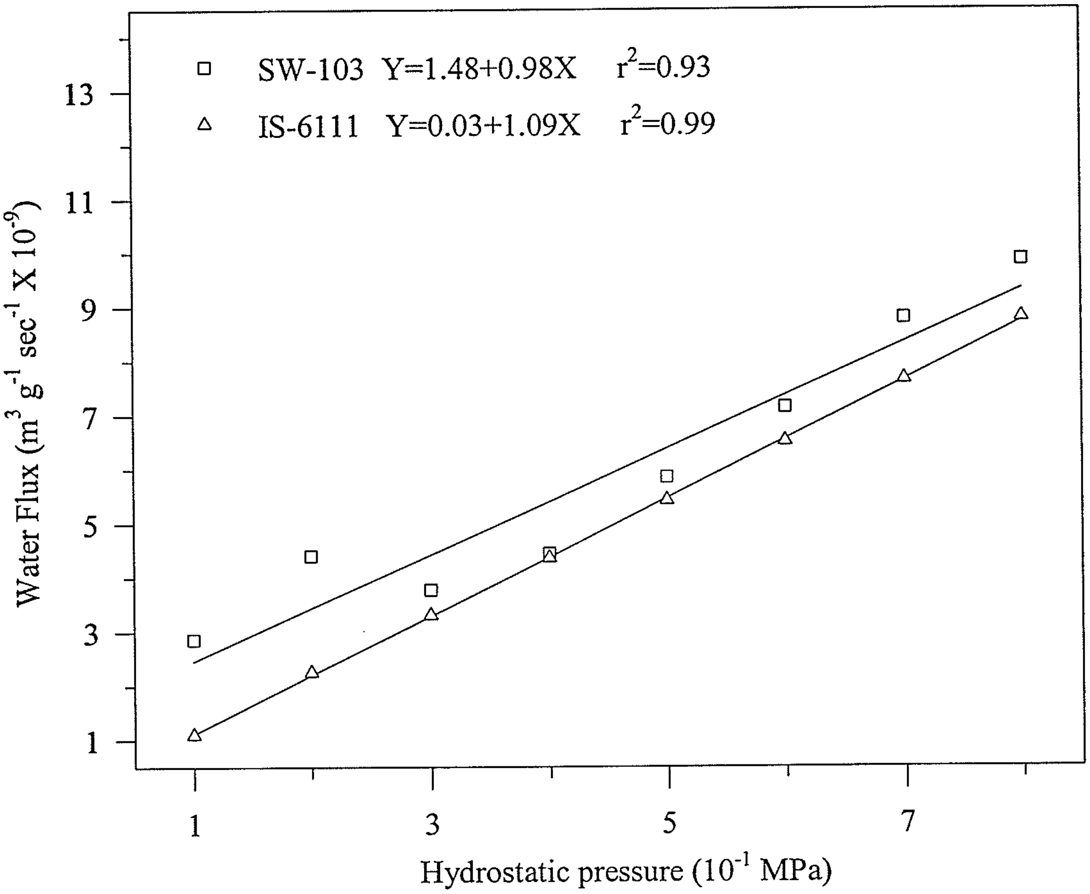

Figure 4.4. Root hydraulic conductance, slope of the relationship between root water flux and hydrostatic pressure, of different height sunflower cultivars in the 1996 greenhouse study.

root hydraulic conductance has been reported in sunflower (Hernandez and Orioli, 1985). Therefore, the root hydraulic conductances of SW-103 and IS-6111, cultivars with different root parameters, were studied in the greenhouse. Results indicated no effect of plant stature on the root hydraulic conductance (Fig. 4.4). This suggests that, based on observations in this study, the effect of reducing plant height on the root system is mainly restricted to the physical root system and not to the root activity.

4.3.4 Soil Water Extraction Pattern

4.3.4.1 Soil Water Extraction Front

Water extraction front has been used to assess rooting depth in a number of crops including sunflower. A close relation between rooting depth and water extraction front has been observed in wheat on the Canadian Prairie (Entz et al., 1992). Therefore, rooting depths in field trials were assessed by measuring extraction front.

Space Planted Trials. Among the cultivars compared, IS-6111 had the deepest extraction front (1.00 to 1.80 m), which was significantly deeper (0.20 to 0.60 m) than SW-103 (Fig. 4.5 and 4.6). A rooting depth of 1.88 m, similar to IS-6111 in the present study, has been observed by Merrill et al., (1996) by using minirhizotrons in Mandan, North Dakota. However, the extraction front of Aurora was similar to IS-6111 in three out of four trials. Genotypic variation for extraction front was observed at the beginning of flowering and it was maintained till maturity. All space planted sunflower cultivars reached their maximum rooting depth between 85 and 95 days after seeding in all environments with some exceptions. The location effect was greater on the extraction front than the effect of season. For example, a deeper extraction front was observed at Winnipeg than at Carman. Maximum

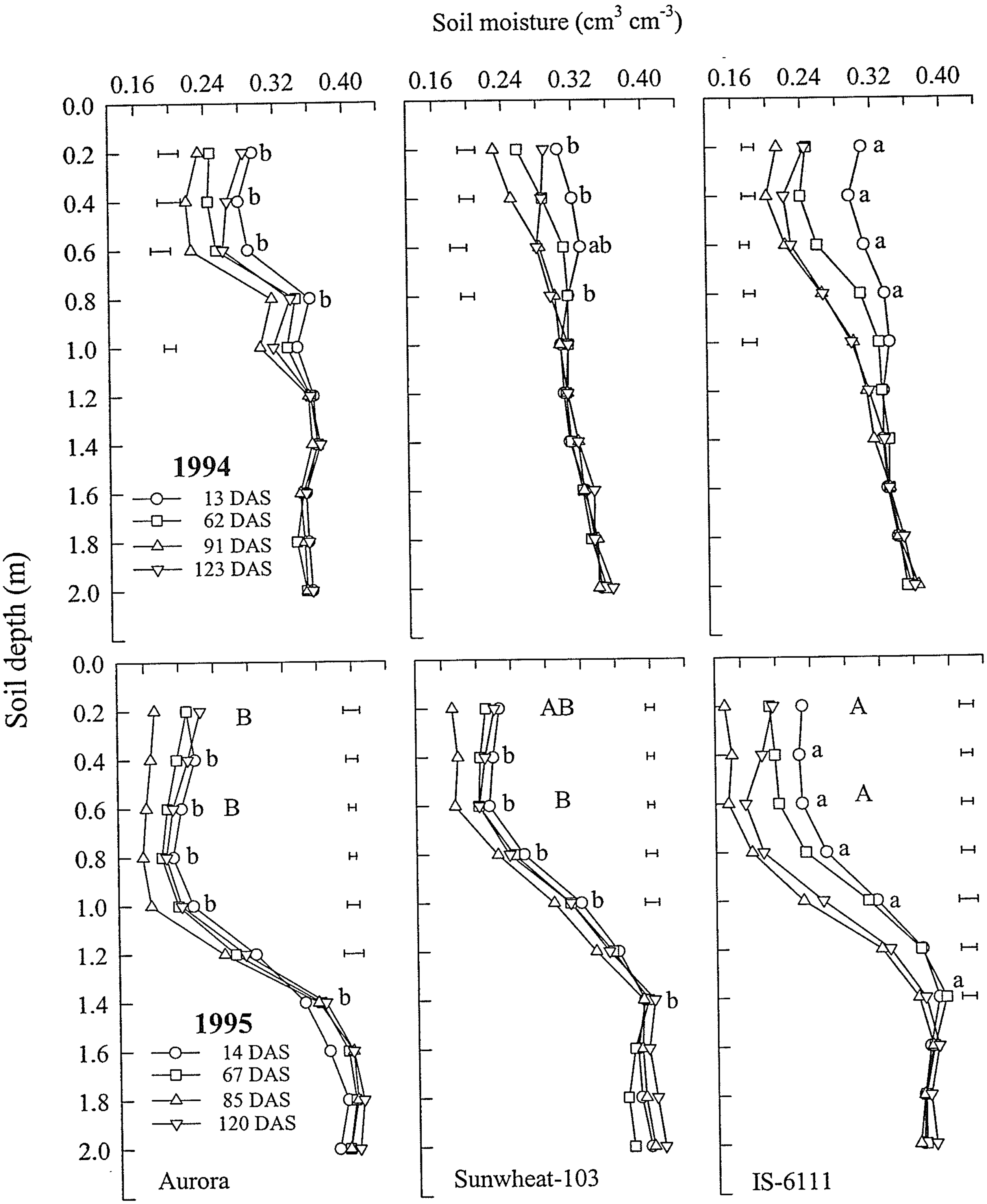

Figure 4.5. Soil profile water content of different height sunflower cultivars in space planted trials at Carman in 1994 (top) and 1995 (bottom). LSD bars (P=0.05) indicate the significance of water depletion between dates. Cultivars followed by different capital and small letters had significant differences (P=0.05) for soil water depletion between seeding to flowering and seeding to harvest at those depths, respectively.

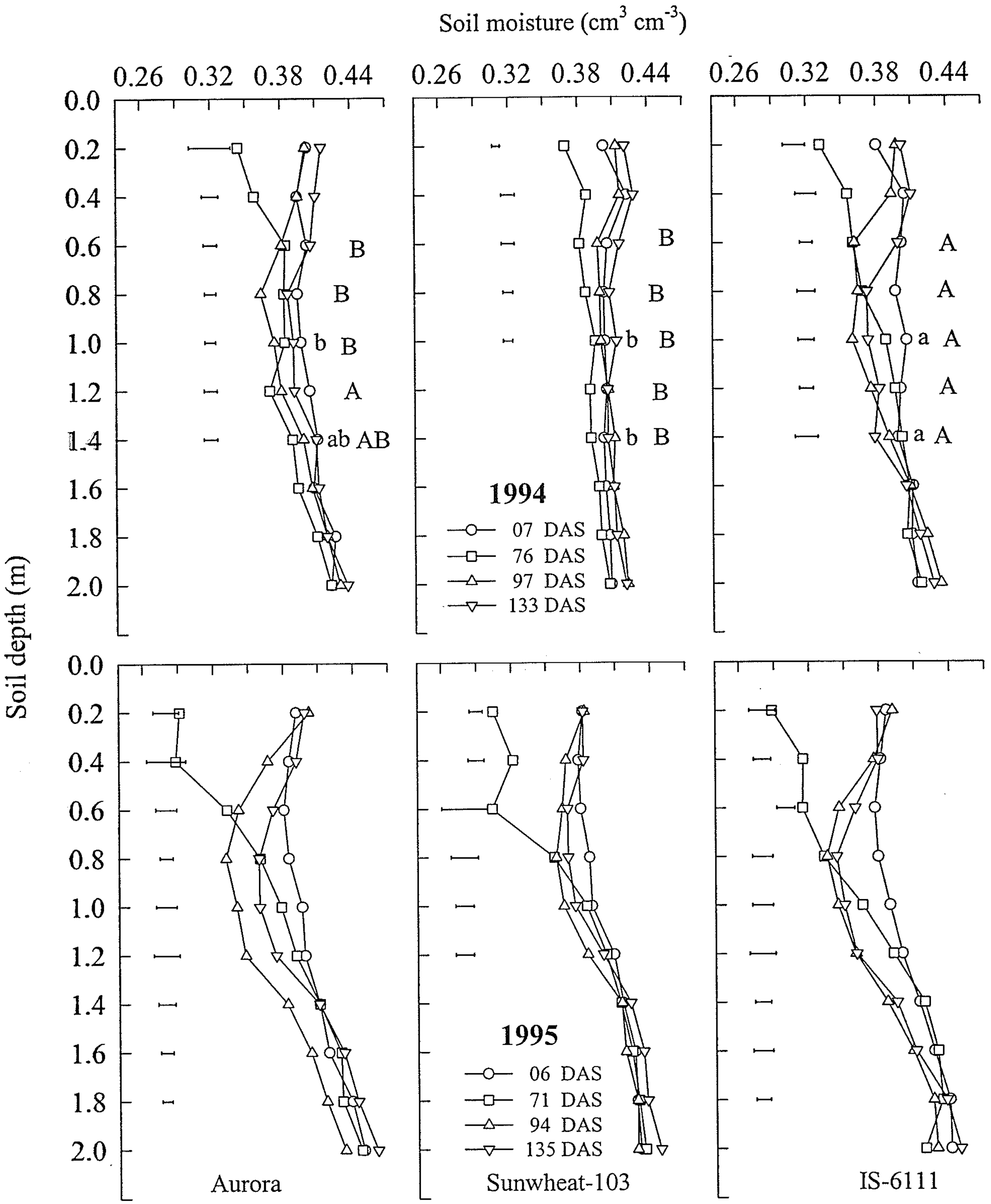

Figure 4.6. Soil profile water content of different height sunflower cultivars in space planted trials at Winnipeg in 1994 (top) and 1995 (bottom). LSD bars (P=0.05) indicate the significance of water depletion between dates. Cultivars followed by different capital and small letters had significant differences (P=0.05) for soil moisture depletion between seeding to flowering and seeding to harvest at those depths, respectively.

depth of the extraction front in sunflower is dependent on either soil or crop characteristics (Meinke et al., 1993). Lower hydraulic conductance in fine textured soil compared to coarse textured soil has been reported (Jackson et al., 2000). Therefore, sunflower extracted more water at each depth at Carman compared to Winnipeg. However at Winnipeg, to compensate for lower hydraulic conductance, sunflower rooted deeper than at Carman. In the present study, biomass production by sunflower cultivars was higher at Winnipeg compared to Carman in each year (Table 3.4). Therefore, both crop water demand and the soil textural differences which influence water release characteristics of the soil, appear responsible for the differences in the maximum depth of extraction front at two locations. Small variations for extraction front within sunolas or sunwheats were observed at Carman in 1994 (data not presented).

Agronomy Trials. As in the space planted trials, SW-103 had a shallower extraction front than IS-6111 in agronomy trials, while contrary to the space planted trials, Aurora had significantly shallower extraction front than IS-6111 (Fig. 4.7 and 4.8). The standard height hybrids had 0.20 to 0.40 m and 0.20 to 0.80 m deeper root system than sunwheat and sunola, respectively. Although additional cultivars of each height class presented smaller interclass variations, overall ranking of height classes remained the same. Thus, the results of agronomy trials imply that 0.20 to 0.80 m of the soil profile remain unexplored by using dwarf sunflower cultivars.

4.3.4.2 Extraction Front Velocity

Depth of the water extraction front increased in a linear fashion with time for all cultivars tested (Fig. 4.9). The extraction front velocity was higher in 1995 than in 1994.

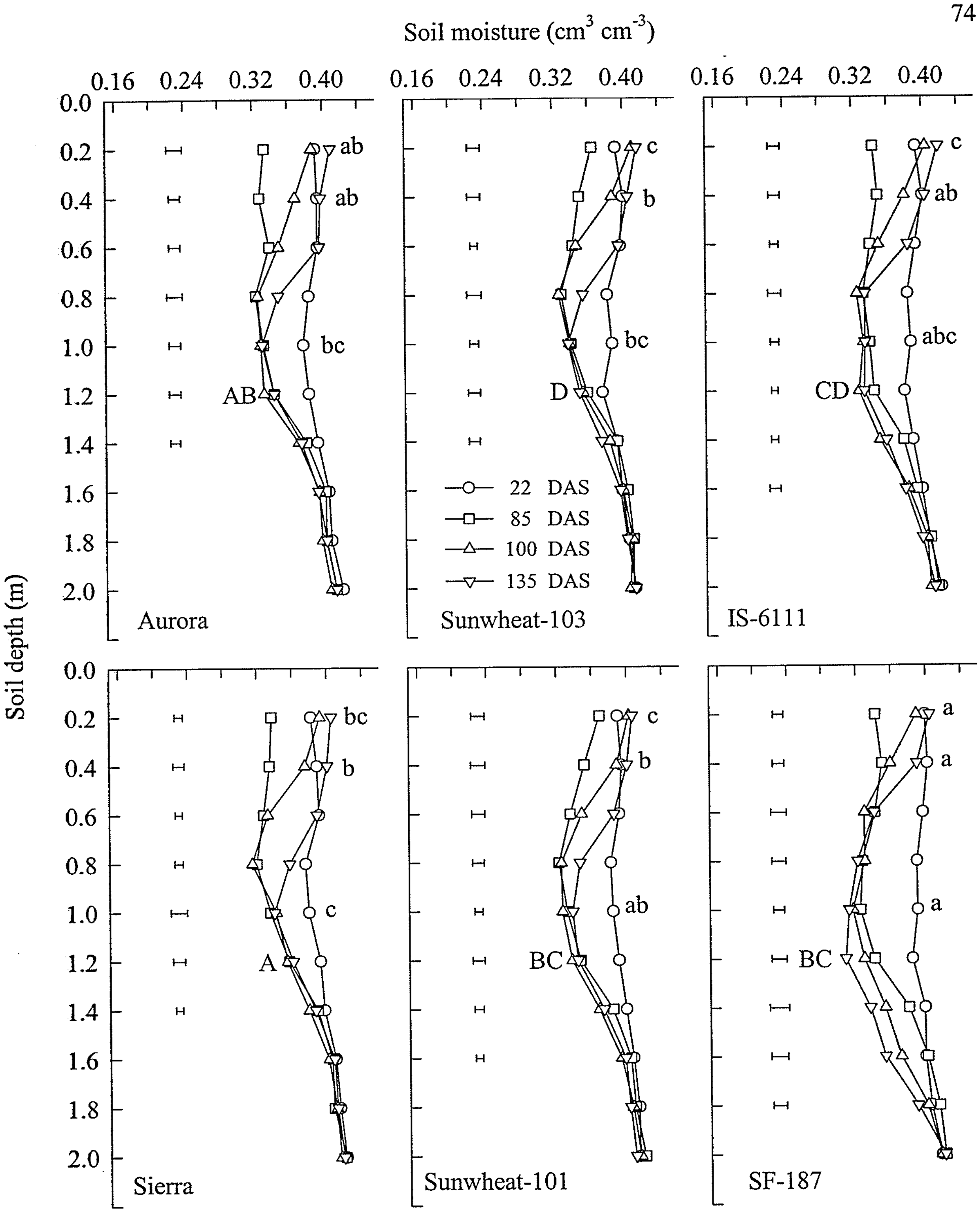

Figure 4.7. Soil profile water content of three height classes of sunflower cultivars in the agronomy trial at Winnipeg in 1994. LSD bars (P=0.05) indicate the significance of water depletion. Cultivars followed by different capital or small letters had significant differences (P=0.05) for soil moisture depletion between seeding to flowering and seeding to harvest, respectively.

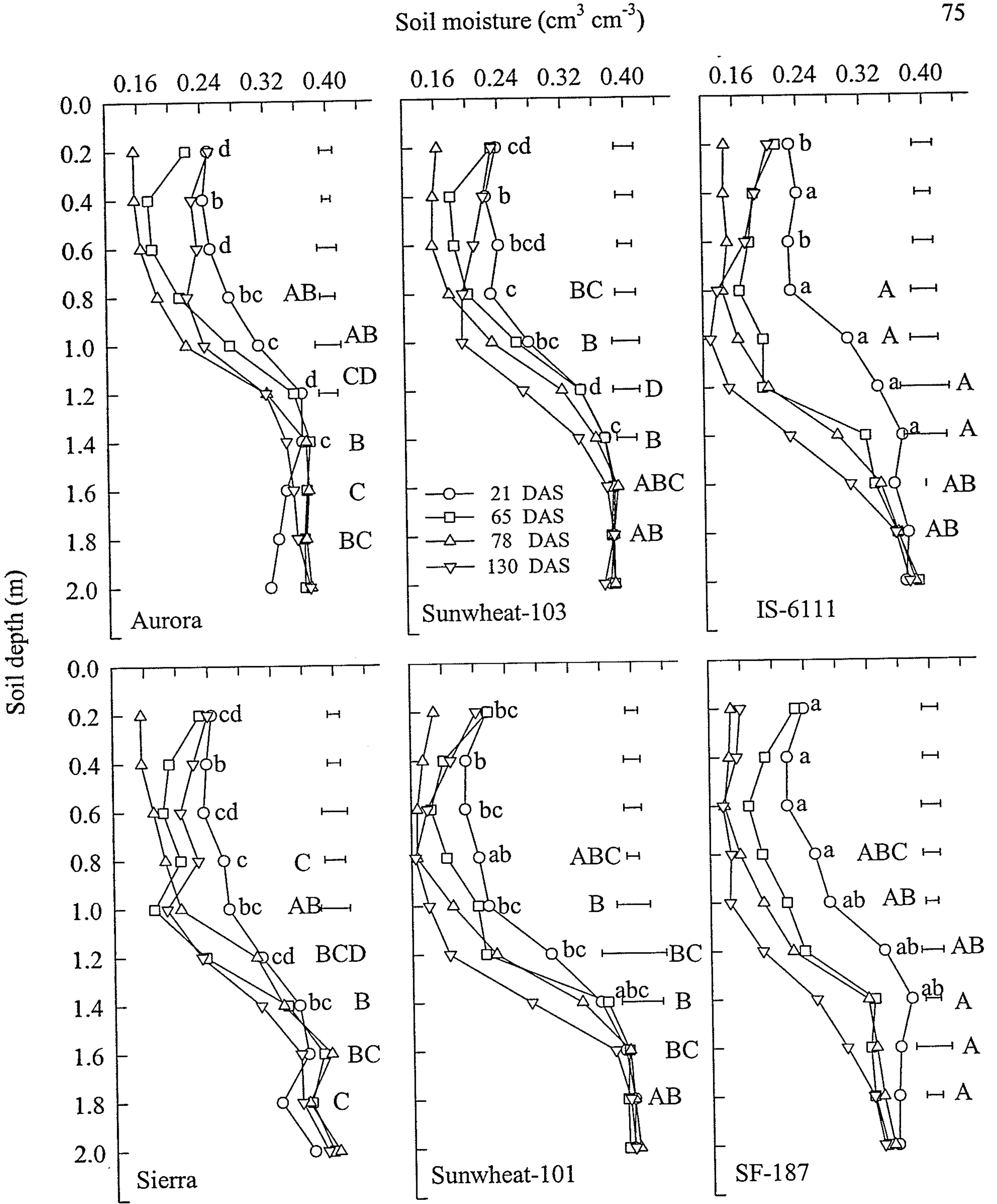

Figure 4.8. Soil profile water content of three height classes of sunflower cultivars in the agronomy trial at Carman in 1995. LSD bars (P=0.05) indicate the significance of water depletion. Cultivars followed by different capital and small letters had significant differences (P=0.05) for soil moisture depletion between seeding to flowering and seeding to harvest at those depths, respectively.

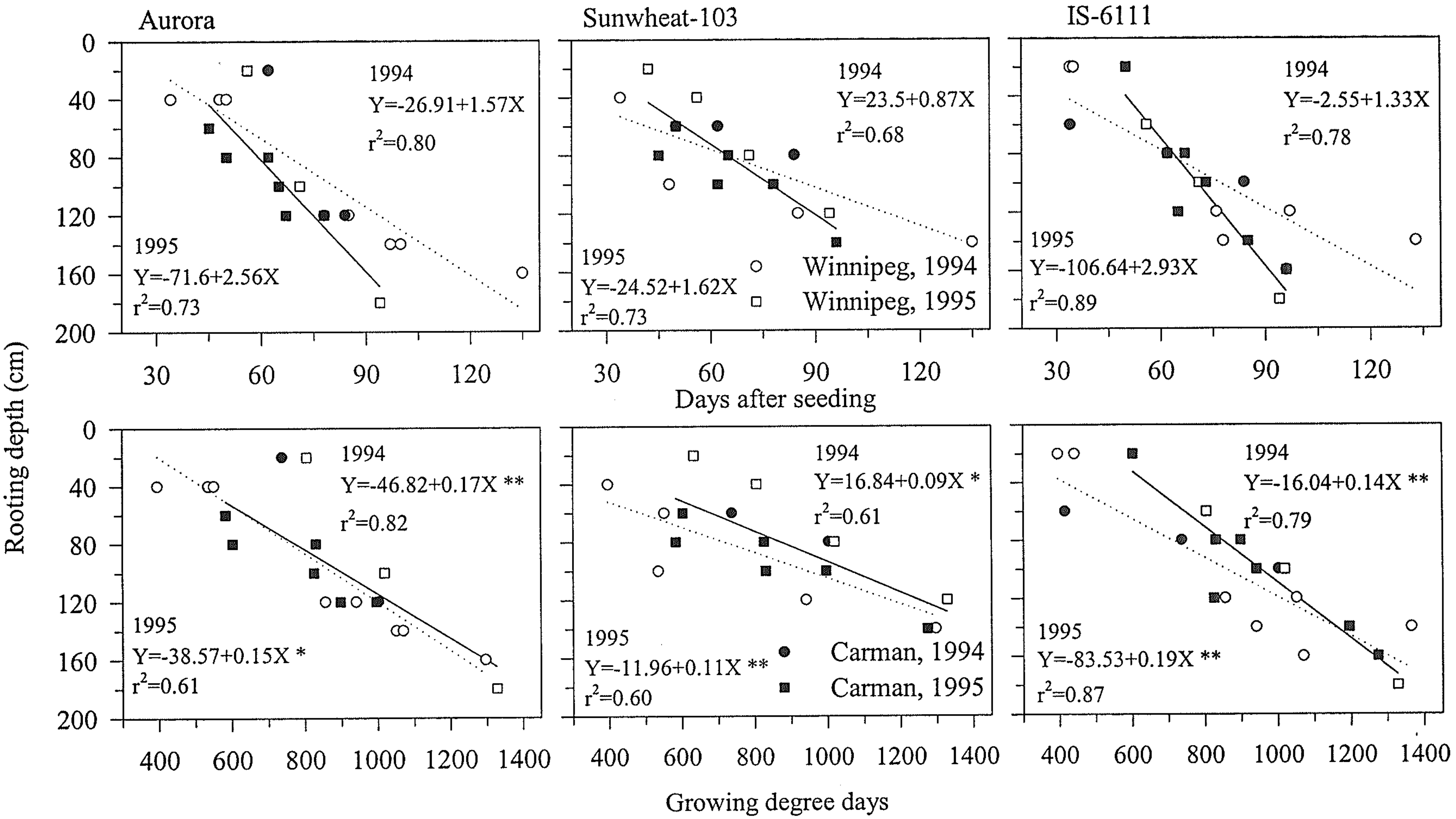

Figure 4.9. The relationship between depth of rooting front and days after seeding (top) and growing degree days (bottom) for different sunflower cultivars in space planted trials in 1994 (dotted line) and 1995 (solid line). * and ** indicate significance of the model at 0.05 and 0.01 P, respectively.

However, expressing the time in accumulated degree days (6.7 °C base temperature) narrowed differences between years significantly, indicating that thermal time more closely described extraction front than calender time.

Cultivars regulated extraction front velocities in the present trial (Fig. 4.9). The three height classes of sunflower, Aurora, SW-103 and IS-6111, pooled over two years had significantly different slopes ($P=0.04$) and intercepts ($P=0.04$). For each heat unit accumulated, the rooting depth increased by 0.14 to 0.19 cm for IS-6111, which was more than 0.09 to 0.11 cm for SW-103. However, Aurora had an extraction front velocity (0.15 to 0.17 cm) similar to IS-6111, indicating that the height was not the only factor influencing root penetration. The extraction front velocity of the standard height hybrid of 29.3 mm day^{-1} in 1995 was slightly lower than 44 mm day^{-1} observed for sunflower by Dardanelli et al. (1997), but comparable to 36 mm day^{-1} reported by Meinke et al. (1993).

4.3.4.3 Water Depletion From Different Soil Depths

At all locations, the profile was wet in the beginning of the season, and a gradual depletion of soil moisture was observed with the crop development. Rainfall during the growing season, especially at the later stages, saturated top layers and confounded water extraction observations from different depths and at different developmental stages. Therefore, soil moisture depletion, as determined by the difference in soil moisture between two observation dates, were used for cultivar comparisons.

Space Planted Trials. A better developed root system, deeper rooting depth and higher extraction front velocity of IS-6111 were reflected in more water depleted from the soil profile compared to the dwarf cultivars in general, and SW-103 in particular (Table 4.1). The

Table 4.1. Soil moisture depletion (mm) by different height sunflower cultivars before and after flowering from above and below 1.10 m soil depth in space planted trials.

Cultivar	Pre-flowering†			Post-flowering			Total
Depth(m)	0.10-1.10	1.10-1.90	0.10-1.90	0.10-1.10	1.10-1.90	0.10-1.90	10-190
Winnipeg 1994							
Aurora	27.0b††	10.6a	37.6b	-30.2a	-7.2a	-37.5a	0.0a
SW-103	22.6b	3.7a	26.4b	-32.4a	-7.3a	-39.7a	-13.3a
IS-6111	42.6a	9.5a	52.2a	-35.9a	-2.0a	-38.0a	14.2a
Carman 1994							
Aurora	29.6a	3.9a	33.5a	-9.1b	-4.0a	-13.0a	20.4b
Sierra	29.2a	-0.5a	28.7a	-1.9b	-1.9a	-3.8a	24.9b
SW-101	12.9a	-5.2a	7.7a	25.1a	2.0a	23.1a	30.8b
SW-103	18.4a	0.6a	19.0a	4.2ab	-5.2a	-1.1a	17.9b
IS-6111	42.4a	-1.9a	40.6a	25.0a	3.4a	28.4a	69.0a
Winnipeg 1995							
Aurora	57.6a	1.0a	58.7a	-46.0b	0.3b	-45.7b	13.0ab
SW-103	49.0a	1.8a	50.8a	-41.1b	-4.5b	-45.6b	5.2b
IS-6111	59.3a	1.3a	60.6a	-39.0b	14.1a	-24.9a	35.7a
Carman 1995							
Aurora	13.4b	-5.4a	8.0a	-8.7b	-5.0a	-16.2b	-7.8b
SW-103	13.2b	-0.4a	14.3a	-2.2b	-8.8a	-12.1b	4.6b
IS-6111	25.1a	-2.5a	22.7a	29.8a	9.8a	39.6a	62.3a

† Pre-flower growth periods were 13-65, 7-76, 14-67 and 06-71 DAS and post-flower period were 65-123, 76-133, 67-120 and 71-135 DAS at Carman 1994, Winnipeg 1994, Carman 1995 and Winnipeg 1995, respectively. Negative values indicate greater rainfall than water extraction.

†† Values within a column followed by the same small letter and mean values followed by same capital letters are not significantly different at $P<0.05$.

differences in water depletion were significant in 2 out of 4 times in the post-flowering period, while the difference was observed only once in the pre-flowering period. Further, separating water extraction into 0.10 to 1.10 m (rooting depths of most annual crops on the

Canadian Prairie are about 1.10 to 1.20 m) and 1.10 to 1.90 m, indicated more water depletion by IS-6111 over dwarf cultivars in both layers, although significance was more often observed in the 0.10 to1.10 m layer (Table 4.1). In the driest environment (Winnipeg, 1995), IS-6111 extracted a greater amount of water from deep in the soil profile compared to dwarf cultivars. Although, such comparisons can be used to identify the genetic variations, care should be exercised while using absolute values because of differences in rainfall (Dardanelli et al., 1997; Meinke et al., 1993).

The higher water extraction by IS-6111 was attributed not only to the deeper rooting depth, but also to the higher extraction efficiency at each depth (Fig. 4.5 to 4.6). For example, the water extraction by IS-6111 at Carman in 1995 was significantly higher than that of dwarf cultivars at each 0.20 m layer to a depth of 1.10 m (Fig. 4.5). A similar trend was observed at other locations, though the differences were not significant at all depths (Fig. 4.5 and 4.6).

In general, at the end of the season sunflower cultivars did not deplete the soil moisture reserve significantly (less than 30 mm) except for IS-6111, which, in spite of over 100 mm rainfall received in the last 30 days (Fig. 4.1), drained up to 69 mm from the soil moisture reserve (Table 4.1). Thus, the soil moisture depletion, which was contributing up to half of consumptive water use during the flowering stage, contributed only about 25 % of seasonal consumptive water use. Entz and Fowler (1989) observed that soil water reserve in spring account for a 25% of total seasonal consumptive water use in wheat.

Agronomy Trials. Genotypic variations for total soil moisture depletion were observed in the agronomy trials (Table 4.2; Fig. 4.7 and 4.8). Similar to space planted trials, standard

Table 4.2. Soil moisture depletion (mm) by different height classes of sunflower cultivars before and after flowering from above and below 110 cm soil profiles in agronomy trials.

Cultivar	Pre-flowering†			Post-flowering			Total
	10-110	110-190	10-190	10-110	110-190	10-190	10-190
Winnipeg 1994							
Aurora	53.5a††	17.4a	70.9a	-41.8c	-2.2bc	-44.0cd	27.0bc
Sierra	46.8a	23.5a	70.3a	-40.2c	-12.2c	-52.4d	17.6c
SW-101	46.1a	15.4a	61.4ab	-33.3bc	2.9b	-30.4bc	31.0bc
SW-103	43.1a	13.9a	57.0b	-33.0bc	-3.8c	-36.8c	32.1bc
IS-6111	41.7a	13.6a	55.4b	-25.5b	7.0b	-18.4b	37.0b
SF-187	46.8a	15.9a	62.7ab	-5.1a	24.1a	19.0a	81.8a
Carman 1995							
Aurora	53.5a	-11.8c	41.7c	-23.4d	18.3a	-5.1d	36.6c
Sierra	39.0a	-3.0bc	36.0c	-6.7cd	32.7a	26.0c	53.8c
SW-101	21.8a	8.3b	30.1c	22.0b	34.2a	56.3b	94.1b
SW-103	30.1a	1.1bc	31.3c	1.8c	22.2a	24.0c	55.3c
IS-6111	58.5a	46.2a	104.7a	21.2b	34.3a	55.5b	160.2a
SF-187	38.4a	42.2a	80.6b	51.8a	37.7a	89.6a	170.2a

† Pre-flower growth period was 22-85 and 21-65 DAS and post-flower period was 65-135 and 65-130 DAS at Winnipeg and Carman, respectively. Negative values indicate greater rainfall than water extraction.

†† Values within a column followed by the same small letter and mean values followed by same capital letters are not significantly different at $P<0.05$.

height hybrids depleted more soil moisture than the dwarf cultivars. Greater water depletion by standard height cultivars than dwarf cultivars was significant during the post-flowering stage at Winnipeg, and during both pre- and post-flowering periods at Carman. The differences during post-flowering period might be related to the longer duration of standard height cultivars. Although the cultivars were good representatives of their height class, some variations within height classes were observed (Table 4.2). For example, among dwarf cultivars, SW-101 extracted more water than SW-103, and among standard height hybrids SF-187 depleted more soil water than IS-6111.

Extraction of water from deep in the soil profile (110-190 cm) was influenced by both cultivar and location. The tall cultivars tended to use significantly more water from this soil zone than dwarf types. At Carman, which had a coarse textured soil with quick release of water, the major difference in water depletion among cultivars in the 1.10 to 1.90 m profile was observed before flowering. In contrast, the differences at Winnipeg, where the soil was a clay with slow release of water, cultivar differences were observed during post-flowering period only. In addition to the soil texture, lower rainfall at Carman compared to Winnipeg location might have affected the soil moisture depletion patterns.

The higher soil moisture depletions by standard height cultivars were due to efficient water extraction as well as deeper rooting than shorter statured cultivars. The efficient water extraction was evident from significantly higher water extraction by standard height cultivars up to 1.10 m depth at Winnipeg (Fig. 4.7) and up to 1.50 m depth at Carman (Fig. 4.8) compared to dwarf hybrids and/or dwarf open pollinated cultivars. Some of these differences were evident by flowering stage. Similar to space planted trials, higher extraction front velocity and occupation of soil profile by the root system for longer time might be responsible for the efficient water depletion (Monteith, 1986).

Thus, standard height hybrids were depleting up to 134 mm more water compared to dwarf cultivars, which was approximately 30 % of the consumptive water use of the standard height sunflower (Table 3.8). Although the soil moisture depletion values reported here are less than 200-300 mm extraction reported in the literature (Bremner et al., 1986; Cox and Jolliff, 1986 and Zaffaroni and Schneiter, 1989), >100 mm of extra water extracted by the standard height sunflower types will have a significant role in stabilising yields during the dry years on the Canadian Prairie.

4.4 Discussion

In sunflower, information on the effect of plant stature on root system does not exist. This is the first study to compare root system of sunflower cultivars in western Canada. Results of this study indicated that reducing plant height reduced the root system of sunflower cultivars, however, the genetic background and/or dwarfing genes significantly modified the stature effects. IS-6111 had a better developed root system compared to the dwarf hybrid, SW-103, while it was similar to the dwarf open pollinated cultivar, Aurora. Recently, plant stature effects on the root system have been systematically studied in wheat by using isogenic lines for plant height and similar to the results, Ehdaie and Waines (1996) observed the effect of genetic background and/or dwarfing gene in modifying plant stature effects. Even in wheat, where a number of studies have been conducted using isogenic or near isogenic lines, a strong relationship between root system and plant height has not been reported (McCaig and Morgan, 1993; Mirelles et al., 1997 and Siddique et al., 1990). Therefore, the possibility of producing dwarf sunflower cultivars without losing the strong root system of sunflower exists.

Rooting depth is an important root trait that determines soil moisture use by crops. In sunflower, greater rooting depth is generally attributed to the longer growth duration (Fereres et al., 1986; Schneiter, 1992). Dardanelli et al. (1997) reported that extraction front velocity was similar among short and long season cultivars, and rooting depth was a function of growth duration. However, in the present study the rooting depth was not related to growth duration alone. Higher extraction front velocities in IS-6111, a taller and longer growth duration cultivar, or Aurora, a cultivar with similar height and duration, compared to SW-103 indicated that neither the plant stature nor the growth duration regulated extraction front completely. Therefore, this study identified genetic variation for extraction front velocity and rooting depth independent of height genes in sunflower.

Temperature has a significant influence on the root development in crops (McMicheal and Burke, 1996) including sunflower (Seiler, 1998). Low soil temperature is one of the major factors limiting root growth in the Canadian Prairie (Entz et al., 1992). The higher air temperature can influence root growth directly by increasing soil temperature or indirectly by influencing the plant growth. The effect of air temperature on sunflower root growth was evident from the significant differences in extraction front velocities (expressed in days) between years (Fig. 4.9). However, in the absence of observation of soil temperature, it was not possible to separate the effect of air temperature into direct and indirect effects. Studies should be conducted to assess the direct and indirect effects.

Genotypic variations in extraction front velocities were observed even when regressed against thermal time. This indicates the presence of genetic variation for low temperature tolerance in sunflower. Although, similar results have been observed with diverse sunflower genotypes in the laboratory, field observations are lacking (Seiler, 1998). Sunola cultivars were developed in the cooler Canadian Prairie. Therefore, root growth of sunola cultivars may be less sensitive to cooler temperatures than the other cultivars tested here. Thus, the genetic background of the dwarf sunflower cultivar was important in determining rooting characteristics.

The use of heat accumulation to correct seasonal differences in extraction front velocities may have implications for modelling root development in different environments. Some of the differences reported in the extraction front velocities can be attributed to temperature differences. For example, Thomos et al., (1995) observed 30 % reduction in extraction front velocities of chickpea and barley by winter seeded crop compared to spring seeded crop in Australia. Similarly, the mean temperature during the growing season in Argentina (Dardanelli, et al., 1997) was 20 to 24 °C and that led to higher extraction front velocity compared to the present study where the temperatures were frequently lower than 20 °C (Fig. 4.1). This indicates that when factors like soil moisture, nutrients, soil physical properties are relatively similar, temperature differences across agro-climatic conditions can be corrected by using heat accumulation. However, further experiments are needed to establish the relationship between extraction front velocity and air temperature.

Soil moisture depletion by the standard height hybrid was greater than dwarf cultivars. The tap root thickness indicated a better channel for transporting water. However, contrary to the expectations, higher hydraulic conductance was not observed in IS-6111. Therefore, higher water depletion by IS-6111 compared to dwarf cultivars was likely due to a combination of traits such as deeper rooting, higher root length density, better root distribution and thicker tap root for IS-6111 and greater transpirational leaf surface area. Longer growth duration of IS-6111 might also have contributed to the higher water extraction compared to Aurora.

The primary reason for adopting sunflower in drought prone areas of the world is its ability to maintain water supply during dry periods with the help of its strong root system, provided soil moisture is available. This ability was documented by Cabelguenne and Debaeke (1998), who observed 70 to 100% exhaustion of available water by sunflower in 10 out of 13 years. Although no extremely dry years were encountered in the present field studies, the rainfall varied and 1995 was the driest season. When we compare the seasonal water depletion of different height sunflower cultivars, the standard height hybrids were depleting 130 mm more soil moisture in 1995 compared to dwarf cultivars. This indicates that when rainfall failed to supply the water needed, the standard height hybrids managed to obtain that water from the soil profile. Dwarf hybrids, on the other hand, were not efficient in obtaining extra water so their consumptive water use was reduced (Table 3.8). This can be substantiated with close observation of the water extraction during the longest dry period of the study. At Carman in 1995 between 65 and 85 DAS only 7.4 mm rainfall was received and 270 GDD was accumulated. The dwarf cultivars extracted 31 mm and 40 mm (Aurora and SW-103, respectively) of soil moisture in that period compared to 75 mm by the standard height hybrid, IS-6111 (Fig. 4.7). Further, observing the soil profile from where the water was extracted by IS-6111 revealed that about 9% was coming from below the rooting depth of dwarf sunflower (1.50 m). The Standard height sunflower is known to exhaust water from the entire profile, compared to other annual crops which leave considerable water at depth (Bremner et al., 1986; Cabelguenne and Debaeke, 1998). Significantly higher water extraction by standard height hybrids compared to dwarf cultivars to a depth of 1.50 m, suggests that extraction pattern of standard height hybrids resembled sunflower in other published studies, while the soil moisture extraction pattern of dwarf cultivars are comparable to other annual crops (shallower and less efficient). Thus, both efficient extraction and deeper rooting contributed to the higher water extraction by standard height hybrid. The extra water obtained by standard height hybrids (about 100 mm) may relieve stress at critical periods. In addition, a crop like standard height sunflower can be used in a cropping system for environmental benefits such as extracting deep leached nitrate.

4.5 Conclusion

In sunflower, although reducing plant height reduced root length density, rooting depth and root distribution, genetic background of the cultivar was important. Therefore, IS-6111 had significantly deeper and explorative root system compared to SW-103, but was similar to Aurora. The differences in root parameters were reflected in the depth of extraction front. The rate of root penetration was dependent on cultivar and temperature. However, soil moisture depletion of the standard height hybrid, especially under water stress conditions, was significantly higher than for the dwarf cultivars. The extra water absorbed by the standard height cultivar was due to efficient water extraction and deeper rooting depth. Observation of additional cultivars, in spite of smaller differences, indicated similar trends. Thus, the standard height sunflower was favoured if the stability of production under intermittent stress was the primary objective and water was available at depth. Dwarf cultivars were favoured if there is no water at depth and/or a shorter season and crop managements are the primary concern. Therefore, in southern Manitoba, where the duration of the growing season is long enough for a standard height sunflower, standard height hybrids are preferred because of their yield stability. In the western Prairie region, where the season is too short for standard height hybrids, dwarf sunflowers can be grown. However, the same yield stability cannot be expected. These results indicate that it is possible to reduce plant height of sunflower without losing rooting depth, and hence additional breeding efforts to combine these desirable traits should be encouraged.

5.0 WATER RELATIONS OF DIFFERENT HEIGHT SUNFLOWER CULTIVARS

ABSTRACT

Development of early maturing short stature sunflower (*Helianthus annuus* L.) cultivars followed the success of dwarf cereals. Although, a number of breeding programs have recently released dwarf sunflower cultivars in western Canada, the drought adaptability of short stature cultivars have not been studied. Therefore, field studies were conducted in western Canada during 1994 and 1995 to compare seasonal water relations of Sunwheat-103 (SW-103), a dwarf hybrid, and AC-Aurora (Aurora), an open pollinated dwarf cultivar, with IS-6111, a standard height hybrid. Results revealed lower water stress experienced by the dwarf hybrid, SW-103, than the tall hybrid, IS-6111. However, the role of plant architecture and/or genetic background in regulating water stress was indicated by another dwarf cultivar, Aurora. Genotypic variation for osmotic adjustment was observed. Dwarf cultivars initiated osmotic adjustment earlier than IS-6111. Comparison of osmotic adjustment per unit of water stress indicated that osmotic response of Aurora was superior compared to other cultivars. All cultivars maintained positive turgor during the study, although the strategy was different for each cultivar. IS-6111, in spite of experiencing higher stress, produced higher photosynthesis and stomatal conductivity to maintain higher productivity. As reported in the literature, water extraction was the most important factor determining productivity in sunflower. The differences within the dwarf height classes for water relation parameters were small and less frequently observed among dwarf classes. Thus, the dwarf sunflower cultivars were either better or equal to standard height sunflower cultivars in drought tolerance under southern Manitoba conditions.

5.1 INTRODUCTION

Water stress is a major abiotic factor limiting plant growth; in the past several millennia, plants have evolved to cope with water deficits (Araus and Buxo, 1993). In annual plants, mechanisms that aid in plant survival have ecological significance, while mechanisms that help maintain the plant productivity have agronomic significance (Turner, 1986). Plant breeding efforts have applied selection pressure for the productivity aspect of the evolutionary process.

Sunflower (*Helianthus annuus* L.) is a highly adaptive crop, with the natural habitat ranging from desert to marsh (Seiler and Rieseberg, 1997). The adaptation in different agroclimatic conditions has produced genetic variations for stress tolerance in sunflower cultivars (Fereres et al., 1986). Generally, sunflower avoids water deficit by extracting water deeper from the soil profile (Bremner et al., 1986; Connor and Sadras, 1992; Dardanelli et al., 1997; Merril et al., 1996). Use of physiological and morphological modifications by sunflower to regulate water use has also been reported (Connor and Sadras, 1992; Sadras et al.,1993b). The ability of sunflower to survive and produce stable yields under periods of drought is responsible for the increase in acreage of sunflower in hot and dry environments.

The success of semi-dwarf genes in cereals, has prompted scientists to consider height reduction in many other crops including sunflower. While the genetics of plant height and agronomic benefits of dwarf sunflowers have been reported (Johnston et al., 1995; Miller, 1992; Miller and Hammond, 1991), the implications of dwarfing genes for plant water relations in sunflower have not been previously explored. The conventional interpretation with cereal crops is that shorter plants are best suited to highly productive environments, while taller plants are best suited for yield stability under adverse conditions, although critical evidence for this is lacking (Blum et al., 1988). In cereals, a limited number of studies indicated a reduction in water stress experienced by reduced stature plants (Kirkham and Smith, 1978; Blum and Sullivan, 1997), while others reported no effect of plant stature on plant water stress (Entz and Fowler, 1990a). Information on the effects of varying stature on sunflower water relations is important for adoption of short stature sunflowers in stress prone environments.

The effect of dwarfing genes on the morphology and physiology of cereals depends on the genetic background of the cultivar (Ehdaie and Waines, 1996; Blum and Sullivan, 1997). In sunflower, semidwarf and dwarf phenotypes have been recently developed (Schneiter, 1992). The plant architecture from different breeding programs and different cultivars from the same breeding program vary, indicating the role of different genes (Miller and Hammond, 1991; Miller, 1992) or differences in the genetic background of the cultivar (Ehdaie and Waines, 1996; Blum and Sullivan, 1997). A new group of open pollinated dwarf sunflower cultivars, referred as sunola, have been developed in western Canada and have been registered for cultivation since 1992. Sunola plants are characterised by reduced plant height, leaf size, head and stem diameter (Beckie and Brandt, 1996). The canopy of sunola cultivars are more open due to smaller leaves and longer petioles. Such an open canopy can alter radiation penetration and air movement, which may affect the soil-plant-air continuum. Therefore, it is essential to study inter- and intra-height class variations for water stress tolerance in sunflower.

The first objective of the study was to observe variations among different height sunflower cultivars for water relations. The second objective was to observe the effect of plant stature on photosynthesis and stomatal conductivity.

5.2 MATERIALS AND METHODS

5.2.1 Experimental Details

Studies were conducted in 1994 and 1995 at Carman (49.5°N, 98.0°W) and Winnipeg (49.8°N, 97.2°W) to monitor sunflower water relations under prevailing conditions in the field in southern Manitoba. The soil at Winnipeg was clay (Riverdale series, Entisol, Cumulic Regosol) with gradual release of water and slow development of stress, while that at Carman was sandy clay loam (Denham and Eigenhof series, Udic Boroll, Orthic Black Chernozem) with characteristic quick release of water and rapid development of stress. The typical relative water deficit for a long duration crop like corn (*Zea mays* L.) at Carman is 50 mm more than at Winnipeg (Ash et al., 1992). Plants were fertilised as per the soil test results (Norwest Lab, Winnipeg; Appendix 2) and were kept free from weeds and insects.

Three commercial cultivars, AC-Aurora (an open pollinated sunola cultivar; referred as Aurora), Sunwheat-103 (a dwarf hybrid; referred as SW-103) and IS-6111 (a standard height hybrid) were used in the study. Additional cultivars, AC-Sierra (a dwarf open pollinated; referred as Sierra) and, Sunwheat-101 (a dwarf hybrid; referred as SW-101) were included in 1994 trials to study variations within the dwarf height classes. All cultivars were hand seeded between May 23 and June 2 in 5 m x 8 m plots at a spacing of 1 m x 1 m. Plots were over seeded and the extra seedlings were thinned at V_2 to V_4 stages (Appendix 2). The top-most fully expanded sunlit leaves were used for all water relation measurements and observations were made between 1100 and 1600 (mostly between 1100 and 1400) hrs (daylight saving time). All field observations were made on clear, sunny days with midday solar radiation levels ≥1600 µmol $m^{-2}sec^{-1}$ and daily maximum temperatures ≥ 25 °C.

5.2.2 Observations

Leaf water potential (ψ_l) was measured as the negative of the hydrostatic pressure required to bring the xylem sap to the cut end of the petiole (Turner, 1981) using a Scholander type pressure bomb (Model 1002, PMS Instrument Company, Corvallis, Oregan, USA). Sample leaves were sealed in a plastic bag and the petiole was cut 2.5-3.5 cm below the leaf blade (Turner, 1981). Sunflower leaves in the field trials were larger than the sample chamber. Therefore, the leaves were carefully rolled, avoiding damage to veins, and inserted into the pressure chamber. The chamber was pressurised at a rate of 0.01 to 0.02 MPa sec^{-1}. The whole process of cutting leaf to appearance of xylem sap (balancing pressure) on the cut end took 3 to 5 min for each leaf.

Leaf osmotic potential (ψ_π) was measured by the psychrometric method (Turner, 1981). The sample leaf was cut into two pieces, avoiding the midrib, and each piece of leaf lamina approximately 5 cm X 5 cm in size was placed into a 5 mL disposable syringe. The syringe tips were sealed with parafilm and packed in ice. Within 2 to 4 hours, the samples were moved to a freezer at -20 °C. The leaf material was frozen to disrupt the cell membrane, thereby eliminating turgor potential of the cell. At a later date the frozen syringes were thawed for about 30 min and the sap was expressed by using similar force on the syringe plunger for all samples. A filter paper disc (0.5 cm) was saturated with the expressed sap. Care was taken to retain a similar amount of sap on the paper disk for all the samples (approximately 7 to10 μL). Osmotic potential of the discs was read with a Wescor Vapour Pressure Osmometer (Model Wescor 5500XR, Logan, Utah, USA). The osmometer was calibrated with standard salt solutions of known osmotic potential. Contamination of the thermocouple was checked every 12 to 15 samples by running standard salt solutions. No effort was made to account for the dilution effect of apoplastic water. Means of two samples from the same leaf were used for statistical comparisons.

Relative water content was measured along with other water relation measurements. A fully expanded leaf along with 2.5 to 4.0 cm petiole was cut from each plot and immediately sealed in a pre-weighed zip lock bag to avoid moisture loss. The fresh weights of the leaves were recorded in the laboratory and then the petioles were immersed into 30 mL test tubes filled with distilled water. The leaves were hydrated (which was evident from visual observation) over night (12 to 14 hours) in the dark. The next morning, after recording the turgid weight, the leaves were transferred to a oven maintained at 70 °C. The dry weights were recorded after 48 hrs of drying. The relative water content was calculated as follows.

$$\text{Relative Water Content} = \frac{\text{Fresh Weight} - \text{Dry Weight}}{\text{Turgid Weight} - \text{Dry Weight}} \times 100 \quad \ldots\ldots\ldots\ldots \quad (1)$$

Turgor potential (ψ_p) was calculated by subtracting osmotic potential from the leaf water potential.

$$\psi_p = \psi_l - \psi_\pi \quad \ldots\ldots\ldots\ldots \quad (2)$$

Relative water content was used to convert ψ_π to osmotic potential at full turgor ($\psi_{\pi 100}$). The differences in $\psi_{\pi 100}$ during various stages of growing season indicates the osmotic adjustment due to active solute accumulation.

$$\psi_{\pi 100} = \frac{\psi_\pi \text{ X Relative water content}}{100} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (3)$$

Stomatal conductance and photosynthesis were measured on clear and sunny days using a closed portable photosynthesis system (LI 6200/6050, LI-COR Instruments, Lincoln, Nebraska). The top most, fully expanded, illuminated leaves were selected for the photosynthesis readings. At each sampling time, 2 to 3 leaves were sampled in each plot and the equipment was set up to record 3 readings on each leaf. Selected leaf was clamped into a one litre leaf chamber with an approximate measurement area of 40 cm^2. Measurement of three readings on each leaf took about 45 to 60 s. Means of all observations for each plot were used for statistical analysis. The infrared CO_2 analyser (LI-6050) was calibrated by feeding a known concentration of CO_2 into the chamber before each sampling date.

Data collected from different environments (and on different dates) were analysed separately by using an analysis of variance procedure (GLM procedure, SAS Institute Inc., Cary, NC, 1985). The statistical design was a randomised complete block design (RCB) with four replications. A Fisher's protected LSD test (P=0.05) was used for mean comparison. Effect of ψ_l on stomatal conductance, photosynthesis and $\psi_{\pi 100}$ were analysed using regression. Mean values were used for regression analysis (Gomez and Gomez, 1984). Slopes of regression equations were tested for statistical significance using JMP software (Sall and Lehman, 1996).

5.3 RESULTS

5.3.1 Weather Conditions

The weather data for Carman and Winnipeg during the years of experimentation are presented in Fig. 4.1 and Table 3.2. In general, 1994 growing season was cooler and received either above normal (Winnipeg) or slightly below normal (Carman) rainfall compared to 1995 season, which was warmer with intermittent dry spells. In addition, a greater portion of seasonal rainfall in 1995 was received late in the season. Water relation observations vary in response to short term weather changes. Therefore, details of weather conditions that prevailed during the water relation observations are presented in Appendix 6 and 7. With the exception of few days, the maximum temperature on the day of observation was above 25 °C with a negligible amount of rainfall in the preceding 72 hrs. However, a few rainfall events 72 hrs before observation period were observed at the beginning or end of the observation period.

5.3.2 Leaf Water Potential

Leaf water potential is the most commonly used parameter to estimate plant water stress. Midday ψ_l in the field ranged from -0.48 (Aurora at Carman 1994) to -1.74 MPa (IS-6111 at Carman 1994) (Fig. 5.1 and 5.2). Similar ranges of ψ_l have been reported in sunflower under different agroclimatic conditions (Bremner and Preston, 1990; Martin et al., 1992; Prasad et al., 1985), although, under severe stress ψ_l can drop below -3.0 MPa (Connor and Jones, 1985; Gimenez and Fereres, 1986; Wise et al., 1990). Therefore, sunflower cultivars in this study experienced only moderate water stress.

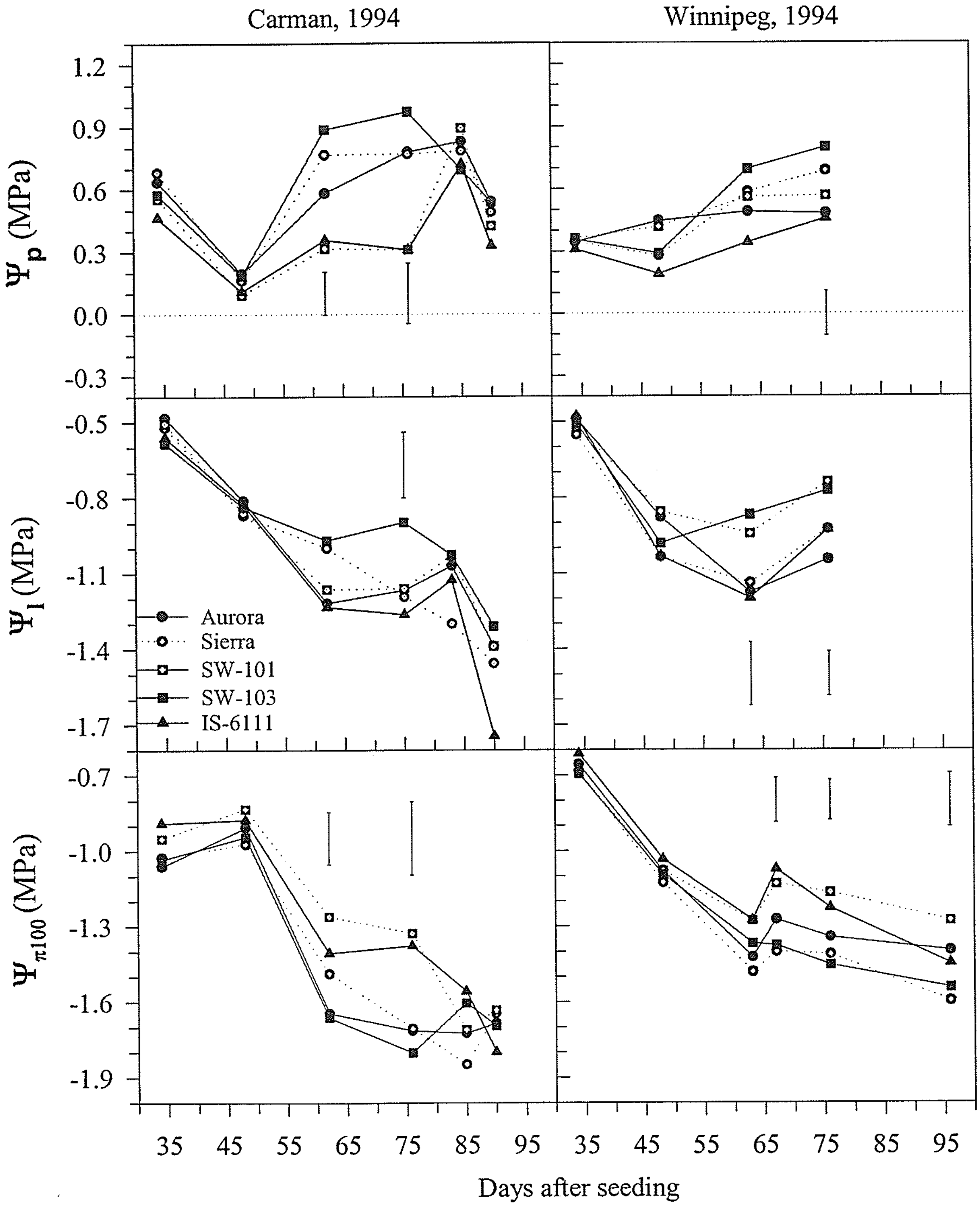

Figure 5.1. Seasonal pattern of turgor potential (ψ_p), water potential (ψ_l) and osmotic potential at full turgor ($\psi_{\pi100}$) of space planted sunflower cultivars in 1994. Additional cultivars of the same height class are shown with the same symbol with a open dot in the centre and a dotted line. The vertical bar represents LSD value (P=0.05). Absence of LSD bar indicates non-significant differences between cultivars.

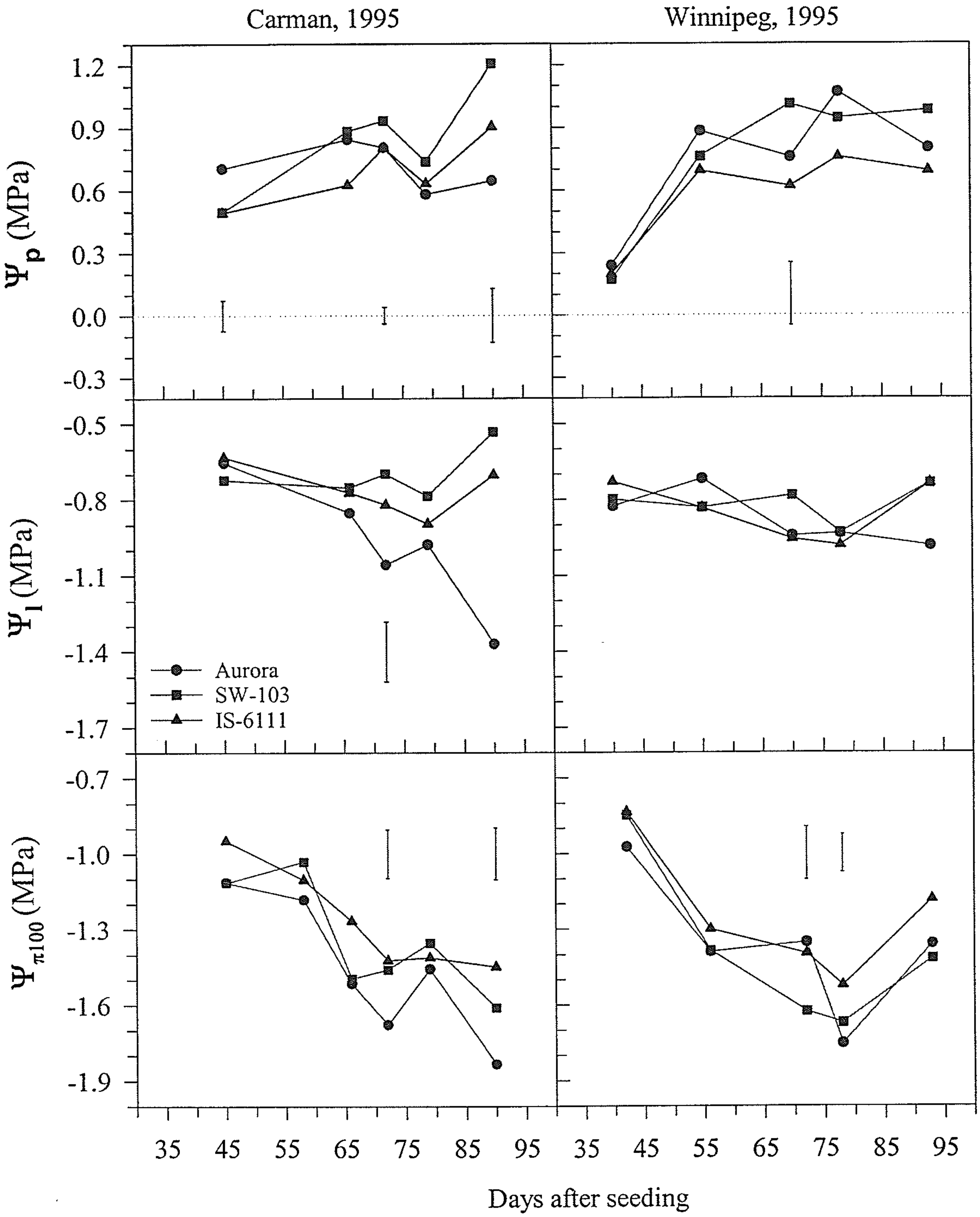

Figure 5.2. Seasonal pattern of turgor potential (ψ_p), water potential (ψ_l) and osmotic potential at full turgor ($\psi_{\pi 100}$) of space planted sunflower cultivars in 1995. The vertical bar represents LSD value (P=0.05). Absence of LSD bar indicates non-significant difference between cultivars.

Significant differences in ψ_l among sunflower cultivars on a number of observation dates indicate that sunflower cultivars experienced different levels of water stress in this study. The dwarf hybrid, SW-103, consistently had the highest ψ_l (i.e., least water stress) among the cultivars compared (Fig. 5.1 and 5.2). For example, at Carman in 1994, ψ_l decreased by 1.19 MPa for IS-6111 during the course of the growing season compared to 0.73 MPa for SW-103. Higher leaf area for transpiration, as indicated by higher dry matter levels (Table 3.4), might have resulted in lower ψ_l in IS-6111 (Gimenez and Fereres, 1986). Similar to these results, Blum and Sullivan (1997) observed increase in plant water stress with increase in plant height among wheat isogenic lines. However, ψ_l of the dwarf open pollinated cultivar, Aurora, was lower than or in some cases similar to IS-6111 (Fig. 5.1 and 5.2). This observation indicates that plant architecture and/or genetic background also plays an important role in determining levels of plant water stress.

The Winnipeg location in 1995 received the lowest amount of precipitation during the early part of the growing season (Fig. 4.1). However, no differences among cultivars for ψ_l were observed (Fig. 5.1). In sunflower, leaf area is more sensitive to water stress than stomatal activity (Cox and Jolliff, 1987). Therefore, early stress at Winnipeg might have reduced leaf area, thereby reducing the effect on water stress. Similar morphological adjustment to match water availability is often observed in sunflower (Connor and Jones, 1985). In general, differences for ψ_l within dwarf height classes were not observed except at 76 days after seeding at Carman in 1994, when SW-101 was more stressed compared to SW-103 (Fig. 5.1). These observations suggest that the cultivars selected represented respective height classes fairly well and that in general the dwarf hybrids experienced the least water stress, followed by IS-6111 and Aurora.

5.3.3 Osmotic Adjustment

Osmotic adjustment by solute accumulation is an important drought response by crops (Morgan, 1984). Genotypic variations for osmotic adjustment were observed in the present investigation (Fig. 5.1 and 5.2). The $\psi_{\pi 100}$ of dwarf cultivars, Aurora and SW-103, were often lower than that for the tall cultivar, IS-6111 indicating that the shorter statured cultivars had a more positive stress response than the standard height cultivar. Solute accumulation in response to water stress however, depicted the further differences among cultivars (Fig. 5.3). Significant differences in slopes ($P<0.05$) indicated that solute accumulation in Aurora was 0.25 to 0.29 MPa higher than SW-103 and IS-6111 for each MPa decrease in ψ_l, respectively. Similar to ψ_l, these observations suggest the role of genetic background in drought response.

While genotypic variations for osmotic adjustment in sunflower have been reported (Chapman and Auge, 1994; Chimenti and Hall, 1993), plant stature effect on osmotic adjustment has not been previously investigated. Limited research on the effect of plant size on the osmotic adjustment in wheat have contradictory results. Blum et al. (1999) reported delayed osmotic adjustment in wheat cultivars capable of extracting more water from depth. This is similar to observation of IS-6111 in this study, as IS-6111 also was capable of extracting more soil water than short stature cultivars, and this may have reduced the need to osmotically adjust. In contrast, Blum and Sullivan (1997), Entz and Fowler (1990a) and Kirkham and Smith (1978) observed better osmotic adjustment with taller wheat cultivars.

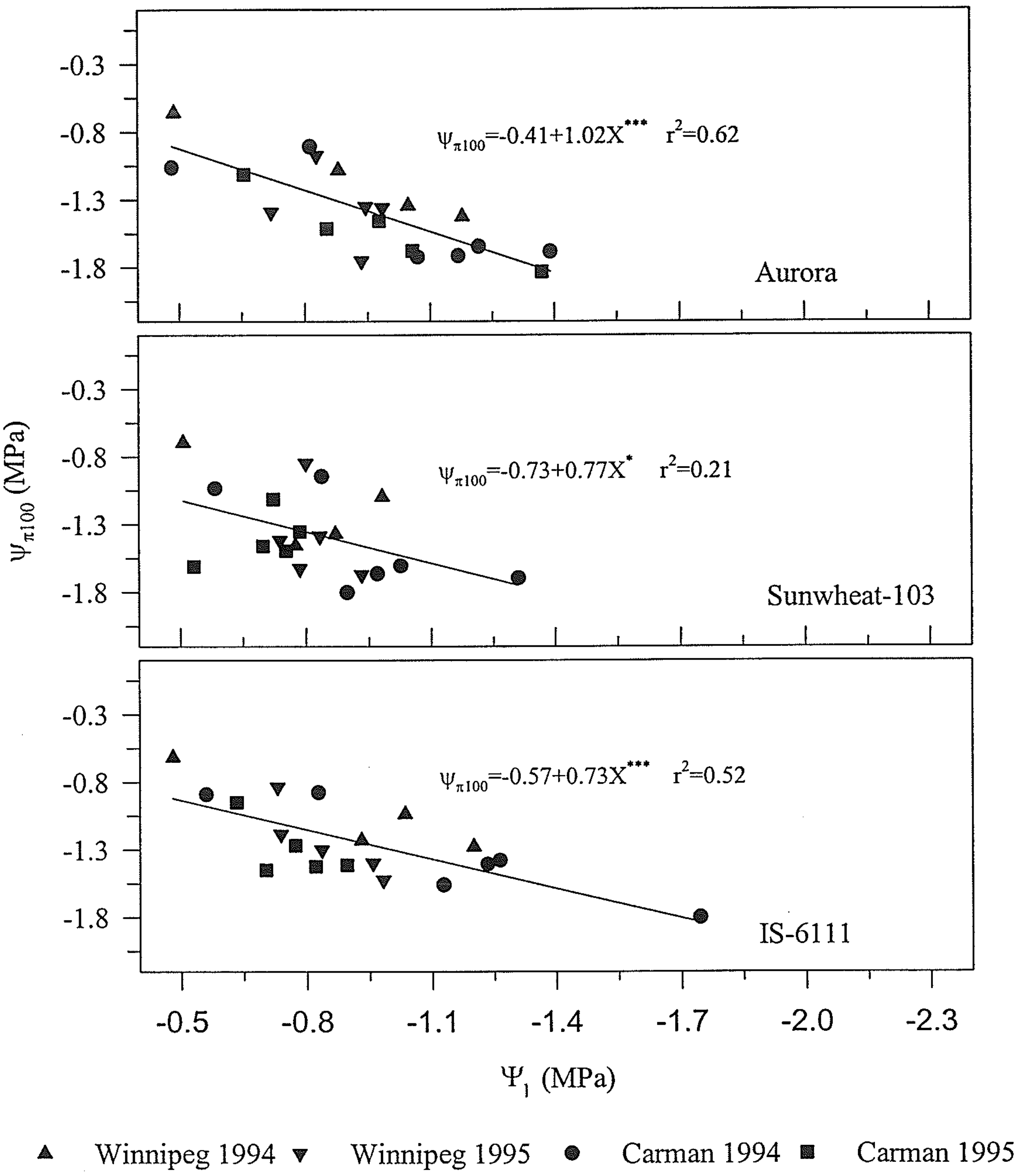

Figure 5.3. The relationship between leaf water potential (ψ_l) and osmotic adjustment ($\psi_{\pi100}$) by different height sunflower cultivars in the trials. * and *** indicate significance at 0.05 and 0.001P, respectively.

Therefore, a crop that delays water stress either by extracting more water or by reducing water loss by smaller leaf area, delays initiation of osmotic adjustment. The only significant difference in $\psi_{\pi 100}$ within the height class was observed in sunwheats, where SW-103 was more efficient in osmotic adjustment compared to SW-101 (Fig. 5.1).

5.3.4 Leaf Turgor Potential

All three height classes of sunflower maintained positive turgor (ψ_p) in all field trials (Fig. 5.1 and 5.2). Whenever significant differences in ψ_p among height classes were observed, SW-103 had higher ψ_p levels than IS-6111. Higher levels of ψ_p for SW-103 vs IS-6111 were not unexpected as SW-103 had higher levels of both ψ_l and osmotic adjustment. The ψ_p of Aurora was intermediate between SW-103 and IS-6111 and on a few occasions, Aurora experienced higher ψ_p than IS-6111. Turgor potentials within height classes were similar with a few exceptions. Whenever significant differences within height class were observed, SW-103 maintained significantly higher ψ_p than SW-101. Lower osmotic adjustment by SW-101 compared to SW-103 was responsible for the differences in ψ_p. Thus, a superior osmotic adjustment and/or lower stress level enabled the dwarf cultivars to maintain higher ψ_p than IS-6111 in this study.

5.3.5 Stomatal Conductance and Net Photosynthesis

Seasonal trends in midday stomatal conductance and net photosynthesis are presented in Fig. 5.4. Due to frequent rainfall, seasonal trends in stomatal conductance and photosynthesis were not observed in 1994. Observation periods in 1995 coincided with 21 and 32 day long dry cycles at Carman and Winnipeg (about 7 mm of rainfall received during

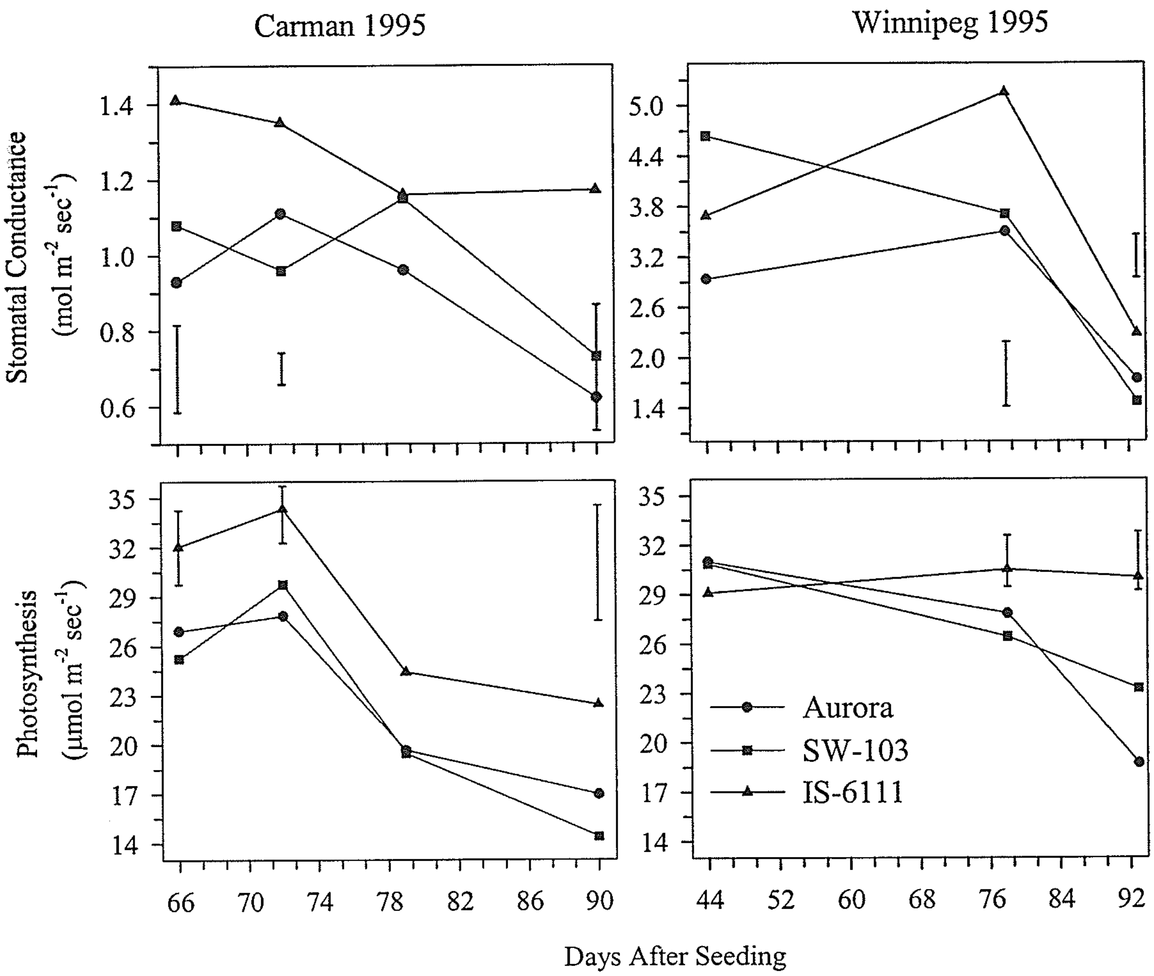

Figure 5.4. The seasonal trends in stomatal conductance and net photosynthesis rate by different height sunflower cultivars at Carman and Winnipeg in 1995. Amount of precipitation between 66 and 86 days after seeding at Carman and between 47 and 78 days after seeding at Winnipeg were only 7.6 and 7.4 mm, respectively. The vertical bars represent LSD at 0.05P. Absence of LSD indicates non-significant difference between cultivars.

the period), respectively (Fig. 4.1). In spite of lower rainfall and a longer stress period, effects of the drying cycle at Winnipeg were less obvious than at Carman. The differences in soil moisture release characteristics of soils at the two locations might be responsible for the differences in stomatal conductance. For example, fine textured soil at Winnipeg supported higher levels of stomatal conductance (up to 5.14 mol m^{-2} sec^{-1}) than coarse textured soils at Carman (up to 1.41 mol m^{-2} sec^{-1}) during the observation period. However, differences in net photosynthesis between locations were small, indicating the insensitivity of photosynthesis to water availability as reported by Connor and Hall (1997).

Cultivar differences were observed in seasonal trends in photosynthesis and stomatal conductance (Fig. 5.4). In general, IS-6111 maintained higher stomatal conductance and photosynthesis than dwarf cultivars in the present investigation. Sadras et al. (1991a) also reported higher transpiration in the standard height sunflower compared to semidwarf sunflower cultivars. This contrasts to observations in wheat, where comparison of isogenic lines for height under controlled conditions either revealed higher stomatal conductance and photosynthesis with dwarfing genes (Bishop and Bugbee, 1998; LeCain et al., 1989; Morgan et al., 1990) or no change (Blum and Sullivan, 1997). When water stress was imposed, taller wheat cultivars reduced stomatal conductance more than shorter cultivars (Blum and Sullivan, 1997). Thus, different height sunflower cultivars had different stomatal conductance and photosynthesis responses compared to different height wheat cultivars.

5.4 DISCUSSION

5.4.1. Plant Stature Effect on Water Stress

Reduced plant height in sunflower was predicted to influence plant water relations by reducing leaf area for transpiration and compressing canopy for air movement. The dwarf hybrid, SW-103, had compressed canopy, lower leaf number and dry matter load (Chapter 3). However, in spite of lower water extraction, SW-103 often experienced significantly lower water stress compared to IS-6111. Recently, plant stature effects on plant water relations have been studied systematically in wheat by using isogenic lines for height and the results concur with the present study (Blum and Sullivan, 1997). Although, no studies on plant height effect on water relations have been reported in sunflower, higher stress has been attributed to the greater leaf area in sunflower (Giminez and Fererez, 1986). Thus, contrary to traditional belief, dwarf sunflower cultivars were able to maintain better plant water status than standard height cultivars.

However, the open pollinated sunola cultivar, Aurora experienced stress levels similar to or greater than IS-6111. This suggests that plant architecture and/or genetic background of the cultivar played a significant role in sunflower water relations. Cultivated sunflower is a unique crop with large horizontal leaves, strong stem (less swinging movements) and non-branching or non-tillering habit (Seiler, 1997). In such crops, the open canopy of sunola will have a distinct influence on plant water relations compared to a crop like wheat. Sunola cultivars are from a different breeding program compared to sunwheats. Higher light penetration and better air circulation, due to a more open canopy, might have increased water loss from the lower leaves in the canopy in Aurora. Therefore, in spite of the lowest dry matter load of Aurora compared with the other cultivars (Table 3.4), Aurora experienced stress similar to or more than IS-6111. The lower water extraction ability of Aurora compared to IS-6111 (Table 4.1) might have contributed for the higher stress experienced by it. There was no difference between two sunola cultivars. Thus, sunola cultivars presented genetic variations for plant water relations within dwarf sunflower cultivars.

5.4.2. Plant Stature Effect on Stress Response

Plant stature had significant influence on osmoregulation strategies of dwarf and standard height cultivars to counter the water stress effects. In general, the dwarf sunflower cultivars Aurora and SW-103 initiated osmotic adjustment earlier than IS-6111. The difference in water extraction ability, as seen from the faster root penetration and greater water extraction in IS-6111 compared to SW-103, suggested that initiation of solute accumulation by IS-6111 was delayed relative to SW-103 due to greater water supply (Table 4.1). Similar plant responses were observed in wheat by Blum et. al. (1999). This hypothesis was supported by the observation that the relationship between $\psi_{\pi 100}$ and ψ_l was similar in SW-103 and IS-6111 (Fig. 5.3). Therefore, early initiation of osmotic adjustment in SW-103 was mainly related to the early experience of stress by SW-103. However, the ψ_l of SW-103 was always higher than IS-6111. Therefore, either different threshold levels of ψ_l or of non-hydraulic root signals (Blum and Sullivan, 1997) might have initiated osmotic adjustment in different height sunflower cultivars. Further studies under regulated moisture supply, preferably under rainout shelter, are needed to elucidate osmotic adjustment responses. At any rate, both dwarf sunflower cultivars were quicker and/or more efficient in using osmotic adjustment to reduce water stress effects.

Stomatal conductance is regulated by environmental demand, controls within the plant system and supply capacity of the soil (Tardieu and Simonneau, 1998). IS-6111, with a deeper and more explorative root system, supported higher stomatal conductance than dwarf cultivars under moderate water limited conditions. Genetic variations for stomatal conductance in sunflower have been reported (Fambrini et al., 1994). As reported by Giminez and Fereres (1986), stomatal regulation restricted further decrease in ψ_l in 1995 trials. It was not possible to assess the threshold ψ_l for stomatal closure in the present study, as it requires a ψ_l lower than -2.8 MPa (Sadras and Milroy, 1996). Stress levels in the present study were moderate (>-1.74 MPa) and no significant relationships between ψ_l and stomatal conductance or net photosynthesis were observed (data not presented). Osmotic adjustment observed in this study is reported to interfere with stomatal regulation (Entz and Fowler, 1990a; Turner et al., 1978), leading to a gradual closing of stomata (Bittman and Simpson, 1989). Thus, although, genetic variations, seasonal trends and differences between locations were observed for stomatal conductance, as reported in the literature (Connor and Sadras, 1992), stomata appeared to play a secondary role in regulating stress response in the present study.

An interesting discovery in this thesis was to learn that sunflower cultivars adopted different strategies to maintain positive turgor. The standard height hybrid relied more on extracting water from depth (Fig. 4.7 and 4.8), followed by osmotic adjustment and stomatal regulation to maintain positive ψ_p. Strong dependence on soil water extraction for turgor maintenance is often reported in sunflower (Conner and Sadras, 1992). The two dwarf classes on the other hand, depended more on osmotic adjustment and stomatal regulation to maintain plant water status. Therefore, the present investigation added to knowledge by identifying that the dwarf sunflower cultivars use of osmotic adjustment for maintaining tissue water status.

Crop productivity is an integration of whole season growth and it is independent of water stress under moderate stress conditions (Passoura, 1994). Blum and Sullivan (1997) reported that, in wheat, the higher production potential of tall cultivars sustains the productivity over the stress-tolerant dwarf cultivars under mild stress, while stress tolerance of the dwarf cultivars takes over when stress is severe. Similar to those results, SW-103, in spite of the highest ψ_l, had the lower photosynthesis rate and dry matter accumulation, while IS-6111 had the lowest ψ_l, but managed to produce the higher photosynthesis rate and dry matter than SW-103 (Table 3.4). In the present study, soil moisture was available at depth and the dry cycles were not long enough to exhaust the water (Bremner et al., 1986). Therefore, IS-6111, the cultivar with deepest root system could maintain better water extraction (Table 4.1) to avoid critical stress at sensitive stages, which enabled standard height hybrids to accumulate higher dry matter compared to dwarf cultivars. Therefore, superior productivity of standard height cultivars in space planted trials was attributed to greater water use in standard height sunflower.

5.5 Conclusions

The present study revealed the presence of significant variations in sunflower drought tolerance mechanisms among different height sunflower cultivars. The reduction of plant stature, in spite of reducing its water extraction ability, maintained or improved water relation parameters. However, the tall hybrid had greater photosynthesis rate and stomatal conductivity than dwarf cultivars, hence was more productive. Therefore, water stress experience and productivity seem to be independent under the mild stress (typical of southern Manitoba) conditions experienced in this study. All cultivars in the present study adopted a drought avoidance strategy and as far as possible relied on the root system to deliver water to the shoot, which was followed by the osmotic regulation and the stomatal regulation to maintain positive turgor. Although, the dwarf cultivars failed to yield more than the standard height hybrid, variations observed within short stature cultivars and lack of a strong relation between plant stature and yield creates a hope for the higher yielding dwarf cultivars in the future. The potential dwarf cultivars should be similar to standard height hybrids in water extraction pattern and photosynthesis, but should have better stomatal regulation, osmotic adjustment to tolerate water stress under field conditions.

6.0 GENERAL DISCUSSION

This thesis reports on the first comprehensive study on newly developed dwarf sunflower cultivars.Therefore, results of the present investigation have both agronomic and physiological significance. The discussion will focus on water, the most limiting factor for crop productivity in the prairie region. The study covered water extraction, water relations and productivity aspects of sunflower cultivars of different stature.

Plant stature effects on the root system have not been studied in sunflower. The direct observation of root systems of the standard height hybrid (IS-6111) and the dwarf hybrid (SW-103) indicated reduction in root size with the reduction in plant height. This conclusion was further supported by the indirect observation of soil water extraction. However, similar root length density, rooting depth, and extraction front velocity between the dwarf open pollinated sunflower cultivar (Aurora) and the standard height cultivar indicated that the genetic background of the cultivar modified the stature effect on root growth. Similarly, deeper rooting and higher root length density in sunflower are attributed to the longer growth duration of the cultivar. Although the above statement applies when comparing the standard height hybrid with the dwarf hybrid, the statement does not hold when the dwarf open pollinated cultivar is included in the comparison. Aurora, the earliest maturing cultivar in the test (Chapter 3), had an extraction front velocity and rooting depth comparable to those of IS-6111. Thus, this study identified genotypic variation in root systems of sunflower cultivars which was neither dependent on plant stature nor on growth duration. These results also suggest that it is possible to develop a dwarf sunflower cultivar without losing the strong root system of standard height cultivars.

Wide variation in the natural habitat and differences in physiological responses due to adaption to diverse habitats have been reported in sunflower. Different rates of root development in response to temperature variations in diverse sunflower cultivars have been observed. Therefore, it is possible that sunola which was bred under cooler conditions of the Prairie may have better tolerance to low temperature or may have a lower temperature optimum than sunwheat which was bred under warmer conditions. Therefore, the cultivars bred in cooler climates and warmer climates should be used in testing the relationship between root growth and air temperature.

The variations in extraction front velocities during the two years identified the importance of temperature in determining rooting depth in sunflower (Chapter 4). It has often been stated that cooler soil temperatures limit the root penetration of annual crops on the Prairie (e.g. Entz et al., 1992). Observations of slower root penetration in 1994 compared to 1995 and differences between extraction front velocities in the present study versus those from trials in warmer conditions, provided evidence to support this claim for sunflower. The temperature and root penetration relationship observed in this study has many agronomic implications. For example, no-till practices under which soil warms up more slowly than under tilled soil conditions, or early spring and dormant fall seeding which are being tried in a number of different crops to shift or extend the growing season, will reduce the extraction front velocity of sunflower. However, adoption of those practices has significant advantages for the sustainability of crop production. Therefore, genetic variations in the root developmental responses to low temperature needs to be exploited for developing cultivars for the Canadian Prairie.

In this study, accumulated degree days accounted for most of the differences in extraction front velocity observed in the two years (Chapter 4). This relationship has significant implications in modeling root penetration in cooler environments and will probably account for the differences observed in extraction front velocities between cooler (e.g. Canadian Prairie) and warmer environments (e.g. Southern United States/Southern Spain) or between cooler (winter) and warmer (summer) seasons (e.g. Southern Australia). The above relation needs to be confirmed by studies in different environments, different seasons (in a Canadian context, different seeding times) and with diverse cultivars, including close observation of soil temperature, air temperature and microclimate.

The present study identified a plant stature influence on soil water depletion. Under agronomic conditions presently used by farmers (i.e., each cultivar grown under optimum plant population), the standard height hybrids extracted about 100 mm more soil water than the dwarf cultivars tested. In addition to deeper rooting depth, efficient extraction of water from the top soil layers by the tall cultivars was also responsible for the more water depleted from the soil profile. Although, smaller variations among the dwarf cultivars (i.e., between as well as among sunolas and sunwheats) were observed, it was possible to conclude that the dwarf sunflower cultivars depend less on soil moisture for their total water needs compared to the standard height sunflower. However, total water use of dwarf cultivars was comparable to other annual crops in the region. Therefore, introduction of dwarf cultivars adds an alternative heat and water stress tolerant crop for the region. This has a significant implication for cropping systems in the region, where the standard height sunflower is considered to exhaust the entire soil water supply. Hence, the soil profile needs to be recharged with water before the next crop is grown. Therefore, standard height and dwarf cultivars will have different niches within cropping systems. For example, a dwarf sunflower is suitable where lower dependence on soil moisture is compensated by regular rainfall (or irrigation) or where complete exhaustion of the soil profile is not acceptable. In contrast, a standard height sunflower is better adapted to where sunflower is grown on fully recharged soil profile and the crop is expected to rely on soil moisture for a considerable portion of evapotranspiration (long intermittent stress or terminal stress periods).

This is the first study for sunflower with the specific objective of investigating the effect of plant stature on plant water relations. In general, the stress experienced by the dwarf hybrid, SW-103 was lower compared to the standard height hybrid, IS-6111 (chapter 5). This does not conform to the traditional notion of lower stress tolerance by dwarf cultivars compared with standard height cultivars. Similar information is not reported in sunflower, although recent results in cereals concur with these observations. The lower stress in the dwarf sunflower cultivar was observed in spite of lower water extraction compared to the standard height hybrid. A possible explanation for this is that the dwarf cultivar perceived water stress earlier and initiated other drought tolerance mechanisms, while standard height hybrids relied on soil water extraction and allowed water potential to drop to a lower level. Higher leaf area for transpiration might also have contributed to the greater loss of water and lower water potential in IS-6111. On the contrary, lowering leaf water potential may be a strategy for standard height hybrids to extract more water from the soil profile. In the cohesion theory of water extraction, water potential differential between leaf and soil is the driving force for water extraction. Therefore, the standard height hybrid which had lower leaf water potential than dwarf cultivars most of the time, in spite of similarity in root hydraulic conductivity, was able to extract more water during those periods.

The differences in stress levels between Aurora and SW-103 may be related to their plant architecture. Aurora is reported to have a more open canopy compared to the dwarf hybrids or standard height cultivars. However, plant architecture and its effect on the aerodynamics of the crop canopy was not studied in the present investigation. Therefore, observations on microclimate within the canopy and real time transpiration response through sap flow measurements will help in assessing the effect of plant architecture on plant water relations.

Drought responses, both osmotic and stomatal, were observed earlier in the dwarf cultivars compared to the standard height cultivar. This suggests that the dwarf cultivars failed to meet the demand of its transpiring surface (although it was smaller) and resorted to osmotic adjustment and stomatal closure to maintain positive turgor. Greater osmotic adjustment per unit of water stress for Aurora than SW-103 (Figure 5.3), indicated significant variation in drought adaptation among short statured cultivars. The lower stomatal conductivity of SW-103 and Aurora was related to limited water extraction and/or stomatal sensitivity. This suggests a more conservative strategy of water use by dwarf cultivars compared to the standard height cultivar. Osmotic adjustment has been reported to increase productivity under water stress conditions in many crops. Therefore, greater osmotic adjustment of dwarf sunflower cultivars should be helpful under Prairie conditions where crops have to face intermittent water stress. However, the observation of osmotic adjustment at relatively high ψ_l levels for SW-103 suggests that other, non-hydraulic, messages were involved in sensing water shortage in the soil and initiating drought response. Non-hydraulic messages have been identified in a number of crops like wheat, lupins (Turner, 1997), including sunflower (Fambrini et al., 1994). Future studies should focus on differences in the ability to sense water shortage among different stature sunflower cultivars.

The results from water relation observations have implications for cropping systems. The standard height sunflower hybrid like canola, is a water user. It relies more on its root system and depends less on stomatal regulation to reduce water loss. Osmotic adjustment is initiated later in standard height cultivars than in dwarf sunflower cultivars. Therefore, as long as moisture was available to meet its water requirement, a standard height hybrid should perform very well. On the contrary, dwarf sunflower cultivars, like dwarf wheat cultivars, are more water conserving. They initiate stomatal and osmotic regulation earlier in the season than standard height cultivars. While osmotic regulation maintains productivity, stomatal regulation in dwarf sunflower conserves water for later stages. Thus, under conditions where there is no moisture deep in the profile and/or severe terminal stress is faced, the dwarf cultivars should be better able to conserve water for grain filling period than the standard height cultivars. In contrast, under the above conditions standard height cultivars may senesce prematurely, and face a significant yield reduction.

The seed yield of sunflower crops depended on the genetic potential of the cultivar and not on the plant stature. The photosynthesis conserved by reducing plant height was not translated into higher yields in the dwarf sunflower. The lower genetic potential of the dwarf stature sunflower in biomass production can be compensated by adopting appropriate management practices (solid seeding) to produce seed yields comparable to the standard height sunflower. Therefore, under typical Manitoba conditions. dwarf sunflower can be adopted to realise the management benefits like solid seeding, shorter duration and rotational benefits.

However, the main reason for not realising the yield advantages with a dwarf sunflower was the presence of the complex capitulum, which utilized about 50% of the head dry matter. In the present study, only one out of four dwarf cultivars had a higher harvest index than standard height cultivars. In sunflower, intermediate storage of photosynthates is more important for yield formation than in small grain cereals. In cereals, reducing stem height diverts photosynthates to the head. However in sunflower, retranslocating assimilate from the stem to the seed head depended on cultivar (not on stature). Aurora diverted a greater proportion of photosynthates to the head than all other cultivars tested, however retranslocation from head biomass into seeds was different among all cultivars compared. This independence between plant stature and biomass partitioning has a positive element, as it indicates that reduced height sunflowers with a higher harvest index can be developed. This suggests that more breeding effort is warranted to improve the harvest index in both dwarf and standard height cultivars.

Seed yield is an integral of the entire growing season and therefore variation in one-time physiological measurement may not account for the yield variations observed under mild stress conditions. Thus, the cultivar with a better water supply (IS-6111) had seed yield similar to Aurora, a cultivar with lower water supply. Similarly, the cultivar with better drought response, SW-103, had lower seed yield than IS-6111, the cultivar that experienced higher water stress. These observations indicate that different cultivars used in this study achieved yield levels by adopting different strategies. Under such moderate stress, the different strategies adopted by SW-103, Aurora or IS-6111 averted critical stress. For example, IS-6111 responded to short periods of stress by lowering water potential and extracting more water from soil profile. On the other hand, dwarf cultivars resorted to osmotic adjustment and stomatal regulation. In different stature wheat it has been observed that under moderate stress, potential of the cultivar regulates yield formation while under severe stress drought tolerance regulates yield formation. The same may be true in sunflower.

The ideal dwarf sunflower cultivar for the Prairie should have water extraction like IS-6111, a smaller head and thin stem similar to Aurora, higher harvest index like SW-103 and the stress responses of dwarf sunflower cultivars. Thus, a sunflower crop growing in the sub-humid regions with more assured moisture supply should be able to meet its water needs during dry cycles and should have drought tolerance traits like osmotic adjustment and stomatal regulation to prolong the grain development. In contrast, a crop growing in more arid conditions should have deeper rooting to provide better seed yield stability under extended stress along with drought tolerance traits to complete the grain development under terminal stress. However, both situations will benefit from smaller head and thin stem of Aurora, which diverts most of the biomass into reproductive parts. Finally, the ideal cultivar should be able to retranslocate an optimum amount of photosynthate from intermediate storage organs like stems, roots, leaves and heads into seeds. However, precaution is necessary to avoid excessive retranslocation, which results in pith autolysis and stem breakage. Thus, presently available dwarf sunflower can be adopted in the Canadian Prairie because of management benefits and shorter growth period.

6.1 Conclusions

Evaluation of divergent sunflower cultivars under different environments in this study has produced many unique results and has confirmed results of previous studies. The following points identify the unique contributions of this study to the adaptive physiology of sunflower under temperate subhumid conditions.

- Reducing plant height reduced root growth of the dwarf hybrid.
- Rate of root penetration in sunflower was related to seasonal temperature.
- Root systems of different dwarf cultivars were different, which indicates role of dwarfing gene and/or genetic background in rooting system.
- Standard height cultivars were more efficient than dwarf types in extracting soil moisture.
- The dwarf hybrid, SW-103 experienced lower water stress compared to standard height cultivars under field conditions.
- In addition to plant stature, plant architecture and/or genetic background of cultivars influenced water stress levels.
- Short stature cultivars initiated stress responses like osmotic adjustment and stomatal regulation earlier than standard height cultivars.
- Genotypic differences in osmotic adjustment were observed.
- All sunflower cultivars maintained positive turgor under the typical conditions of the region, although the strategies adopted were different.
- Harvest index, unlike in wheat, was not higher in all short stature sunflower cultivars compared to standard height cultivars. However, higher harvest index

observed in SW-103 indicated the possibility of breeding short stature cultivars with higher harvest index.

- Nearly half of the dry matter stored in the head was not utilised for seed formation in sunflower.

-Seed yield of presently available different height sunflower cultivars depend on genetic background and not on plant stature.

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APPENDICES

Appendix 1. Details of fertilizer used in different experiments.

Trial	Fertilizer kg ha^{-1}† N	P_2O_5	K_2O	S
Winnipeg 1993	90	45	0	20
Carman 1994	0	43	0	22
Winnipeg 1994	93	27	0	24
Carman 1995	60	30	0	9
Winnipeg 1995	96	33	0	17
Greenhouse Trials	80	38	0	20
Carman Root Study	87	36	0	11

† Based on soil test results (Norwest Lab, Winnipeg).

Appendix 2. Description of Sunflower Growth Stages (Schneiter and Miller, 1981).

Vegetative Stages		Reproductive Stages	
VE	The hypocotyl arch and cotyledons have emerged through the surface and the first true leaf blade is < 4 cm	R1	Miniature floral head surrounded by immature bracts.
		R2	The internode directly below the base of the inflorescence elongates 0.5 to 2.0 cm above the nearest leaf
$V_{(n)}$	Number of true leaves (> 4 cm) are counted and expressed as V_1, V_2, V_3....	R3	Internode lifts inflorescence above 2.0 cm
		R4	Inflorescence begins to open. Small ray florets are visible from the top.
		R5	Beginning of anthesis. This stage is further divided into substages. eg. 5.2, 5.5, 5.9 when 20, 50 and 90 % disk florets completed flowering or in anthesis.
		R6	Anthesis complete, ray florets wilting
		R7	Back of inflorescence started to turn light yellow.
		R8	Back of head is yellow. Bracts are still green
		R9	Bracts yellow and brown. Head may turn brown. Considered physiological maturity.

Appendix 3. Summary of experimental locations, dates of seeding, dates of harvest and duration of different experiments.

Location	Year	Sowing Date	Harvest Date	Duration
Space Planted Trials:				
Carman	1994	May 26	September 28	123 DAS
Winnipeg	1994	June 02	October 06	126 DAS
Carman	1995	May 23	September 14	113 DAS
Winnipeg	1995	May 31	October 04	128 DAS
Root Study:				
Carman†	1994	June 01	August 30††	90 DAS
Agronomy Trials:				
Morden‡	1993	May 13	September 11-October 11	120-150 DAS
Winnipeg‡	1993	May 25	October 12-19	140-147 DAS
Winnipeg	1994	May 30	September 20-October 06	114-129 DAS
Carman	1995	May 13	August 29-September 16	103-121 DAS
Green House Studies: Small Pots:				
Winnipeg¶	1996	January 20	February 19	30 DAS

† : Separate space planted trial for field assessment of root system.

††: The plants were sampled at 90 DAS for root length density observation.

‡ : The water use data from these study showed no root activity due to continuous rainfall during the season. Data not presented.

¶ : Small pot (2.0 L) studies for hydraulic conductivity.

Appendix 4. Summary of different soil moisture and water relation measurements made in both space planted and agronomy field trials along with dates and crop stage at the observation time.

Observation	Space planted trials				Agronomy trials	
	Carman 94	Carman 95	Winnipeg 94	Winnipeg 95	Winnipeg 94	Carman95
Soil moisture						
1	08th June(13)†	06th June(14)	09th June(07)	05th June(06)	21st June(22)	07th June(21)
2	29th June(34)	07th July(45)	06th July(35)	11th July(42)	05th July(35)	06th July(50)
3	13th July(48)	24th July(62)	19th July(46)	25th July(56)	18th July(50)	21st July(65)
4	27th July(62)	29th July(67)	17th Aug(76)	08th Aug(71)	22nd Aug(85)	03rd Aug(78)
5	18th Aug(84)	04th Aug(73)	07th Sept(97)	31st Aug(94)	06th Sept(100)	21st Aug(96)
6	25th Aug(91)	17th Aug(85)	13th Oct(133)	12th Oct(135)	12th Oct(135)	23rd Sept(130)
7	29th Sept(123)	21st Sept(120)				
Leaf water potential						
1	29th June(34)	07th July(45)	06th July(35)	10th July(41)	05th July(35)	04th Aug(79)
2	13th July(48)	28th July(66)	20th July(47)	25th July(56)	18th July(56)	10th Aug(85)
3	27th July(62)	03rd Aug(72)	05th Aug(63)	08th Aug(71)	01st Aug(65)	21st Aug(96)
4	09th Aug(75)	10th Aug(79)	17th Aug(76)	16th Aug(78)	15th Aug(77)	
5	18th Aug(84)	21st Aug(90)		31st Aug(94)		
6	24th Aug(90)					
Leaf osmotic potential						
1	29th June(34)	20th June(28)	06th July(35)	10th July(41)	05th July(35)	07th July(51)
2	13th July(48)	07th July(45)	21th July(47)	25th July(56)	18th July(56)	20th July(64)
3	27th July(62)	20th July(58)	05th Aug(63)	09th Aug(72)	01st Aug(65)	28th July(72)
4	10th Aug(76)	28th July(66)	08th Aug(66)	16th Aug(78)	14th Aug(76)	04th Aug(79)
5	18th Aug(84)	03rd Aug(72)	17th Aug(75)	31st Aug(94)	06th Sept(100)	21st Aug(96)
6	24th Aug(90)	10th Aug(79)	06th Sept(96)			
7		21st Aug(90)				

Contd

Appendix 4. Summary of different soil moisture and water relation measurements in different field trials along with dates and crop stage at the observation time. (Continued).

Observation	Space planted trials				Agronomy trials	
	Carman 94	Carman 95	Winnipeg 94	Winnipeg 95	Winnipeg 94	Carman95
Relative water content						
1	29th June(34)†	07th July(45)	06th July(35)	11th July(42)	05th July(35)	07th July(51)
2	13th July(48)	20th July(58)	21th July(47)	25th July(56)	18th July(56)	20th July(64)
3	27th July(62)	28th July(66)	05th Aug(63)	09th Aug(72)	01st Aug(65)	28th July(72)
4	09th Aug(75)	03rd Aug(72)	08th Aug(66)	16th Aug(78)	14th Aug(76)	04th Aug(79)
5	18th Aug(84)	10th Aug(79)	17th Aug(75)	31st Aug(94)	06th Sept(100)	21st Aug(96)
6	24th Aug(90)	21st Aug(90)	06th Sept(96)			
Portable photosynthesis equipment readings						
1	23rd July(58)	28th July(66)	05th Aug(63)	10th July(41)	04th July(34)	28th July(72)
2	18th Aug(84)	03rd Aug(72)	17th Aug(75)	13th July(44)	07th July(37)	21st Aug(96)
3		10th Aug(79)		09th Aug(72)	15th Aug(77)	
4		15th Aug(84)		16th Aug(78)		
5		21st Aug(90)		31st Aug(94)		

† Numbers in the bracket are days after seeding.

Appendix 5. Surface shield used for measuring 0-10 cm soil moisture.

Appendix 6. Summary of weather parameters during different water relations observations in space planted and agronomy trials.

Sl	Date	Temperature			Ppt.†	Wind	Solar Rad.
		Max. (°C)	Min. (°C)	Mean (°C)	(mm)	(km)	(MJ/m^2)
Space Planted Trials							
Carman 1994							
1	29th June(34)††	21.9	9.5	15.8	11.0	-	25.6
2	13th July(48)	24.7	9.5	15.9	0.0	-	14.9
3	27th July(62)	29.6	11.1	19.7	0.0	-	23.7
4	09th Aug(75)	22.8	4.9	14.3	11.0	-	21.2
5	18th Aug(84)	26.8	10.8	17.1	0.0	-	14.8
6	24th Aug(90)	30.0	12.4	21.2	0.0	-	22.5
Carman 1995							
1	07th July(45)	30.2	10.9	19.4	2.0	-	-
2	28th July(66)	26.3	12.4	19.8	0.0	-	-
3	03rd Aug(72)	26.8	10.6	18.5	0.0	-	-
4	10th Aug(79)	23.5	11.3	17.4	0.0	-	-
5	21st Aug(90)	25.4	10.4	18.0	65.6	-	-
Winnipeg 1994							
1	06th July(35)	21.2	9.3	15.3	68.2	12.9	-
2	20th July(47)	23.5	16.2	19.9	7.6	16.8	-
3	05th Aug(63)	25.3	9.1	17.2	5.2	16.0	-
4	17th Aug(76)	23.1	10.4	16.8	0.0	13.0	-
Winnipeg 1995							
1	10th July(41)	27.6	16.6	22.8	0.0	-	-
2	25th July(56)	25.7	12.0	18.8	0.7	-	-
3	09th Aug(72)	27.1	14.7	20.8	0.0	-	-
4	16th Aug(78)	31.3	18.0	24.9	2.2	-	-
5	31st Aug(94)	23.2	11.7	17.0	26.6	-	-
Agronomy Trials							
Winnipeg 1994							
1	05th July(35)	26.2	15.0	20.6	68.2	10.5	-
2	18th July(56)	24.1	15.3	19.7	4.3	16.8	-
3	01st Aug(65)	28.7	12.9	20.8	5.8	6.1	-
4	15th Aug(78)	29.4	9.8	19.6	0.0	13.2	-
Carman 1995							
1	04th Aug(79)	29.7	10.3	20.1	0.0	-	-
2	10th Aug(85)	23.5	11.3	17.4	0.0	-	-
3	21st Aug(96)	25.4	10.4	18.4	65.6	-	-

† Precipitation received in the previous 72 hours.

†† Numbers in the bracket are days after seeding.

Appendix 7. Summary of weather parameters during photosynthesis observations in space planted and agronomy trials.

Sl No	Date	Temperature			Ppt.*	Wind	Solar Rad.
		Max. (°C)	Min. (°C)	Mean (°C)	(mm)	(km)	(MJ/m^2)
Space Planted Trials							
Carman 1994							
1	23rd July(58)†	27.8	13.2	20.3	1.0	-	28.1
2	18th Aug(84)	26.8	10.8	17.1	0.0	-	14.8
Carman 1995							
1	28th July(66)	26.3	12.4	19.8	0.0	-	-
2	03rd Aug(72)	26.8	10.6	18.5	0.0	-	-
3	10th Aug(79)	23.5	11.3	17.4	0.0	-	-
4	17th Aug(86)	33.5	19.1	24.3	0.0	-	-
5	21st Aug(90)	25.4	10.4	18.0	65.6	-	-
Winnipeg 1994							
1	05th Aug(63)	25.3	9.1	17.2	4.0	16.0	-
2	17th Aug(75)	23.1	10.4	16.8	0.0	13.0	-
Winnipeg 1995							
1	10th July(41)	27.6	16.6	22.8	0.0	-	-
2	13th July(44)	30.7	19.5	24.8	3.0	-	-
3	09th Aug(72)	27.1	14.7	20.8	3.0	-	-
4	16th Aug(78)	31.3	18.0	24.9	2.2	-	-
5	31st Aug(94)	23.2	11.7	17.0	26.6	-	-
Agronomy Trials							
Winnipeg 1994							
1	04th July(34)	25.8	16.7	21.3	68.2	10.0	-
2	07th July(37)	17.1	9.3	13.2	0.0	16.2	-
3	15th Aug(78)	29.4	9.8	19.6	0.0	13.2	-
Carman 1995							
1	28th July(72)	26.3	12.4	19.8	0.0	-	-
2	21st Aug(96)	25.4	10.4	18.4	65.6	-	-

* Precipitation received in the previous 72 hours

† Numbers in the bracket are days after seeding.