FRUIT QUALITY AND COMPOSITION, GROWTH, WATER RELATIONS, AND POSTHARVEST PERFORMANCE OF 'BRAEBURN' APPLES (*Malus Domestica* BORKH.) UNDER REDUCED IRRIGATION

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ABSTRACT

Benefits of reduced irrigation in apple production include decreased costs, control of vegetative growth, possible improvement in fruit quality, and reduced leaching of nutrients and pesticides into ground water. This study was on the effects of withholding irrigation at different times of the growing season on water relations, photosynthesis, growth, fruit quality and composition, and postharvest performance of 'Braeburn' apples (*Malus domestica* Borkh.).

Seven-year-old trees on MM. 106 rootstock were subjected to four irrigation treatments in a randomized complete block design. The treatments were: fully watered control (C); early withholding (EW) of irrigation from full bloom until 104 days after full bloom (DAFB); late withholding (LW) of irrigation from 104 DAFB up to final harvest at 194 DAFB; and nonirrigated (NI), where trees were not irrigated during the entire growing season.

Trees not receiving irrigation at any stage developed a lower predawn and midday leaf water potential relative to the well-watered control. For LW and NI trees towards the end of the growing season, water stress caused a reduction in the rate of photosynthesis (*Pn*), stomatal conductance (g_s), and the rate of transpiration. The reduction in *Pn* was caused by non-stomatal factors in addition to a reduction in g_s. Withholding irrigation caused an increase in canopy temperature and canopy-air temperature difference in LW and NI possibly due to the reduction in the rate of transpiration.

Fruit growth and fruit growth rate measured from 42 DAFB up to harvest were not affected by the treatments although shoot growth and increase in trunk circumference were significantly reduced by withholding irrigation during the early and entire season. Mean fruit weight at harvest and return bloom were reduced in EW and NI relative to C and LW. The treatments had no effect on total yield per tree, crop density or yield efficiency.

At final harvest, total soluble solids, soluble sugars (fructose, sucrose, and sorbitol), flesh firmness, and red skin colour intensity were higher in NI and LW than in C. The concentration of glucose and minerals (N, P, Ca^{2+}, Mg^{2+}, and K^{+}) in the fruit was not affected by the treatments.

Withholding irrigation during the late and entire growing season resulted in more advanced fruit maturity as indicated by an earlier ethylene climacteric, more yellow background skin colour, and increased total soluble solids concentration. Firmness remained higher in LW and NI than in EW and C during a 12-week storage period at 1 °C. Weight loss was higher in C than in the reduced irrigation treatments. Skin permeance to water vapour was higher in C relative to EW and NI.

This study showed that withholding irrigation late in the season may be used in apple production with improved fruit quality in terms of increased total soluble solids, firmness, soluble sugars, and intensified red skin colour without adverse effects on fruit size and yield. For the control of vegetative growth, withholding irrigation early in the season is best but this treatment may adversely affect fruit size. Reduced irrigation is also potentially beneficial in terms of reduced weight loss and increased firmness in storage.

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GLOSSARY OF ABBREVIATIONS

A	- Surface area of the fruit (m^2)
ACC	- 1-aminocyclopropane-1-carboxylic acid
ANOVA	- Analysis of variance
C	- Control
CD	- Crop density (g of fruit per unit trunk cross sectional area)
C_a	- External CO_2 concentration ($\mu mol\ mol^{-1}$)
C_i	- Intercellular CO_2 concentration ($\mu mol\ mol^{-1}$)
DAFB	- Days after full bloom
ET	- Evapotranspiration
EW	- Early withholding of irrigation
FGR	- Fruit growth rate ($mm\ day^{-1}$, $g\ day^{-1}$, or $cm^{-3}\ day^{-1}$)
Ft_1	- Fruit size at time 1 (mm, cm^{-3}, or g)
Ft_2	- Fruit size at time 2 (mm, cm^{-3}, or g)
FW	- Initial fresh weight
GLC	- Gas liquid chromatography
GLM	- General linear models
g_s	- Stomatal conductance ($mol\ CO_2\ m^{-2}\ s^{-1}$)
H	- Hue angle (°)
HPLC	- High performance liquid chromatography
IR	- Infrared
L	- Lightness (%)
LW	- Late withholding of irrigation
MPa	- Mega Pascal (1 MPa = 10 bars)
n	- Number of observations
NI	- Nonirrigated
PAR	- Photosynthetically active radiation ($\mu mol\ quanta\ m^{-2}\ s^{-1}$)
Pn	- Rate of photosynthesis ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)

P'_{H2O} - Skin permeance to water vapour (mol s^{-1} m^{-2} Pa^{-1})

RCBD - Randomized complete block design

RDI - Regulated deficit irrigation

RH - Relative humidity (%)

r'_{H2O} - Rate of water loss (mol s^{-1})

SAM - S-adenosylmethionine

SEM - Standard error of the mean

T - Rate of transpiration (mmol m^{-2} s^{-1})

TA - Titratable acidity (% malic acid)

T_a - Air temperature (°C)

T_c - Canopy temperature (°C)

T_c-T_a - Canopy-air temperature difference (°C)

T_1 - Time 1 (day)

T_2 - Time 2 (day)

TCA - Trunk cross-sectional area

TDR - Time domain reflectometry

TSS - Total soluble solids

θ - Soil volumetric water content (m^3 m^{-3})

VPD - Vapour pressure deficit (kPa)

VP_{air} - Actual water vapour pressure (kPa)

VP_{sat} - Water vapour pressure at saturation (kPa)

YE - Yield efficiency (g of fruit cm^{-2} TCA)

Ψ - Leaf water potential

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CHAPTER ONE

GENERAL INTRODUCTION

Apple production is important in many regions of the world with varied climatic conditions. The apple has a diverse climatic adaptation which makes it the most widely planted fruit crop of the temperate zone (Westwood, 1993, p. 52). Important apple production areas include Southeastern Europe, Southwestern Siberia, Central Asia and North America (Westwood, 1993, p. 52). In some apple growing regions, water resources are under severe strain, because water is being pumped from its source at a higher rate than it is being recharged (Solley, 1993). With increasing populations, especially in urban areas, and increased industrial and commercial activities, less water is or will be available for agricultural use. Dwindling available water resources create problems not only for the general public and governmental agencies, but also for scientists working on water research and crop production (Csizinski, 1993). Scientists need to conduct research and find methods to produce crops with less water without reducing yield quantity and quality.

In some countries or states, there are legislations restricting the amount of nutrients and/or pesticides which may be leached into the ground water. For example, in California, the primary water issues affecting growers are: 1) water availability and cost during drought periods, 2) water runoff, and 3) nitrate and pesticide pollution of groundwater and bodies of water (Kabashima, 1993). According to Kabashima (1993), these problems have caused nurseries to change their management practices to adhere to public policy, or discontinue business in their geographic areas. The use of reduced irrigation strategies in crop production is a management practice that reduces leaching of nutrients and pesticides into the groundwater and is thus an

environmentally beneficial practice.

An additional benefit of using less water in apple production is the reduction of pruning costs. Any management system that tends to reduce vegetative growth gives an opportunity for reducing production cost and improving productivity. Considerable work has been done on the effect of regulated deficit irrigation (RDI) on the vegetative growth of fruit crops such as peaches and pears (e.g., Chalmers et al., 1981). Regulated deficit irrigation is the return of less water than the trees are evapotranspiring during particular periods (Boland et al., 1993). Studies have shown that RDI applied at the right time may limit shoot growth while stimulating subsequent fruit growth (Mitchell et al., 1984). According to Chalmers (1989), the vegetative vigour of the crop may be suppressed by RDI in favour of fruit growth. The result is less need for pruning or use of dwarfing rootstocks with often an increase in yield especially in high density orchards. These results are based on fruit crops such as peaches and pears which have a distinct phenological separation of shoot and fruit growth (Chalmers, 1989). In apples, there is no such clear separation and the rapid growth phases of the two organs sometimes overlap (Fig. 1.1). In this thesis, the responses of the vegetative and reproductive growth of apple trees to withholding irrigation at different times of the growing season are discussed.

This thesis also explores the effect of reduced irrigation on photosynthesis, stomatal conductance, canopy temperature (T_c) and canopy-air temperature difference (T_c-T_a). The use of T_c and T_c-T_a as a measure of plant water status has hitherto been largely confined to field crops with very little application in deciduous fruit crops (Jackson, 1982).

Although reduced irrigation, either as RDI or application of less water through trickle irrigation systems has shown benefits in terms of reduced vegetative growth and increased yield in some fruit crops, there is limited information regarding its effect on fruit quality. If this practice is to be used

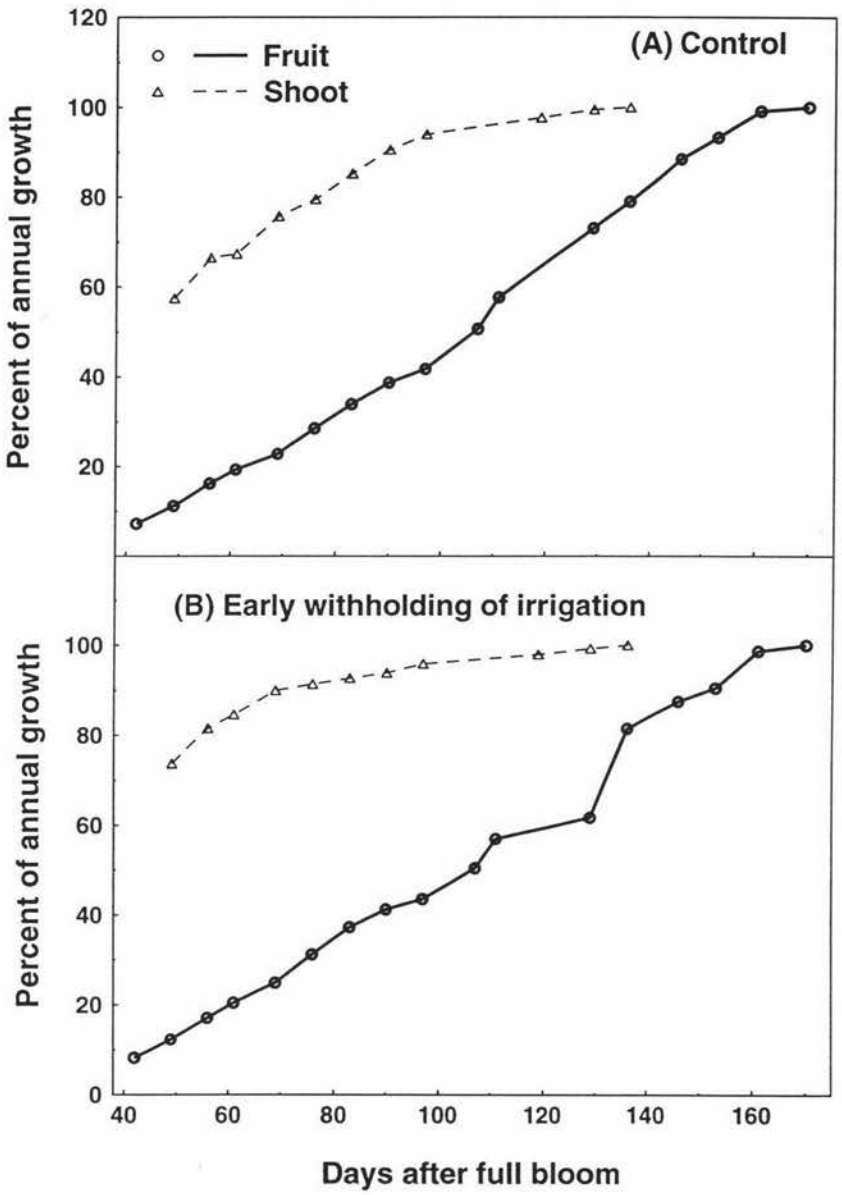

Figure 1.1: Cumulative growth of annual shoots and fruit of 'Braeburn' apples expressed as a proportion of the total seasonal growth. The trees in (B) were subjected to withholding of irrigation from full bloom to 104 days after full bloom.

successfully as a management tool, there is need to quantify its effects not only on fruit quality and composition at harvest but also, and perhaps more importantly, on the postharvest behaviour of the fruit. The capacity to maintain quality during storage is important for horticultural products, and the predictability and manipulation of storage quality has considerable commercial benefit through reduction in storage loss. Some of the important postharvest quality attributes for which literature is limited or nonexistent include the effect of preharvest irrigation amount and frequency on postharvest weight loss of the fruit. This is important because it leads to a reduction in the marketable weight of the fruit and is a major cause of deterioration in storage (Woods, 1990).

Given the limited work done on the effects of reduced irrigation on fruit quality, this study was conducted to gain further understanding on the effect of withholding irrigation at different times of the season on the quality of 'Braeburn' apples.

This study focused on the following areas:

I. Water relations, photosynthesis, and growth of 'Braeburn' apple trees grown under different irrigation regimes,

II. the effect of withholding irrigation during the early, late and the entire growing season on the quality and composition of 'Braeburn' apples, and

III. evaluating the postharvest behaviour in terms of maturity, ripening, and weight loss of 'Braeburn' apples grown under different irrigation regimes.

The approach taken was to withhold irrigation and to prevent rainwater from reaching the rootzone at different times of the growing season. Data were collected on plant water status, growth, yield, fruit quality, maturity, and postharvest weight loss characteristics of the fruit. The 'Braeburn' cultivar was chosen because of its importance in the New Zealand export industry.

For example, 'Braeburn' production in New Zealand increased from 3.5 million tonnes in 1994 to 5.2 million tonnes in 1995. The 'Braeburn' export quantity rose from 724,000 tonnes in 1994 to 1.19 million tonnes in 1995 (Horticulture News, October 1995).

CHAPTER TWO

LITERATURE REVIEW

The need to reduce pollution of groundwater by nutrients and pesticides, the limited availability of good quality water, and the demand for more efficient fruit production has encouraged the search for an improved understanding of plant water requirements. Regulated deficit irrigation (RDI) strategy was suggested by Chalmers and co-workers (Chalmers et al., 1981) and has attracted considerable attention from horticulturalists due to its ability to control excessive vegetative growth and for increasing water use efficiency without negative effects on yield. Regulated deficit irrigation is an irrigation strategy based on reducing the water applied during certain growth stages to levels which cause the water potential of the plant to decline to a predetermined level below the maximum water potential at that time and applying the water that the crop uses during the rest of the growing season. Regulated deficit irrigation was initially developed as an approach to irrigation management for the control of vegetative vigour in high-density plantings of peaches. The principle concept of RDI is to establish a controlled water deficit in the plant during periods of rapid shoot and/or slow fruit growth. This water deficit is achieved by irrigating the trees at a rate of water replacement lower than the actual water use. Water is then made readily available during subsequent period of rapid fruit expansion. The first experiments were conducted on late-maturing 'Golden Queen' peaches (Chalmers et al., 1981; Mitchell and Chalmers, 1982), and later applied successfully to 'Bartlett' pears (Mitchell et al., 1984).

2.1 PHYSIOLOGICAL BASIS OF RDI

Regulated deficit irrigation embodies a number of complementary

physiological principles. These are:

2.2.1 Phenological Separation of Shoot and Fruit Growth

Since most events in the development of perennial crops are seasonal and are sensitive to reduced leaf water potential (Ψ) only during active times, periods can be identified during the season when low Ψ can affect one process but not others. For example, the phenologies of fruit and vegetative growth are separated in some fruit crops such that at the beginning of the growth season, fruit development follows shoot development and, in terms of assimilate demand, there is a significant separation between the early active periods of vegetative growth and fruit growth (Chalmers, 1989). Hence one can target vegetative growth with reduced Ψ without affecting fruit growth.

2.2.2 Differential Sensitivities of Tissues, Organs and Processes

Chalmers (1989) has identified the differential sensitivity of tissues, organs and processes as a key factor for the beneficial effects of RDI. The capacity of two or more processes to compete for leaf and/or root products depends on the relative extent to which each process is inhibited by reduced Ψ. Water availability can therefore be manipulated in a variety of ways to beneficially modify developmental processes in fruit trees.

One of the areas where this idea has been put into practice is in fruit growth in relation to vegetative growth. Cell expansion occurs as a result of the uptake of solutes and/or increased cell wall elasticity when they absorb water to restore the balance between the turgor potential of the cell and the negative pressure exerted by the resistances to stretching of the cell wall (Serpe and Matthews, 1994). Therefore cell expansion is very sensitive to reduced plant Ψ. Although fruit cells expand by a similar mechanism and therefore are also sensitive to water stress, they are strong solute sinks and are able to attract water more strongly (Chalmers, 1989).

There is ample evidence of the above phenomenon in studies conducted on a variety of fruits and growing regions. Irving and Drost (1987) found that water stress, if applied after the cell division phase, reduced the terminal shoot growth but did not affect fruit growth and they concluded that shoot extension in the apple is more sensitive to water stress than fruit growth. Similarly, Ebel et al. (1995) used RDI to produce midseason drought stress to restrict vegetative growth of 'Delicious' apples without a reduction in fruit size or yield. Proebsting et al. (1984) induced low Ψ in apple trees by use of trickle irrigation and found that these trees had less vegetative growth, equal or higher yields, and similar fruit size to those receiving ample water. In peaches and pears, RDI reduced excessive vegetative growth without reducing fruit growth and yield (Chalmers et al., 1981, 1986; Mitchell and Chalmers, 1982; Mitchell et al., 1984).

2.2.3 Functional Equilibrium Between Shoot and Root Growth

The vegetative growth of plants is usually limited by the growth potential of the root system (Chalmers, 1989) thus restricting root growth will tend to restrict shoot growth. It has been demonstrated that root growth can be inhibited by limiting the root volume and this results in an increased ratio of fruit growth to vegetative growth per unit tree size (Richards, 1985). Deficit irrigation may cause the roots in the dry soil to become physiologically inactive, effectively decreasing rooting volume (Mitchell and Chalmers, 1983). Indeed, drip irrigation increased yield efficiency while reducing shoot growth compared to overhead sprinklers in apple (Proebsting et al., 1977) which suggests it may have been having an impact by way of root restriction.

2.2 PLANT RESPONSES TO WATER STRESS

2.2.1 Leaf/xylem Water Potential

The leaf and/or xylem water potential, Ψ, is a widely accepted parameter for the measurement of plant water status. The xylem water potential of water stressed plants is generally lower than in plants receiving adequate water. Brun et al. (1985) subjected pear trees to wet, normal and dry treatments and found that the Ψ of the trees under dry treatment decreased steadily after full bloom and continued as soil water was depleted whilst the values remained higher in the normal and wet treatments. In 'Braeburn' apples, differences of up to 0.7 MPa in Ψ between irrigated and nonirrigated trees were observed by Mills .et al. (1994). In a study by Chalmers et al. (1986), withholding irrigation reduced the leaf water potential of 'Bartlett' pear trees at dawn and midday by about 0.1 and 0.5 MPa respectively compared to control.

In many plant species, there is a diurnal variation in Ψ (Jones et al., 1985). Goode and Higgs (1973) compared the leaf water potentials of irrigated and non-irrigated apple trees and obtained a considerable diurnal change in Ψ (from between -0.1 and -0.2 MPa before sunrise to between -1.5 and -2.5 MPa after midday) even when the soil moisture tension was low. This is an indication that Ψ is also dependent on the evaporative demand of the atmosphere in addition to the soil water status. Indeed, Smart and Barrs (1973) demonstrated that the diurnal variation in environmental parameters such as radiation, temperature and saturation vapour pressure deficit (VPD) accounted for 74% to 99% of the diurnal variation in Ψ in peaches, prunes, citrus and grapes. Similarly, Chalmers et al. (1983) found that the diurnal maximum values in Ψ of peach trees paralleled those of soil water potential whilst the minimum values did not change greatly with the decrease in soil water potential during the drying cycle. McCutchan and Shackel (1992) have suggested that the variability associated with changing environmental

conditions can be reduced by the use of predawn Ψ measurements. According to these authors, predawn Ψ measures the integrated effect of soil, plant, and atmospheric conditions on water availability within the plant itself. The predawn Ψ, however, may not indicate the soil-water status over the entire root zone because it tends to be biased towards the water status of the wettest part (Jones, 1990).

In this study, measurements of both predawn and midday Ψ were taken to determine plant water status. These were complemented by measurements of volumetric soil water content.

2.2.2 Physiological Processes

When soil water is adequate, the movement of water in plants is controlled by transpiration which is regulated by both stomatal aperture and the evaporative demand. When the soil dries out however, the movement through the plant system is regulated primarily by soil water supply and root conductivity (Syvertsen, 1985). Water stress occurs when absorption lags behind transpiration (Kramer and Boyer, 1995, p. 183) and is characterized by a decrease in water content, turgor, and total plant water potential resulting in wilting, partial or complete stomatal closure and a decrease in cell enlargement and plant growth. Severe water stress conditions may cause cessation of growth, decrease or cessation of photosynthesis, disturbance of many metabolic processes and even death of the plant. This section discusses some of the physiological processes that are affected by water stress in the plant system.

2.2.2.1 Stomatal Conductance

Given that the leaf water potential is usually much higher than the water potential in the atmosphere, plants have developed characteristics and structures such as stomata which control the balance between water loss and

carbon gain (Hinkley and Braatne, 1994). Stomata are have a very important role to play with regard to plant water status. Stomatal conductance (g_s) is influenced by environmental and plant factors such as the level and quality of light, the concentration of CO_2 and relative humidity in the surrounding atmosphere, soil water status, plant water status, and plant growth regulators (Hinkley and Braatne, 1994; Kramer and Boyer, 1995, p. 265).

In general, stomatal conductance decreases in response to loss of turgor upon exposure to low soil-water potentials and/or low humidity. In several plant species, stomatal closure has been observed in response to the dryness of the air regardless of the leaf water potential (e.g., Cohen and Cohen, 1983). Low levels of soil moisture have also been shown to induce stomatal closure even when the leaf water potential was kept high under experimental conditions (Gollan et al., 1986). This has led to speculations that g_s can be controlled by a chemical message, originating in dehydrating roots and conveyed by the water flux towards the stomatal complex. It has been suggested that abscisic acid (ABA) may be the chemical message produced by the root tip and translocated to the leaves where it induces stomatal closure (Shulze, 1993). According to this theory, an increase in ABA concentration within leaf tissue under deficit conditions stimulates rapid ion efflux from the guard cells leading to stomatal closure (Rashke and Hedrich, 1985). Indeed, increases in ABA concentration in plants under water stress is well documented (e.g., Zhang and Davies, 1987). Although there is considerable evidence to support this theory, there is still some controversy (Kramer, 1988; Passioura, 1988; Saliendra et al., 1995) about the nature and source of this signal.

Low leaf water potential also leads to stomatal closure. Reduced g_s in response to low Ψ has been extensively documented, but the underlying mechanism(s) and consequences of this response are still under investigation (Saliendra et al., 1995). In avocado and citrus, a reduction in Ψ below -1.0

MPa initiated stomatal closure (Kriedeman, 1986). Young et al. (1981) found that stomatal closure occurred in peach seedlings when Ψ dropped below -2.6 MPa and no apparent correlation existed between stomatal closure and turgor pressure. Olsson and Milthorpe (1983) however found no clear relationship between stomatal conductance and Ψ of peaches. They thus concluded that Ψ may have only a small effect upon stomatal conductance. Jones et al. (1983) found that, under conditions of lower g_s, Ψ of water stressed apple trees was higher than that of well-watered trees, suggesting that g_s might in fact control Ψ. Also, the diurnal course of g_s does not correlate well with Ψ in apple trees hence Ψ is not a primary regulator of g_s (Lakso, 1985). In some cases, stomatal conductance seems to be relatively unaffected by decreasing Ψ until a threshold value is reached at which stomatal conductance decreases sharply over a narrow range of Ψ (Hsiao, 1973). According to Sylvertsen (1985), Ψ does not regulate g_s of fruit trees until extremely low values of Ψ occur. Thus although it is generally assumed that stomata close in response to soil water deficits through the mediation of Ψ, the relationship between g_s and Ψ can take several forms depending on the species and atmospheric conditions (Garnier and Berger, 1987). Furthermore, this relationship is not always unequivocal since in some cases g_s can be reduced without Ψ mediation (Schulze, 1986), and decreased g_s can act as a regulator of Ψ, leading to more negative Ψ values in well-watered plants than in stressed ones (Jones et al., 1983). The possible feed-back effects between these two parameters can thus lead to misinterpretation when they are not measured simultaneously.

In addition, stomata are also sensitive to relative humidity and VPD. In some cases g_s responds to the dryness of the air independently of the leaf water potential. For example, in apricot leaves, Schulze et al. (1972) found that at high RH, stomata remained open in spite of a decrease in Ψ. Midday closure of stomata on hot days as observed in many plant species might be

a response to high VPD in order to prevent the development of critically low Ψ (Lakso, 1985).

The diurnal pattern of stomatal conductance has been investigated in various fruit trees. Peach trees showed higher values of g_s early in the day, followed by a decrease towards sunset (Chalmers et al., 1983). In this study, leaves in the upper layers, exposed to more irradiance, exhibited higher stomatal conductance than the shaded lower leaves. This response may have been as a result of the effect of light on stomatal mechanisms. Stomatal aperture is affected by both the quality and quantity of light (Kramer and Boyer, 1995, p. 265). Increasing light intensity activates stomatal opening. The action spectrum for stomatal opening involves both red and blue light. When guard cells are irradiated, unidentified receptors of light are activated resulting in the subsequent activation of proton extrusion across the plasma membrane and the hydrolytic and/or phosphorylytic breakdown of starch within guard cell chloroplasts. This leads to a flux of water along a gradient of osmotic potential into the guard cells causing increased turgor pressure of the guard cells and hence stomatal opening (Hinkley and Braatne, 1994).

2.2.2.2 Transpiration

Transpiration may be defined as the loss of water from plants in the form of vapour. Although high rates of transpiration often cause injury, especially in limited soil water availability, transpiration is unavoidable because a leaf structure favourable for the entrance of CO_2 is also favourable for the loss of water vapour. The closure of stomata under low water potential (both soil and leaf) is an adaptive mechanism by the plants to reduce water loss via transpiration (McDermitt, 1990).

The rate of transpiration is controlled by the energy supply, the vapour pressure gradient from leaves to air (VPD), the boundary layer resistance around the leaves or plant canopy, leaf/stomatal resistance, and the water

supply to the roots (Kozlowski et al., 1991). The boundary layer as used here refers to the layer of water vapour and other gases surrounding leaf surfaces in quiet air. The energy required to evaporate water from transpiring structures comes chiefly from incident solar radiation (Hsiao, 1990). The rate of transpiration increases as the steepness of the vapour pressure gradient increases from the plant to air, which depends on temperature and humidity of the atmosphere.

The extent to which stomatal movements affect canopy transpiration is thus dependent on several factors such as energy supply and the proportion of the boundary layer resistance to stomatal resistance (Hsiao, 1990). According to Hsiao (1990), the effect on transpiration by stomatal movement is only high when the stomata are partially closed and when the canopy is closely coupled to the atmosphere in terms of water vapour pressure. A closely coupled canopy is one in which the temperature and the water vapour pressure adjacent to the transpiring surface and the airstream outside the boundary layer are very similar. Thus the gradient in temperature and water vapour pressure between these two locations is very gentle. In a poorly coupled canopy, the boundary layer is relatively thick and gases are not exchanged rapidly with the atmosphere above the canopy. Jarvis and McNaughton (1986) introduced the omega factor Ω, a dimensionless coefficient that varies from 0 to 1 which is indicative of the degree of coupling between the transpiring surface and the free airstream outside the boundary layer. The value approaches 1 when conditions at the leaf or canopy surface are poorly coupled with those of the free airstream or atmosphere. It has been shown that the closer the coupling (the smaller the Ω), the more sensitive is canopy transpiration to stomatal control (Hsiao, 1990). Thus it seems clear that the degree of coupling between the canopy and the atmosphere has a strong effect on the canopy's response to changing environmental conditions and must be understood if we are to gauge

accurately the role of stomatal changes at the leaf level in the process of transpiration. Hinckley and Braatne (1994) cite the Ω for apple trees to be 0.3 indicating a closely coupled canopy.

2.2.2.3 Canopy temperature and canopy-air temperature difference

As indicated earlier, plant water status integrates the effects of available soil water, evaporative demand (ED), and the hydraulic fluxes within the soil-plant-atmosphere continuum. Therefore the measurement of plant water status can be an effective indicator of water stress only if the measurement integrates characteristics of available soil water, potential water use rates, and water flow through the soil-plant system (Spomer, 1985).

According to Jackson (1982), some of the effects of ED have been incorporated in the measurements of plant water status by the use of canopy temperature (T_c) and canopy-air temperature differences (T_c-T_a) as indicators of water stress. It has been shown through energy balance analysis that, (T_c-T_a), is related to the leaf to air vapour pressure deficit and depends on the aerodynamic resistance to water flow and on the net radiation level for a constant T_a (Glenn et al., 1989). In general, the use of canopy-air temperature differences to detect plant water status is based on two assumptions (Jackson, 1982):

i) A well-watered crop will transpire at its maximum potential rate, resulting in leaf temperatures lower than air temperature and,

ii) as water deficits increase, transpiration declines and leaf temperature rises relative to air temperature.

This method is attractive because i) it is relatively easy to use hence one can sample a large number of plants in a relatively short time, ii) it encompasses both plant and environmental factors in the determination of plant water status and may be used for whole plant measurements as well as single leaves or plant parts, and iii) the method is nondestructive.

2.2.2.4 Photosynthesis

In natural or agricultural ecosystems, water is often the most limiting environmental factor for the process of photosynthesis (Salisbury and Ross, 1992, p. 585). Other environmental factors affecting photosynthesis include light, ambient CO_2 and O_2 concentrations, mineral nutrients and leaf temperature (Lawlor, 1987). The process of photosynthesis may be considered conveniently in three stages;

i) diffusion of CO_2 from a gaseous phase in the atmosphere and leaf intercellular spaces into the liquid reaction site at the chloroplast,

ii) photochemical processes and electron transfer, and

iii) biochemical stage, when CO_2 serves as a substrate of reduction processes to organic compounds.

Inhibition of one or more of these stages limits the process as a whole. Plant water deficits may result in low photosynthetic rates in leaves (Sritharan and Lenz, 1989). For example, water stress reduced the rate of photosynthesis in 'Golden Delicious' apples by as much as 50%. In kiwifruit, water deficit reduced the rate of photosynthesis by 53% to 66% in relation to the well-watered control treatment (Chartzoulakis, 1993a).

The process of photosynthesis requires an exchange of gases and this takes place through stomata. Therefore stomatal conductance is an important factor in photosynthesis. The closure of stomata under water stress restricts the uptake of CO_2 and hence the rate of photosynthesis (Farquhar and Sharkey, 1982). Therefore the extent to which stomatal closure affects photosynthetic capacity is indicated by the magnitude of the reduction in intercellular CO_2. In apples, a mild water stress was shown to reduce stomatal conductance and the rate of photosynthesis (Flore et al., 1985).

In some instances however, a low stomatal conductance does not closely correlate to decreased photosynthesis. For example Mills et al. (1994)

found a significant decrease in stomatal conductance in 'Braeburn' apples under water stress, yet photosynthesis was not affected. Chartzoulakis et al. (1993b) working on kiwifruit found that despite large changes in g_s, water stress had little effect upon intercellular CO_2 concentration. Such evidence has led to speculations that photosynthesis may also be under non-stomatal inhibition such that water stress has a direct effect on the rate of photosynthesis even without stomatal closure (Kozlowski et al., 1991). In a study by Janoudi et al. (1993), water stressed cucumber plants had lower stomatal conductances and CO_2 assimilation rates. The authors were able to show that the decrease in the rate of photosynthesis was not solely due to a decrease in CO_2 availability. They showed that some non-stomatal factors were contributing to the decrease in photosynthesis in the stressed plants. Although these 'non-stomatal factors' causing decreases in photosynthesis in stressed plants are not completely understood, several suggestions have been put forth. These include inhibition of the activity of photosynthetic enzymes e.g., fructose-1,6-biphosphate (Berkowitz and Gibbs, 1983) and/or ribulose biphosphate carboxylase oxygenase (RUBISCO) (Von Caemmerer and Farquhar, 1984; Vu and Yelenosky, 1988) and feedback inhibition of photosynthesis due to photoassimilate accumulation (Azcon-Bieto, 1983; Janoudi et al., 1993; Thorne and Koller, 1974).

2.2.3 Plant Growth

2.2.3.1 Vegetative growth

The reduction in growth by water stress has been observed in many studies. Goode and Ingram (1971) studied the growth of apple trees under different irrigation regimes and reported that although shoot growth was reduced in the first season of growth under water deficit, trunk growth was not affected during the first season of growth but was affected in successive seasons. In the long term however, the most marked effect of deficit

irrigation was on shoot number rather than on shoot elongation. Higgs and Jones (1991) showed that when apple trees were subjected to water stress, there was a 40% to 50% reduction in the number of shoots and up to 62% reduction in the weight of shoots removed by summer pruning.

Increase in the trunk cross-sectional area (TCA) of a tree is related to the annual growth of the tree. Westwood and Roberts (1970) found a linear relationship between TCA and the above ground weight of lightly pruned apple trees. Thus a measure of increase in TCA is a good indicator of the vegetative growth of the tree. Water deficit reduces TCA in fruit trees. For example, Girona et al. (1993) reported an 8% reduction in the trunk growth of peach trees subjected to RDI.

Different physiological reasons have been put forward to account for the reduction in vegetative growth in response to water stress. According to Chartzoulakis et al. (1993a and b), the decrease in growth in kiwifruit due to water stress is as a result of a reduction in photosynthesis, leaf area development and photosynthate partitioning. However, according to Kramer (1983, p. 355), the alteration of the pattern of allocation of photosynthates occurs only after prolonged/severe water stress. Hence decreased photosynthesis and altered photosynthate partitioning do not explain the reduction in growth observed under moderate water stress.

The other physiological explanation suggested for reduced growth is that of reduced cell expansion and division. The quantity and quality of plant growth depend on cell division, enlargement, and differentiation, and all these processes are affected by water stress (Kozlowski et al., 1991). Cell division is believed to be the physiological process most sensitive to water stress because a minimum degree of turgor is necessary for cell expansion (Hsiao, 1973; Matthew and Serpe, 1994). Thus water stress reduces growth by reducing cell turgor and hence cell expansion. Cell enlargement is however a complex process that requires simultaneous intake of water, extension of

cell walls, and a sustained supply of solutes necessary to maintain turgor in the expanding cells (Boyer, 1985) hence it is often difficult to find a clear relationship between turgor and cell growth.

The reduction of vegetative growth by water stress has offered the possibility of using irrigation strategies to control vigour of fruit crops. This has been applied successfully in peaches and pears using regulated deficit irrigation (Section 2.1). In this study, the objective was to determine the best time of withholding irrigation during the season for the control of vigour in apple trees.

2.2.3.2 Reproductive growth

In the development of suitable RDI strategies for fruit trees, it is important to understand the effects of water stress on the various processes involved in the reproductive phase of growth. The effects of water stress on the reproductive growth of plants are well documented. Reproduction includes flower bud initiation and development, flowering, pollination and fruit setting, fruit growth and ultimately the yield. All these stages may be affected by water deficits.

Before looking at the effects of water stress on reproductive growth, it is important to understand the stages of fruit growth in apples. The pattern of fruit growth has been estimated for many species by measuring changes in fruit size using either linear dimensions or fluid displacement (Coombe, 1976). Apples display a pattern of growth that follows a single sigmoid growth curve. Here, an initial period of slow growth (stage I) during rapid cell division after anthesis is followed by a period of major increase in size dominated by cell expansion (stage II), and a final period where growth rate decreases and ripening is initiated (stage III) (Rhodes, 1980). Each of these phases is differentially affected by water deficits as discussed in the following subsections.

a) Flower initiation and Fruit development

Water stress may cause serious effects on bud initiation, formation and maturation (Hanan, 1972). In peaches, fruit set was reduced by water stress (Chalmers et al., 1981). According to Powell (1974), initial fruit set is sensitive to water stress. He supported this in a subsequent paper where he reported that the sensitivity of the fruit to outside influences is greatest at the early stages of growth (Powell, 1976). According to Faust (1989, p. 159), severe water stress during the period of flower bud development may decrease return bloom in the following year. Conflicting results were obtained by Mitchell et al. (1984) who reported that RDI increased flower density in pears.

Fruit growth rate is linked to plant water status but little is known of the causes and effects linking water availability and fruit growth (Failla et al., 1992). Generally, fruit of irrigated trees are larger and contain less dry matter than poorly or nonirrigated ones (Guelfat'Reich et al., 1974). According to Failla et al. (1992), water availability can act directly on fruit growth first by reducing cell water content, and indirectly by reducing the biosynthetic capability of the fruit or by reducing the nutritional supply of photosynthates and mineral to the fruit. These mechanisms probably operate at the same time but may have different degrees of importance depending on the intensity and duration of the water deficit, and the phenological stage of fruit growth. Failla et al. (1992) found that fruit growth was reduced progressively with water deficit, whether imposed in stage I or stage II. They found that water deficits decreased fruit growth through two mechanisms depending on whether the fruit was in the phase of cell division (stage I) or of cell enlargement (stage II). When water deficit was imposed on fruit growing by cell division, the decreased growth was directly linked to a lower water uptake, when water deficit was imposed to a fruit in stage II, decrease in growth was linked to a lower dry matter content.

b) Yield

Goode and Ingram (1971) studied the response of 'Cox's Orange Pippin' apples to different soil moisture conditions and found no consistently positive effect of irrigation on fruit size when compared to non-irrigated trees. The irrigated trees, however, generally carried a larger crop, and thus had higher yields. In studies by Guelfat'Reich et al. (1974) and Lötter et al. (1985) 'wet' treatments always yielded larger fruit and higher yields than 'dry' treatments.

Several other studies have however shown increases in yields under RDI treatments. In a study on grapes by Goodwin and Jerie (1989), RDI treatment had more bunches per vine than those on full irrigation. Chalmers et al. (1981) found that high tree density with low rate of water application increased the yield of peaches. They postulated that water stress, if applied at the right time, limited shoot growth but stimulated subsequent fruit growth. Hence the vegetative vigour of the tree was suppressed in favour of fruit growth. In a subsequent paper, Chalmers et al. (1986) suggested that the mechanism by which regulated deficit irrigation reduces vegetative growth but increases fruit yield may be based on the differences in sensitivity to water stress between different tissues or organs. They suggested that RDI during the slow fruit growth phase and the rapid shoot and frame growth would reduce the vegetative growth without loss of fruit size or yield.

In similar studies, Mitchell et al. (1984) reported that final fruit size and yield were not reduced by RDI treatment on pear. Li et al. (1989) showed that it was possible to reduce the vigour of peach trees without affecting fruit size and quality if water stress was imposed at a particular stage of fruit development, normally stage I and II of fruit growth. Beukes and Weber (1982) found that the optimum sequence of water levels necessary to optimize yield in apples was one which indicated a deficit during stage I and stage III of fruit growth and the highest irrigation level in the second

phenological phase of fruit growth. In this study, I attempted to determine if withholding irrigation during the early, late, or entire growing season has any effects of the reproductive growth of 'Braeburn' apples.

2.3 WATER STRESS AND APPLE FRUIT QUALITY

The definition of fruit quality is highly subjective. According to Krishnaprakash et al. (1983), the quality of apples is largely determined by the maturity of the fruit when harvested and on the rate of further maturation, ripening and subsequent behaviour in storage. The maturity of fruit on the other hand is determined by the changes that take place in the fruit during growth and development. As a fruit reaches maturation and ripening several changes take place. These include changes in colour, flesh firmness, fruit respiration rate, internal ethylene concentration, acidity levels and total soluble solids concentration (Kingston, 1992; Westwood, 1993, p. 301).

There is little information regarding the effect of water stress on the quality of the fruit although this is of paramount importance if RDI is to be used as a management tool in fruit production. This section reviews some of the aspects of apple fruit quality and how they are affected by water stress.

2.3.1 Skin Colour

Skin colour in apples is an important quality attribute and is a primary criterion or index used by consumers to determine the degree of fruit maturity (Lancaster et al., 1994). The development of attractive uniformly-coloured fruit is essential in the increasingly competitive international market. In New Zealand, minimum colour standards have been set for red skinned apple varieties destined for export. For example, 'Royal Gala' export standards include a minimum blush of 66% red and a background of light to creamy yellow while 'Braeburn' apples exported from New Zealand must have a blush of 40% red colour (Kupferman, 1994).

Fruit skin colour depends on the amount of pigments in the skin and the type of radiation (Gorski and Creasy, 1977). As fruit matures, it takes the colour characteristic of the cultivar and loses its green under-colour. This normally involves the loss of chlorophyll (Knee, 1972) and either the synthesis of other pigments such as carotenoids or anthocyanins and/or the unmasking of these pigments formed earlier in the development of the fruit (Biale and Young, 1981; Gorski and Creasy, 1977). In some apple cultivars such as 'Braeburn', there is a red blushed side of the fruit that is mainly due to anthocyanins and an unblushed green side (background) that is due to chlorophyll (Gorski and Creasy, 1977).

According to Kingston (1992), the degree of red blush development of the fruit may not be a good indicator of fruit maturity because it varies markedly between fruit positions in the canopy. This is mainly due to the effect of light on fruit colour. Studies have shown that red colour development is higher in apples developing under high light intensities than in apples developing under shade (Jackson et al., 1971; Krishnaprakash et al., 1983; Robinson et al., 1983). Kingston (1992) therefore suggests the use of ground colour, i.e. the colour of the unblushed portion of the fruit, as a more reliable indicator of maturity. Indeed, the yellow background skin colour is widely used as an indicator of maturity in 'Braeburn' apples (Kupferman, 1994). As fruit matures, chlorophyll is broken down and carotenoids are unmasked, hence the ground colour changes from green to yellow (Gorski and Creasy, 1977). Ground colour development may be influenced by nitrogen levels. High nitrogen levels enhance chlorophyll retention hence retarding yellow ground colour development (Magness et al., 1940).

There is no general consensus regarding the effect of reduced irrigation and/or water stress on apple skin colour. Mills et al. (1994) reported that late-season withholding of irrigation enhances the red colour of 'Braeburn' apples. Proebsting et al. (1984) found that deficit irrigation applied throughout the

season did not affect the red colour of 'Delicious' apples. Ebel et al. (1993) applied early season deficit irrigation in 'Delicious' apples and found no effect on skin colour.

These differences could have been a result of withholding irrigation at different times of the growing season. There is need to quantify the effects of water deficit on apple skin colour and to determine the optimum time during the season for withholding irrigation for enhanced skin colour in apples.

2.3.2 Titratable Acidity

Apples contain a number of organic acids the predominant one being malic acid (Kays, 1991, p. 278). During maturation, ripening and storage, the total organic acid content of the fruit gradually declines (Kays, 1991, p. 278; Kingston, 1992). This loss of acids is largely due to the utilization of these compounds as respiratory substrates (Biale and Young, 1981) and as carbon skeletons for the synthesis of new compounds during ripening (Kays,1991, p. 278). A measure of titratable acidity (TA) is thus a useful maturity index in apples. The flavour of the fruit results from the combination of acids, sugars, and volatiles within the fruit (Kingston, 1992). Titratable acidity may therefore be used to predict the eating quality of the fruit after storage.

Several workers have examined the effects of water stress on the TA of apples. However, their results are conflicting. Guelfat'reich et al. (1974) reported that apples from trees subjected to water stress had lower titratable acidity levels than those from the well-watered trees treatments. Similar results were obtained by Ebel et al. (1993) on apple trees stressed during the early growing season. However, Irving and Drost (1987) found that titratable acidity was not affected by water deficit imposed after the cell division phase of fruit growth. Drake et al. (1981) also found that titratable acidity was similar at harvest between fruit receiving adequate moisture and those

receiving deficit irrigation. After five months storage however, the TA was much less in the stressed fruit. Proebsting et al. (1984) report that TA was similar in early harvested fruit for both 'dry' and 'wet' treatments but was less in fruit from trees subjected to a mild water deficit in later harvests (155 days after full bloom or later) and also after storage.

Therefore, the effect of water stress or reduced irrigation on fruit TA is not clear. It is not known whether the time at which water stress or reduced irrigation is applied has any consequence on the TA of the fruit at harvest and during storage.

2.3.3 Total Soluble Solids

As apples mature, starch is converted to simple sugars (Kingston, 1992). These changes occur as a result of the hydrolysis of carbohydrate reserves within the tissue by β-amylase and α-amylase and/or starch phosphorylase (Biale and Young, 1981). This conversion increases soluble solids concentration and fruit sweetness. Since sugar is a major component of soluble solids, it is possible to measure soluble solids in extracted juice by use of a refractometer (Wills et al., 1989).

Most of the work done indicates that water deficit leads to increased total soluble solids concentration in the apple fruit (Assaf et al., 1975; Drake et al., 1981; Guelfat'reich et al., 1974; Irving and Drost, 1987; Mills et al., 1994; Proebsting et al., 1984). Guelfat'reich et al. (1974) suggested that fruit from water stressed trees may have been more mature at harvest than those from plants receiving ample water hence the difference in TSS. However in the study by Proebsting et al. (1984), the soluble solids concentration was higher in the stressed fruit well before maturity (108 days after full bloom). In Asian pears, Behboudian et al. (1994) found a higher TSS in fruit from stressed trees as early as 35 days after full bloom.

The increase in TSS could be due to enhanced conversion of starch to

sugars which occurs as a result of water stress (Kramer, 1983, p. 264) or a dilution effect of solutes in well-watered treatments. Therefore, reduced irrigation can be used to enhance fruit quality in terms of increased TSS and total soluble sugar concentration in apples. It would be of interest to determine whether the seasonal timing of reduced irrigation has any effect on the concentration of TSS.

2.3.4 Flesh Firmness

One of the most important quality alterations associated with maturity and ripening is softening (Ferguson, 1984). Changes in texture of fruit during ripening result from changes in the structure and composition of their cell walls (Rhodes, 1980). Softening affects both the palatability of the fruit and the length of time the fruit may be held (Kays, 1991, p. 269).

Although several authors have reported increased firmness in water stressed fruit (Assaf et al., 1975; Guelfat'reich et al., 1974; Powell, 1976), Ebel et al. (1993) associated the increase in firmness with a decrease in fruit size and hence increased cellular density in fruit from water stressed plants. In their study, when the firmness was adjusted to remove the effect of size, there was no difference in firmness between the treatments. Irving and Drost (1987) and Proebsting et al. (1984) also found that water deficit has no effect on fruit firmness. In this study, I attempted to clarify the effect of reduced irrigation applied at different times of the season on flesh firmness.

2.3.5 Ethylene Production

Ethylene is a plant hormone which regulates many aspects of plant growth, development and senescence. As with other hormones, ethylene is thought to bind to a receptor to form an activated complex which triggers subsequent reaction leading to physiological responses (Yang, 1985). Apples are climacteric (Biale and Young, 1981) i.e they are characterised by transient

increases in ethylene synthesis at an early stage of ripening. Fruit softening, colour changes, development of desirable taste and aromatic flavour are associated with the climacteric cycle (Biale and Young, 1981) and hence the fruit enters the ripe edible stage at or shortly after this peak. The rate of ethylene production and/or internal ethylene concentration is therefore a useful indicator of the physiological state/maturity and the potential storage life of the fruit (Fidler and North, 1971; Wills et al., 1989).

Not much work has been done to study the effect of water stress on the rate ethylene production of the fruit. Guelfat'Reich et al. (1974) reported a higher rate of ethylene production at harvest, storage and on removal from storage in fruits from 'dry' treatments. Ebel et al. (1993) also found that internal ethylene concentrations were higher in RDI apples than in the control apples during most of the developmental period. According to Ebel et al. (1993), the apples receiving deficit irrigation early in the season entered an 'earlier-than-normal' climacteric rise. There is no literature available on the effects of water deficit applied late in the growing season on the internal ethylene concentration.

2.3.6 Fruit Mineral Composition

Low calcium concentration has been associated with the occurrence of many physiological disorders in apples. These include bitter pit, water core, senescent breakdown, internal breakdown, and scald (Shear, 1975). This may be attributed to the role played by calcium in the structure of the cell wall and in the cell membranes (Bangerth, 1979). Calcium binds with the pectin chains in the cell wall to form linkages which enhance the strength of the wall (Ferguson, 1984). Calcium is also important in the cell membranes where it plays a role in the maintenance of membrane integrity (Bower and Cutting, 1988).

The concentrations of other major minerals in the fruit also influence

storage behaviour of the fruit. High K and Mg generally aggravate problems caused by lack of calcium (Bangerth, 1979) while low P increases the risk of low temperature breakdown and is also associated with reduced firmness (Johnson et al., 1987). Too much N leads to decreased fruit firmness, increased chlorophyll and therefore less red and yellow skin colour and may also increase fruit susceptibility to rotting (Kingston, 1992).

Although the effect of environmental factors on mineral plant nutrition is fully recognized, and has been studied in some detail in numerous plant species, rather little attention has been paid to separate organs such as fruits (Tromp and Van Vuure, 1993). Several experiments have been undertaken to investigate the effect of water stress on fruit mineral content. However, results from these studies are conflicting. Goode and Ingram (1971) and Mills et al. (1994) found that water stress led to decreased calcium concentration in the fruit. Goode and Ingram (1971) found an increase in K concentration as a result of water stress whereas Mills et al. (1994) found no effect of water stress on K concentration. Guelfat'Reich et al. (1974) and Lötter et al. (1985) found a lower K in water-stressed fruit at harvest. Irving and Drost (1987) reported that water stress had no effects on the concentrations of N, P, K, Mg or Ca. The results from the different authors may have differed as a result of water stress/deficit irrigation being imposed at different times of the growing season. Therefore further investigation is warranted.

2.3.7 Keeping Quality

An important aspect of fruit quality is the occurrence of fruit disorders, both at harvest and after cold storage. Apples produced under some form of water deficit have been found to show less occurrence of physiological disorders and fungal diseases during and after storage than fruit produced in ample water supply (Failla et al., 1990; Guelfat'Reich et al., 1974; Irving and

Drost, 1987; Lötter et al., 1985). Irving and Drost (1987) found less incidence of bitter pit in fruit that was grown under water stress imposed six weeks after full bloom. When peach fruit were stored at ambient temperatures under home conditions, fruit from deficit-irrigated trees were less affected by fungal rot than fruit from well-watered trees which extended their shelf life (Li et al., 1989). Proebsting et al. (1984) reported equal storage life in fruit from trees under water deficit irrigation and that from trees receiving ample water. Mills et al. (1994) did not observe any effect of water stress on the occurrence of physiological disorders during storage.

The development of many disorders in apple fruit have been attributed to the concentration of minerals, especially Ca (Section 2.3.6). Bitter pit is a particularly important calcium related physiological disorder in 'Braeburn' apples (Kupferman, 1994). Guelfat'Reich et al. (1974) attributed the inferior keeping quality of apples from well-watered trees compared to apples grown under limited water supply to a mineral imbalance in the well-watered fruit i.e a high K:Ca ratio.

The susceptibility of fruit to water loss is also an important factor to consider in reduced irrigation treatments. Water loss is a major cause of deterioration in storage and leads to adverse consequences such as loss of marketable weight, changes in texture due to reduction in cell turgor e.g., loss of succulence and crispness, undesirable changes in colour and palatability, and increased susceptibility to diseases (Ben-Yehoshua, 1987; Grierson and Wardoski, 1978; Hatfield and Knee, 1988; Woods, 1990). In apple, a loss of more than 6% of the harvest weight results in an unattractive, shrivelled appearance (Hatfield and Knee, 1988). There is no information available as to the effect of reduced irrigation on the water loss characteristics of apples. This aspect was therefore studied in this research.

CHAPTER THREE

MATERIALS AND METHODS

3.1 EXPERIMENTAL SITE

The experiment was carried out during the 1994-95 growing season at Massey University's Fruit Crops Unit, Palmerston North, New Zealand (altitude 30 m, Lat. 40.2 °S, long. 175.4 °E).

3.2 ENVIRONMENT

3.2.1 Soil

The soil type in the experimental block is the Manawatu fine sandy loam which comprises of 500 mm fine sandy loam, overlying 400 mm of fine sand with a coarse sand below 900 mm. This textural interface has been shown to impede water transport, yet water drains more freely below (Clothier et al., 1977).

3.2.2 Climate

During the experimental period, meteorological data were collected in a standard electronic weather station (AgResearch Grasslands, Crown Research Institute (CRI), Palmerston North) located approximately 1 km from the experimental site. The parameters recorded included air temperature, air relative humidity, windrun (2 m above ground), sunshine hours, and monthly rainfall. The climatic data of the area based on 30-year monthly means from 1963-1993 is shown in Fig. 3.1. The area experiences a humid temperate climate with the following characteristics:

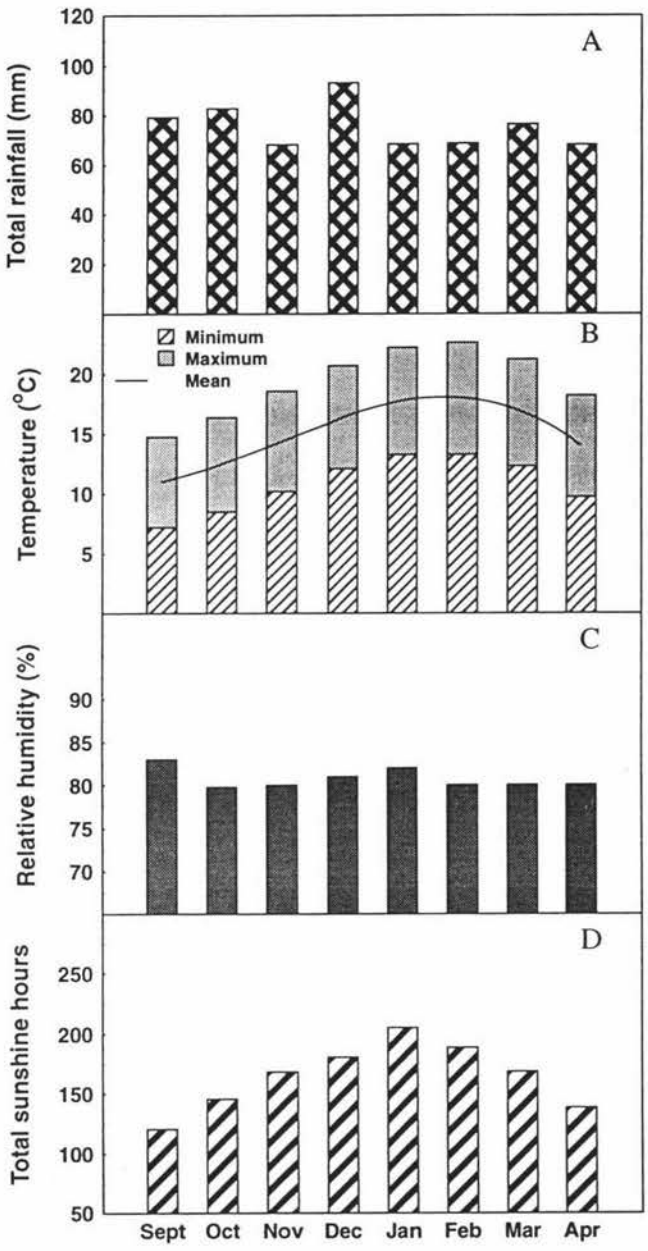

Figure 3.1: Summary of the long-term climatic data (1964-1994) during the months of September to April (growing season) for the Manawatu region.

a) Rainfall

The area receives a total rainfall of approximately 970 mm per year occurring in about 166 days during the year. The highest rainfall is recorded in December (98 mm) and the lowest in April (68 mm). Annual pan evaporation is 995 mm. The highest pan evaporation is recorded in January at 157 mm.

b) Temperature

The lowest mean monthly temperature is recorded in July at 8.4 °C and the highest occurs in February (17.5 °C).

The total annual sunshine hours is approximately 1715 hours with the highest mean monthly sunshine hours occurring in January (205 hours). The lowest sunshine hours occur in June.

c) Relative Humidity

The area experiences a high relative humidity throughout the year in the range of 74% to 87% with the highest relative humidity occurring in June and July. The lowest relative humidity is experienced in December.

3.3 PLANT MATERIAL

Two rows of seven-year-old 'Braeburn' apple trees on MM106 rootstock were used. The trees were spaced at 4.5 m between the rows and 2.2 m within the rows. The trees were trained to a central leader.

3.4 EXPERIMENTAL DESIGN AND TREATMENTS

A total of 36 experimental trees were divided into three blocks of 12 trees each. Each block had four plots of three trees each. Adjacent plots were separated by at least one guard tree to avoid influence from irrigation treatments between neighbouring plots. The design used was a randomized

complete block design with four treatments randomly assigned to each block. The treatments were: Control (C), comprising well-watered trees; early withholding (EW) of irrigation from full boom (20 October 1994) to 104 days after full bloom (DAFB); late withholding (LW) of irrigation from 104 DAFB up to final harvest at 194 DAFB; and nonirrigated (NI), where irrigation was withheld throughout the season.

Clear polythene under-tree covers were installed for NI and EW trees one month before full bloom and at 100 DAFB for LW trees to exclude rainfall. It was necessary to install the covers early due to the high rainfall conditions in winter and the high moisture retentivity of this soil (Clothier et al., 1977). The covers extended 2 m on either side of the tree rows and were held to the ground between the rows by steel pegs. The covers were attached to wires running along the rows at a height of 1 m from the ground level to form tent-like structures which allowed air movement over the ground while excluding rainfall. Cultural practices, except for irrigation, were the same as for other commercial orchards in the area with herbicides being applied under the covers to remove vegetation.

3.5 FRUIT THINNING

Fruitlets were hand-thinned on 22 November 1994 to reduce crop load differences between the trees and ensure adequate fruit size at harvest. Trees were thinned to the following mean fruit numbers per tree (± standard error of the mean (SEM)): 319 ± 23, 336 ± 18, 301 ± 28, and 343 ± 15 for C, EW, LW, and NI respectively. In all cases more fruit were left on trees with a larger trunk circumference.

3.6 SOIL MOISTURE

Soil volumetric water content (θ, $m^3\ m^{-3}$) was determined using time domain reflectometry (TDR) equipment (model 1502 C; Tektronix, Redmond,

Ore.) (Topp et al., 1984; Topp and Davis, 1985a,b). Soil volumetric water content was determined at depths of 300 mm and 1000 mm and at distances of 400 and 500 mm from the tree trunk, respectively. Measurements were taken at 65, 100, 121, 139, and 170 DAFB for the 300 mm depth and at 100, 121, 139, and 170 DAFB for the 1000 mm depth.

Due to practical limitations, only one block was used for soil moisture measurements. Four pairs each of 300 and 1000 mm long transmission lines (probes) were installed around the middle tree of each plot on the four cardinal compass directions. The 300 and 1000 mm probes were respectively installed at 400 and 500 mm from the tree trunk. A customised software was used to interpret the TDR signal as θ.

3.7 LEAF WATER POTENTIAL (Ψ)

Leaf water potential (Ψ) was measured using a Scholander pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, Calif.) following the recommendations of Turner (1988). Measurements commenced at 42 DAFB. Two fully expanded mature leaves per tree were excised from exposed shoots in the middle tree canopy using a sharp scalpel. The leaves were immediately enclosed in small plastic bags to avoid water loss due to evaporation. The excised leaves were placed in the pressure chamber which was humidified with moist tissue paper. Nitrogen gas was used to apply pressure until leaf sap appeared at the cut cross-section of the vascular tissue. The pressure applied was taken as an estimate of bulk leaf water potential. In all cases care was taken to ensure that measurements were taken within 30 seconds of leaf excision.

Predawn Ψ measurements were taken every two weeks between 0500 and 0600 HR. Midday Ψ measurements were made weekly between 1200 and 1300 HR. Diurnal changes of Ψ were monitored between 0600 and 2000 HR at 96, 111, 132, and 151 DAFB.

3.8 PHOTOSYNTHESIS AND STOMATAL CONDUCTANCE

A LI-COR, LI-6200 Portable Photosynthesis System (LI-COR Inc., Neb., USA) was used to determine the net CO_2 assimilation rate (*Pn*) and the stomatal conductance (g_s). The equipment measures the net exchange of CO_2 between a leaf and the atmosphere. The net photosynthetic rate is then calculated using this rate of change and other factors such as the amount of leaf area enclosed in the leaf chamber, volume of the enclosure, temperature and atmospheric pressure. Each leaf was enclosed in a one litre leaf chamber and measurements were started 10 seconds after the CO_2 level in the chamber started falling steadily. Measurements were continued for 30 seconds for each leaf. Other parameters recorded at the time of measurement using the same equipment were: leaf internal CO_2 concentration (μmol CO_2 mol^{-1}), photosynthetically active radiation (PAR in μmol quanta m^{-2} s^{-1}), vapour pressure deficit (VPD in kPa), and the rate of transpiration (mmol m^{-2} s^{-1}).

Measurements were made on two mature fully expanded leaves in the outer middle canopy zone. Measurements were taken weekly between 1200 and 1300 HR local time. On 156 DAFB, diurnal changes in *Pn* and g_s for C and NI were determined between 0800 HR and 1700 HR.

3.9 CANOPY TEMPERATURE AND CANOPY-AIR TEMPERATURE DIFFERENCE

The canopy temperature (T_c) and the canopy-air temperature differences (T_c-T_a) were determined weekly using an infrared (IR) thermometer (Everest Interscience Inc., Tustin, Ca.).

Infrared thermometry is a non-contact method for estimating the surface temperature of a target. The measurement does not interfere with the surface and yields a temperature that is an integrated value over the field of

view of the sensor. The instrument measures the radiation emitted from the target, and relates this radiation (R) to the surface temperature (T_s) by the Stefan-Boltzmann law (Jackson, 1982):

$$\mathbf{R = \varepsilon\delta T_s^4}$$

where ε = Emissivity of the surface

δ = Stefan-Boltzmann constant ($5.674*10^{-8}$ W m^{-2} K^{-4})

T_s= Surface temperature

R = Radiation (W m^{-2})

The thermal IR emittance (emissivity) of most plant surfaces ranges between 0.95 and 1.00 with most plant leaves being 0.97 to 0.98 (Fuchs and Tanner, 1966).

In this experiment T_c and T_c-T_a measurements were mostly made at 1300 HR thus minimizing the effects of sun angle on the foliage temperature and exposing the crop surface to the highest solar radiation, air temperature, and vapour pressure deficit conditions of the diurnal period. On several occasions, diurnal measurements were taken from 0900 to 1700 HR local time. During measurement, the instrument was held horizontally approximately 1.5 m above ground level, 2-3 m from the tree, on the eastern side of the canopy. The instrument was kept at an emissivity setting of 0.98. The T_c and T_c-T_a values were recorded from the display window within 5 seconds after the reading had stabilized.

3.10 VEGETATIVE GROWTH

In order to determine the effect of the treatments on vegetative growth of the trees, the trunk circumference of all experimental trees was measured at a marked point 300 mm above the ground level using a metric tape. This was done at the beginning of the experiment (22 October 1994) and at the

time of final harvest (1 May 1995). The data were used to calculate the change in trunk cross-sectional area (TCA) over the season.

For the measurement of shoot extension, two similar sized shoots per tree were selected at the outer portion of the middle canopy at the beginning of the experiment. The shoots were tagged and their lengths measured at weekly intervals starting 49 DAFB until growth ceased. Growth was assumed to have ceased at 138 DAFB when there was no evidence of further shoot growth.

3.11 REPRODUCTIVE GROWTH

3.11.1 Fruit Diameter and Volume

Two fruit of uniform size were tagged on the eastern side of the middle canopy zone of each experimental tree at 42 DAFB. Fruit diameter was measured once a week across the widest part of the fruit using a pair of digital callipers (Mitutoyo Corp, Japan). Fruit volume as calculated from the diameter data assuming the fruit was spherical, using the following formula:

$$V = \frac{4}{3}\pi r^3$$

Fruit diameter and volume data was used to calculate the growth rate using the following formula (Hunt, 1978):

$$FGR = \frac{(Ft_2 - Ft_1)}{(t_2 - t_1)} \quad ,$$

where

FGR = fruit growth rate (cm^3 day^{-1})

Ft_2 = fruit size at Time 2 (cm^3)

Ft_1 = fruit size at Time 1

t_1 = Time 1 of record in days

t_2 = Time 2 of record in days

3.11.2 Yield

Fruit were harvested at commercial maturity based on the background colour in three separate pickings on 10 April 1995, 19 April 1995 and 1 May 1995. The number and total weight of fruit per tree was recorded at each picking date. Mean fruit weight, yield efficiency (weight of fruit cm^{-2} TCA) and crop density (fruit number cm^{-2} TCA) were calculated.

Yield efficiency was calculated as:

$$YE = \frac{TY}{TCA}$$

where YE = yield efficiency (g of fruit cm^{-2} TCA)

TY = total weight of harvested fruit per tree (g)

TCA = trunk cross-sectional area (cm^2) at harvest

Crop density was calculated as:

$$CD = \frac{NF}{TCA}$$

where CD = crop density (fruit number cm^{-2} TCA)

NF = number of fruit per tree at harvest

TCA = trunk cross-sectional area (cm^2) at harvest

3.11.3 Return Bloom

In Spring 1995 (21 October 1995), the basal circumference of two major tier branches between 1.0 and 2.0 m from the ground for each tree was measured. This was used to calculate the branch basal cross-sectional area. Flowers on each branch were counted and flower density (flower number per branch cross-sectional area) determined for each tree.

3.12 FRUIT QUALITY, COMPOSITION, AND MATURITY

3.12.1 Fruit Sampling

During the season, four fruit per tree (36 per treatment) were randomly sampled at 15-day intervals from the outer portion of the mid-canopy for the evaluation of quality and composition. The first samples were collected at 64 DAFB. Fruit were kept in labelled plastic bags before analysis. At final harvest (194 DAFB), four fruit were sampled from each of the top and bottom canopy positions from each tree for quality determination. The sampled fruit were used for the determination of fruit carbohydrates (fructose, sucrose, glucose, and sorbitol), titratable acidity, skin colour, fruit mineral composition (K^+, Mg^{2+}, Ca^{2+}, N, and P), dry matter content, flesh firmness, and total soluble solids concentration.

3.12.2 Determination of Fruit Carbohydrates

Sugar concentrations were determined for the four major sugar groups in apples: fructose, glucose, sucrose and sorbitol (Chan et al., 1972). One gram of cortical tissue was removed from the equatorial portion of each fruit and mixed together to form composite samples of fruit from each tree. The samples were placed in 20-ml plastic vials with screw lids and boiled in 95% ethanol to inactivate invertase enzyme which may lead to increases in glucose and fructose (Paull et al., 1984). The samples were stored below 0 °C for at least one month to allow for the precipitation of cell components. Aliquots of clear supernatant were then taken and put into 1.5-ml Eppendorf tubes. The samples were completely dried using a concentrator (model RH 40-11; Savant Instruments, Farmingdale, N.Y.). The residue was redissolved in 3-ml Barnstead nano-pure water and then filtered using 0.3-μm nylon membrane filters. For the determination of carbohydrates, 15 μm of each sample was injected into a high-performance liquid chromatography (HPLC) system

(Waters, Milford, MA, USA). The standard used was a mixture of glucose, fructose, sucrose and sorbitol (0.6 mg ml^{-1} of each). The carbohydrate analysis column (Aminex HPX87C; Life Science Group, Hercules, Calif.) was maintained at 85 °C with deashing guard column and the detector (Optilab 5922 RI Chromatography Module, Tekator AB, Hognas, Sweden) at 25 °C. Injected samples were eluted with water at a flow rate of 0.6 ml min^{-1}. The areas under the curves were computed by a β-RAM software package. The results are reported as mg g^{-1} fresh weight.

3.12.3 Titratable Acidity

For the determination of titratable acidity (TA), fruit were peeled and the flesh made into small pieces. The samples from each tree were then homogenised together. Once homogenised, 1 g of fruit pulp was mixed with 39 ml of double-distilled water and titrated with 0.1 N NaOH using an automatic titrator (model DL21; Mettler, Greifensee, Switzerland) to an end point pH of 7.1. The values were expressed as percent malic acid.

3.12.4 Fruit Mineral Composition

Approximately 1 g of cortical tissue was taken from each fruit and placed in a labelled glass vial to make one composite sample from each tree. The fruit samples were dried at 70°C for 14 days and then stored in a dry environment at room temperature prior to analysis. At the time of analysis, fruit samples were ground into powder using a coffee grinder and kept in an oven at 70 °C for about 12 hours to drive away any moisture. Two separate extractions were carried out in different sets of digestion tubes. For each series of analysis, 0.1 g of dried sample was weighed into a labelled digestion tube. Each run in the heating block also had two samples of known concentrations (Standard, Wageningen No. 883). Results are presented as mg g^{-1} dry weight.

a) Analysis of K^+, Ca^+, and Mg^{2+}

All glassware used for K^+, Ca^{2+}, and Mg^{2+} analysis were acid-washed in 2M HCl prior to use and between each series of analysis. Samples were digested by adding 4 ml concentrated nitric acid (70%) to approximately 0.1 g of each sample or standard in a digestion tube. The digestion tubes were set in a heating block with small funnels in the top to cause refluxing, and heated at 150°C until the solution became clear. The funnels were then removed and the temperature raised to 250°C. This reduced the extract to dryness after approximately four hours.

Five ml 2M HCl and 2 ml 25000 ppm Sr/Cs (30.19 g Strontium nitrate, $Sr[NO_3]_2$ and 15.84 g Caesium chloride, CsCl made up to 500 ml with deionised water) were added to each digestion tube while it was still warm. The volume was made up to 50 ml by adding deionised water and well mixed using a vortex mixer. Sufficient volume (approximately 30 ml) was poured into labelled glass vials and K^+, Ca^{2+} and Mg^{2+} were analysed using an atomic absorption spectrometer (model GBC 904AA; GBC Scientific Equipment, Dandenong, Victoria, Australia). Dilution was performed as required to ensure that the results were within the range of a standard curve which was computed at the same time.

b) Analysis of N and P

The amounts of N and P were determined by colorimetric autoanalysis (Technicon Instruments Corp., NY, USA) following Kjeldahl digestion (Twine and Williams, 1971). Kjeldahl solution was made in a fume cupboard by heating a mixture of 250 g K_2SO_4, 2.5 g selenium powder and 2.5 l concentrated H_2SO_4. Four ml of Kjeldahl solution was added to digestion tubes containing preweighed 0.1-g ground fruit sample or standard then heated at 350°C for 4-5 hours until the solution became clear. The volume was made up to 50 ml using distilled water and mixed using a vortex mixer. A

sufficient volume (about 30 ml) was poured into labelled glass vials and the concentrations of N and P were determined within the range of a standard curve.

3.12.5 Dry Matter Content

At harvest, 30 g of cortical tissue was removed from each fruit and placed in an oven at 70°C for 14 days on an aluminium foil. The tissue was weighed and the dry matter calculated in mg g^{-1} fresh wt. Weighing was done using an analytical balance (model AE 200 Greifeinsee, Switzerland).

3.12.6 Flesh Firmness

Approximately 1 mm thick peel section was removed from the equatorial part of two opposite sides of each fruit using a sharp blade. Flesh firmness (the force required to penetrate the cortical tissue in kg) was determined using an Effegi penetrometer (model FT 327; R. Bryce, Alfonsine, Italy) with an 11.1-mm plunger and mounted on a drill stand with a lever to apply a constant and even pressure to the fruit. Fruit firmness was obtained as the mean of the two measurements and converted to newtons (N) by multiplying by 9.807.

After harvest, firmness was determined on 15 fruit per treatment removed from cold storage (1 °C) at 3-weekly intervals for a total of 12 weeks.

3.12.7 Total Soluble Solids (TSS)

The concentration of total soluble solids was determined using an Atago refractometer (0-20% Brix; ATC-1; Atago, Tokyo) with automatic temperature compensation. Total soluble solids concentration was determined on juice squeezed from approximately 5 mm thick apple slices taken from across the equator on two opposite sides of each fruit. The

penetrometer was zeroed with distilled water after each reading. The prism surface and the sunlight plate were thoroughly washed and dried with soft tissue paper after each reading.

After harvest, TSS was determined on 15 fruit per treatment removed from cold storage (1 °C) at 3-weekly intervals for a total of 12 weeks.

3.12.8 Skin Colour

During the growing season, colour was determined as the mean of two measurements per fruit on both the red blush (red) surface and the unblushed (green) surface of the fruit using a portable tristimulus chromameter (CR-200; Minolta, Osaka, Japan). Measurements were made by placing the 8-mm-diameter measuring area of the chromameter at the midpoint between the stem and calyx end of each fruit and recording the L and H values. The meter was calibrated at illuminant condition C (6774K) with the manufacturer's green standard tile before use (Dixon, 1993).

At harvest, 30 fruit per treatment (10 per plot) were randomly selected and placed randomly on trays. The trays were then kept at room temperature (approx. 20 °C) for 18 days. During this time, background skin colour was determined at 2-day intervals on marked points on each fruit. Another group of 30 fruit per treatment was removed from cold storage (1 °C) at weekly intervals and background colour determined for eight weeks.

3.12.9 Internal Ethylene Concentration

Fruit for the determination of internal ethylene concentration were harvested at 170 DAFB. Fifteen uniformly sized fruit per treatment (five per plot) were randomly selected for the measurements. The internal ethylene concentration was measured using the external chamber method which is a non-destructive method used for repeated sampling of internal atmospheres (Banks and Kays, 1988).

The bottom half of 2-ml glass vials was removed and the top fitted with 0.4-ml plastic tubes which were stuck using polyvinyl acetate adhesive (PVA). The vials were then stuck onto each fruit on the surface at the equatorial region with PVA (Fig. 3.2). The chambers were sealed after allowing the adhesive to dry for 24 hours by inserting a rubber septum into the plastic tube fitted onto each chamber. The well formed in the plastic tube after sealing the chamber was filled with water to prevent gas leaks through the septum and atmospheric contamination of gas samples during and between sampling.

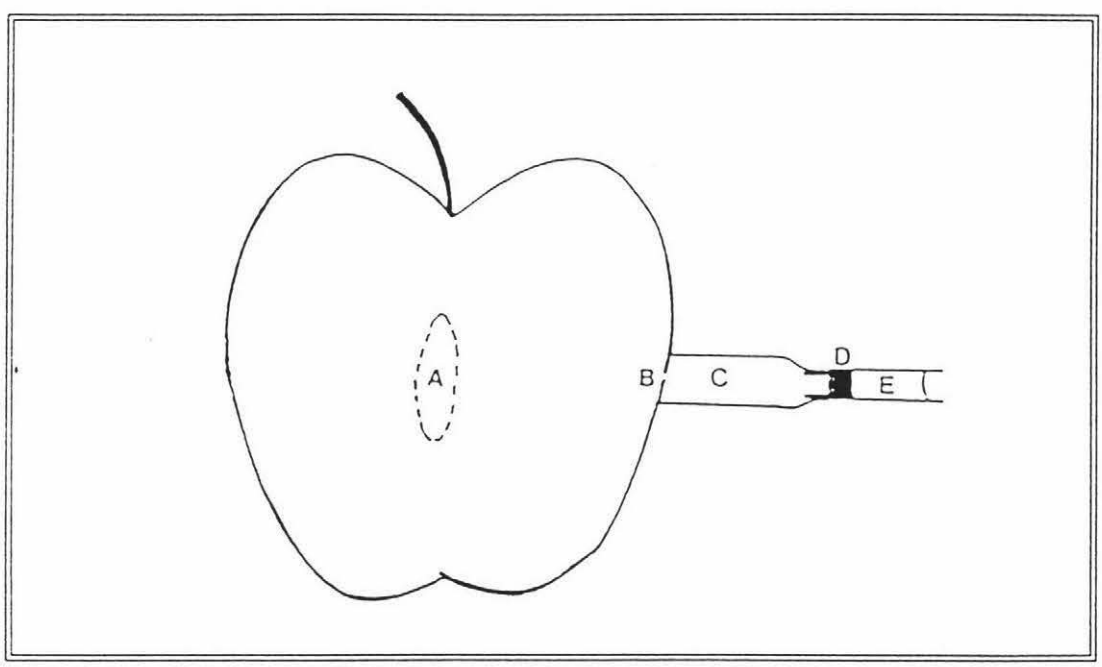

Figure 3.2: Arrangement of gas sampling chamber on the fruit surface. (A) Fruit core cavity; (B) lenticel; (C) glass chamber; (D) rubber septum; (E) plastic tube with water.

3.11.9.1 Taking gas measurements

The sub-epidermal internal gas concentrations were estimated to be the same as the equilibrated gas concentrations in the glass chamber after 40 to

90 hours at room temperature (20 °C) in air (Banks and Kays, 1988). Sampling for ethylene determination started 48 hours after the external chambers were sealed and performed at two-day intervals for 16 days. The fruit were kept at room temperature (20 °C) for the entire period.

Sampling was done by taking 90 µl (0.09 ml) gas samples from each vial using 100-µl gas-tight glass syringes (Hamilton Co., Nev.) fitted with 25-gauge needles. The needle was inserted through the septum into the chamber and flushed before the sample withdrawal.

3.12.9.2 Gas liquid chromatography for ethylene analysis

Ethylene concentration (µl litre^{-1}) in 0.09 ml gas samples was determined within approximately 30 seconds of sample withdrawal using a PYE Unicam gas-liquid chromatography (series 104) fitted with a flame ionization detector (FID) and with a stainless steel activated alumina column (80/100 mesh, 6' long and 1/8 " diameter). The temperature of the column, injector, and detector were 100 °C, 100 °C, and 130 °C respectively. The carrier gas was nitrogen with a flow rate of 30 ml min^{-1}. Hydrogen and air were used for the detector with flow rates of 30 ml min^{-1} and 300 ml min^{-1} respectively. The response to sample injection was measured as peak height using a Hewlett Packard 3393A integrator.

3.12.10 Weight Loss Susceptibility

Sixty uniformly sized fruit per treatment were randomly selected at harvest (194 DAFB) and individually weighed using an analytical balance (Mettler AE200, Greifensee, Switzerland). The initial mean fruit weights (g ± SEM) were: 195.3 ± 3.6, 196.3 ± 4.3, 188 ± 7.5, and 186.7 ± 6.9 for C, EW, LW, and NI, respectively. Thirty fruit per treatment were then stored in air at approximately 1 °C (RH = 93%). The fruit were marked using a felt pen to indicate the treatments and placed randomly in commercial cartons.

The fruit were reweighed at weekly intervals for a total period of nine weeks. Weight loss was calculated as the percent reduction from the original fresh weight.

The remaining 30 fruit per treatment were individually weighed, marked, and placed randomly on open trays. The fruit were kept in a temperature controlled room at 20 °C (RH = 72%). The fruit were reweighed every two days for a total of 14 days and weight loss calculated as the percent reduction from the original fresh weight.

3.12.11 Skin Permeance to Water Vapour

3.12.11.1 Theory

Water loss, which accounts for 95% to 98% of product weight loss after harvest, occurs as a result of transpiration which is a mass transfer process in which water vapour moves from the product surface to the surrounding air (Ben-Yehoshua, 1987). Water vapour moves in accordance to Fick's law of diffusion from a region of high to a region of low concentration or partial pressure. It is assumed that the internal atmosphere of the product has a saturated vapour pressure based on the following assumptions (Van Den Berg, 1987; Woods, 1990):

i) The cell membrane is selectively and perfectly permeable to water,

ii) the cell is under full turgor pressure and,

iii) the surface tension effects in the intercellular spaces are negligible.

The surrounding atmosphere usually has a lower water vapour pressure. The driving force of transpiration is the gradient of the water vapour pressure between the tissue and the surrounding air (Ben-Yehoshua, 1987; Grierson and Wardowski, 1978; Thompson, 1992; Van Den Berg, 1987). This gradient is termed the water vapour pressure deficit (VPD) which may be defined as

the difference between the water vapour at saturation (VP_{sat}) and the actual water vapour pressure at the same temperature (VP_{air}) as follows;

$$\mathbf{VP_{sat} - VP_{air} = VPD}$$

The rate of water loss from a horticultural commodity strongly depends on the condition and surface characteristics of the commodity (Van Den Berg, 1987; Woods, 1990). Therefore, some products lose water at a higher rate than others due to differences in the structure and composition of their surfaces. The ease of water movement across the skin can be quantified, taking into consideration the water vapour pressure deficit, as the skin permeance to water vapour (P'_{H2O}) which is expressed in terms of the quantity of water evaporated per unit surface area per unit water vapour pressure deficit (Van Den Berg, 1987; Woods, 1990). Using P'_{H2O} as a constant of proportionality, the rate of water loss (r'_{H2O}) can be expressed as:

$$\mathbf{r'_{H2O} = P'_{H2O} * VPD} \qquad \text{(Fick's Law)}$$

3.12.11.2 Determination of skin permeance to water vapour

The experiment was carried out in a temperature-controlled room at 22.5 °C (RH = 72%). Fifteen fruit per treatment were randomly selected and weighed immediately after harvest at 194 DAFB. The fruit were marked and randomly placed on an elevated wire mesh on a bench to allow for air movement around each fruit. An electric fan was placed at each end of the table so as to remove the effect of the boundary layer. The fruit were left for 24 hours after which they were reweighed. The data were used to calculate the skin permeance to water vapour in fruit of the various treatments using the following formula:

$$P'_{H20} = \frac{r'_{H2O}}{A \cdot VPD} \quad ,$$

where:

P'_{H2O} = skin permeance to water vapour (mol s^{-1} m^{-2} Pa^{-1})

r'_{H2O} = rate of water loss (mol s^{-1})

A = surface area of the fruit (m^2)

VPD = water vapour pressure deficit (Pa)

Details on the calculation of r'_{H2O}, A, and VPD are given in Appendix 1.

3.13 STATISTICAL ANALYSIS

Analysis of variance (ANOVA) and regression analysis were performed using Statistical Analysis Systems (SAS) software (SAS Institute, Cary, N.C.). Data were analysed as a randomized complete block design (RCBD) (Steel and Torrie, 1981) with three blocks and four treatments. Mean comparisons were carried out using the Duncan's multiple range test at 5% and 1% level of significance. For fruit carbohydrates, TA, and mineral composition measurements, the composite samples from each tree were considered within-block replications. Analysis of variance was done by date of sampling for all variables except ethylene, colour change after harvest, and weight loss which were analysed using repeated measures analysis (Mead, 1988). Ethylene and weight loss data were respectively subjected to logarithmic and arcsine transformation before analysis so as to conform to the assumptions underlying the ANOVA (Gomez and Gomez, 1984). The data were back-transformed for presentation. Data for θ were not subjected to ANOVA due to the limited number of TDR measurements.

CHAPTER FOUR

EFFECT OF IRRIGATION TREATMENT ON WATER RELATIONS, PHOTOSYNTHESIS, AND GROWTH

4.1 INTRODUCTION

Due to the high humidity and rainfall experienced in the Manawatu region where this experiment was conducted, it is often difficult to impose a reduced water status in plants. In this experiment, under-tree covers were installed one month before full bloom so as to achieve a lowered soil water status early in the growing season for EW and NI treatments. Plant water status was determined by measurements of the leaf water potential (Ψ) at midday, predawn, and during the course of the day.

Plant water deficits result in changes in various physiological processes in plants as discussed in Chapter 2. This part of the study attempted to establish if and to what extent water stress develops in 'Braeburn' apples on withholding irrigation at different times of the growing season and to relate this to various physiological responses such as photosynthesis, transpiration, and growth.

4.2 RESULTS

4.2.1 Climatic Conditions

The long term pattern of climatic conditions at the experimental site is presented in Chapter 3. The climatic record of the 1994-95 growing season is shown in Fig. 4.1. The total precipitation between September 1994 and April 1995 was 933 mm, the long term mean precipitation over the same

period is 695 mm. During this period, rainfall was not evenly distributed with the highest rainfall occurring in November (179 mm) and the lowest in December (46 mm). A comparison between the 1994-95 season and the long term (30 year) rainfall pattern is presented in Fig. 4.2B which shows that the area received much more rainfall in September, November, March, and April than usual.

The highest monthly mean temperature was 18.9 °C recorded in February (Fig. 4.1). However, all the months except February and March were cooler than normal (Fig. 4.3).

4.2.2 Soil Volumetric Water Content

Results for θ are presented as the means of four measurements per plot in one of the blocks (Fig. 4.4). Although no statistical analysis was done for these data, certain trends were observed. At the start of measurements, 65 DAFB, θ was highest in C and lowest in NI at the 300 mm depth (Fig. 4.4A). There was a gradual decline in θ in NI during the season to 0.14 m^3 m^{-3} at harvest. The θ for EW was below 0.2 m^3 m^{-3} until the plants were rewatered at 104 DAFB. Thereafter θ for EW increased to 0.3 m^3 m^{-3} at harvest. There was a gradual decline in θ for LW after irrigation was withheld to approximately 0.14 m^3 m^{-3} at harvest. The θ values were generally lower for the 1000 mm depth than for the 300 mm (Fig. 4.4B). At 1000 mm, θ for treatment NI declined to approximately 0.13 m^3 m^{-3} at harvest. The θ for EW was below 0.15 m^3 m^{-3} at 100 DAFB and increased to about 0.2 m^3 m^{-3} on rewatering. There was a decline in θ for LW after irrigation was withheld (Fig. 4.4B). Volumetric water content for irrigated trees was maintained above 0.2 m^3 m^{-3}, values close to field capacity for this soil (Clothier et al., 1977), while θ for trees not receiving irrigation remained below 0.18 m^3 m^{-3} at 300 mm depth and below 0.17 m^3 m^{-3} at 1000 mm.

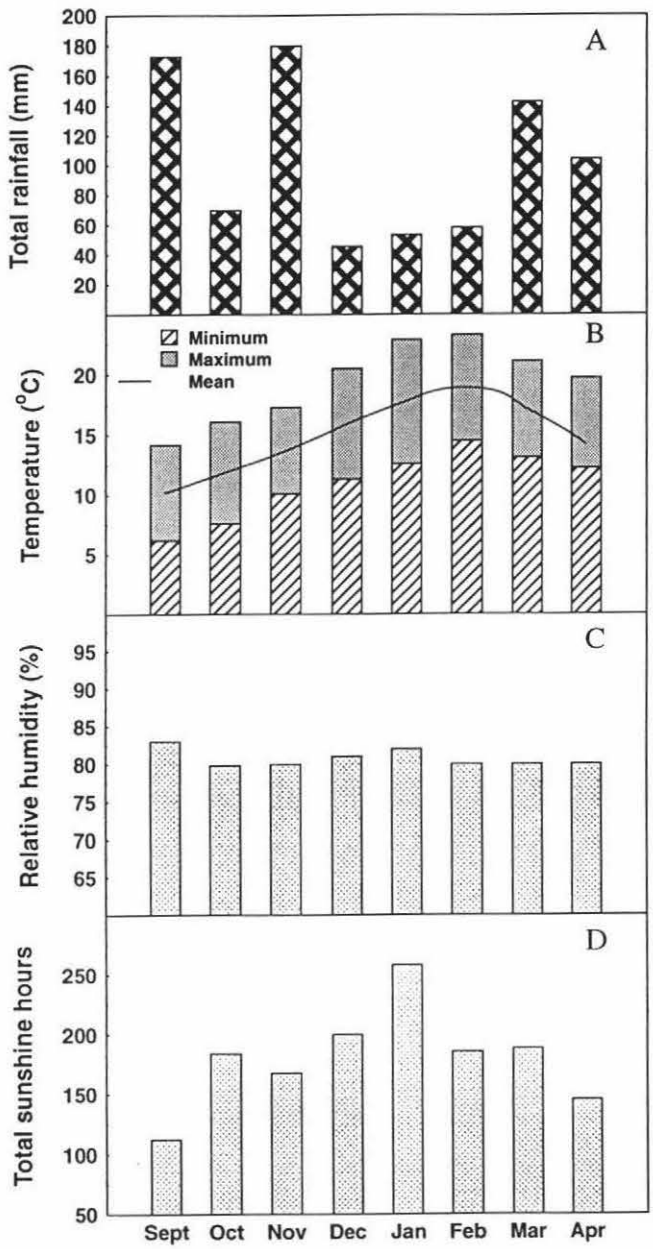

Figure 4.1: Summary of climatic data for the Manawatu region during the 1994-95 growing season.

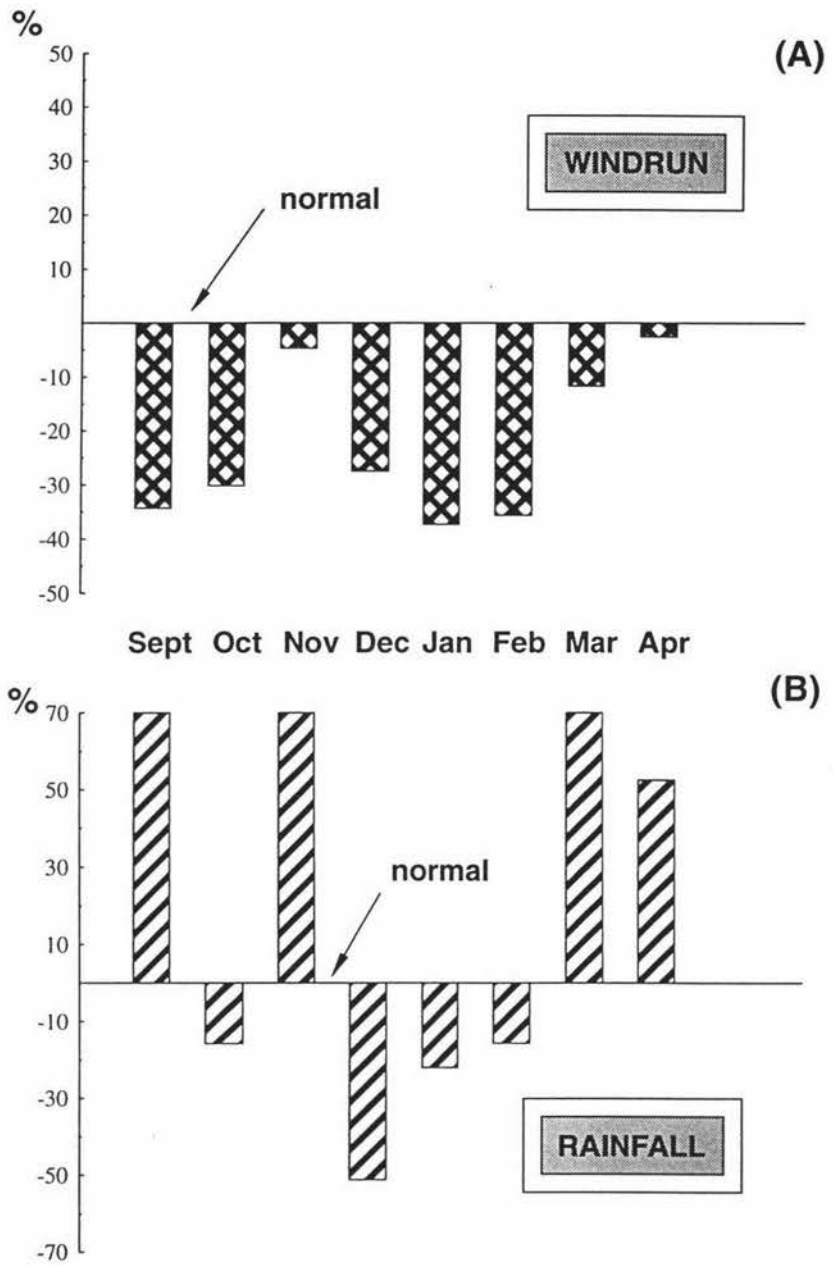

Figure 4.2: A comparison of total windrun (A) and monthly rainfall (B) during the 1994-95 growing season and the normal based on a 30-year average.

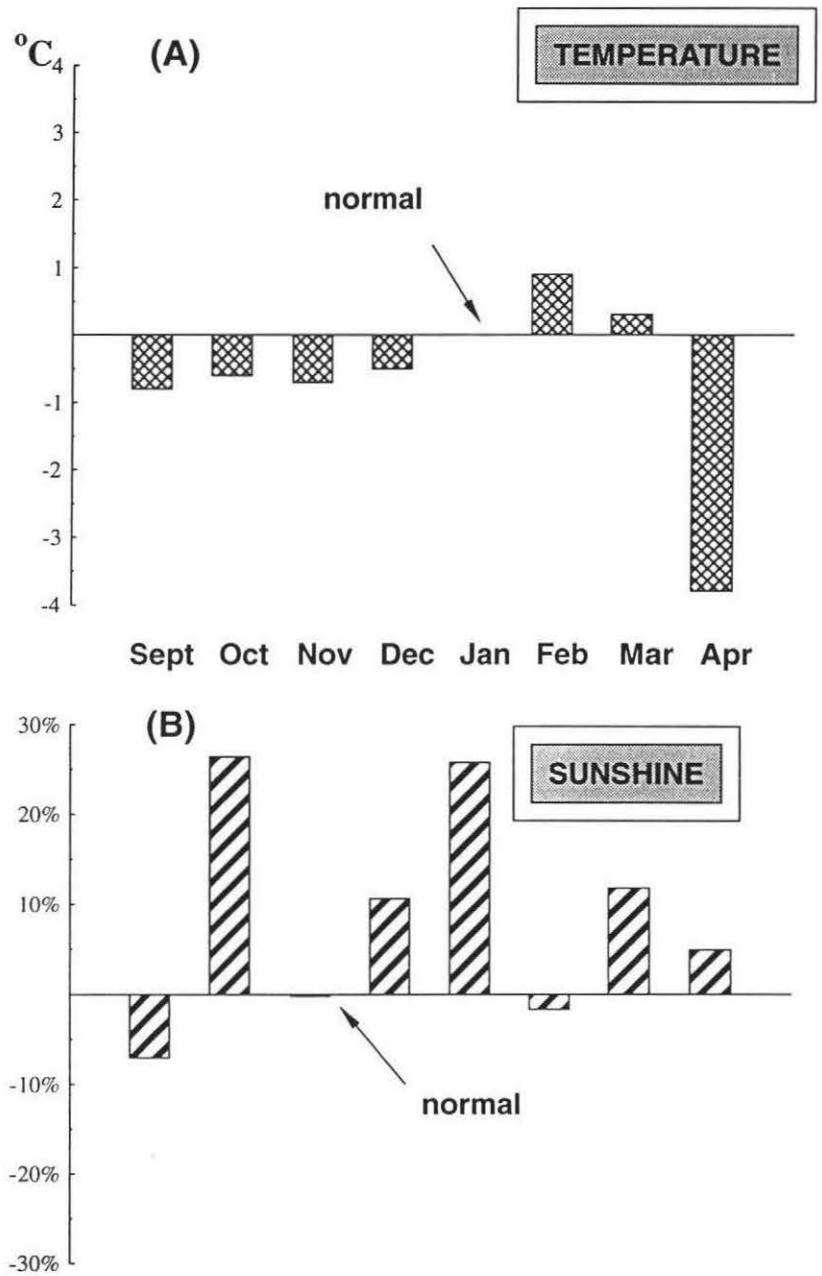

Figure 4.3: A comparison of mean monthly temperature (A) and total sunshine hours (B) during the 1994-95 growing season and the normal based on a 30-year average.

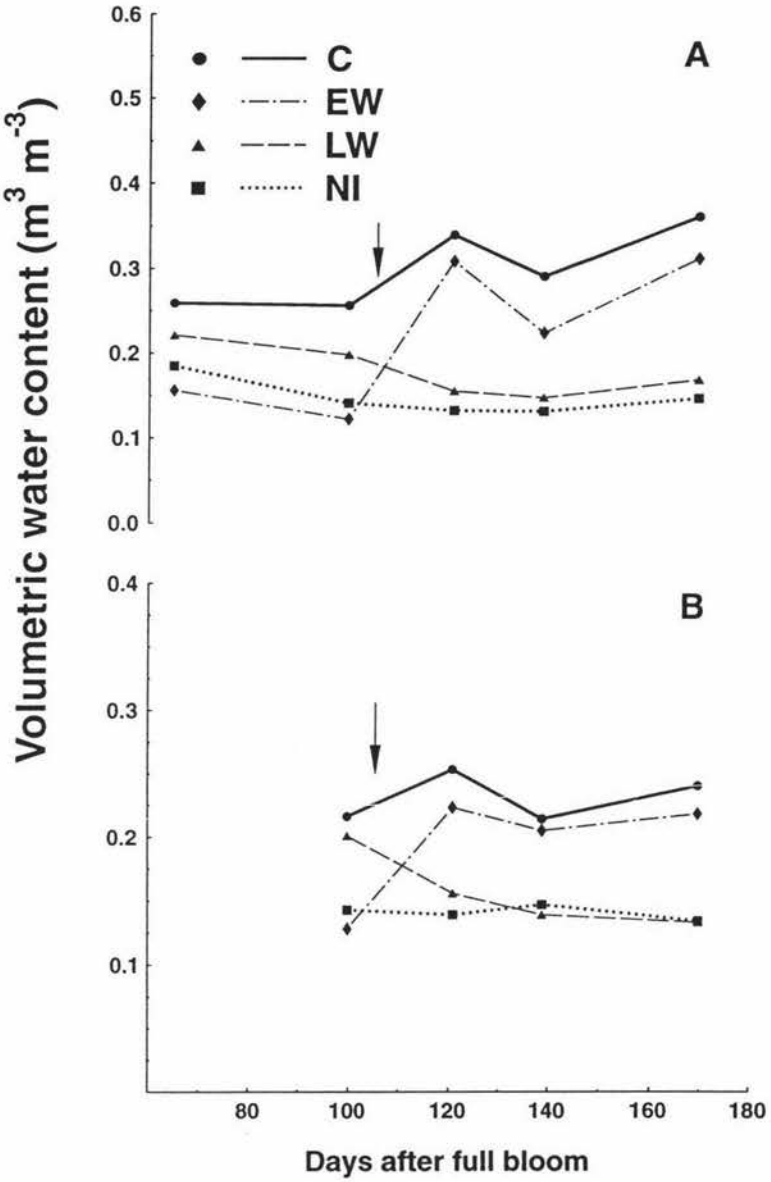

Figure 4.4: Changes in soil volumetric water content at depths of 300 mm (A) and 1000 mm (B) during the season for 'Braeburn' apple trees under different irrigation treatments. Arrows indicate the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Each point is a mean of four measurements.

4.2.3 Leaf Water Potential

Predawn Ψ for C remained high (between -0.2 MPa and -0.3 MPa) for most of the season whereas that of NI was always lower than C (Fig. 4.5A). The lowest predawn Ψ of -0.78 MPa was recorded for NI at 135 DAFB. Predawn Ψ for LW was not significantly different C before 104 DAFB whereas EW was similar NI. There was an increase in predawn Ψ in EW after rewatering at 104 DAFB and a decrease in Ψ of LW on withholding irrigation. The recovery of predawn Ψ for EW after the start of irrigation was slow. During the late season, the largest difference in predawn Ψ of 0.6 MPa was recorded between the trees not receiving irrigation (NI and LW) and the control at 138 DAFB (Fig. 4.5A).

Midday Ψ followed a similar trend as the predawn Ψ (Fig. 4.5B). A significant reduction in midday Ψ was observed in EW and NI treatments as early as 42 DAFB ($P \leq 0.05$). Midday leaf water potential was always higher in C and in LW than in EW and NI during the early season (before 104 DAFB). However, differences between the irrigated trees (C and LW) and the nonirrigated trees (NI and EW) at this time period were generally small being less than 0.3 MPa in most cases. A lower midday Ψ in NI relative to C was maintained until harvest. On resumption of irrigation for EW at 104 DAFB, there was a gradual increase in midday Ψ to the same level as in C at 120 DAFB. On withholding irrigation for LW, the midday Ψ gradually declined to the same level as NI. In the later part of the season (after 104 DAFB), differences of approximately 0.8 MPa were observed between the irrigated (C and EW) and the nonirrigated (LW and NI) treatments. In general, midday Ψ for water stressed trees fell below -2 MPa on several occasions with the lowest midday Ψ of -2.3 MPa being recorded for NI and LW at 163 DAFB (Fig. 4.5B).

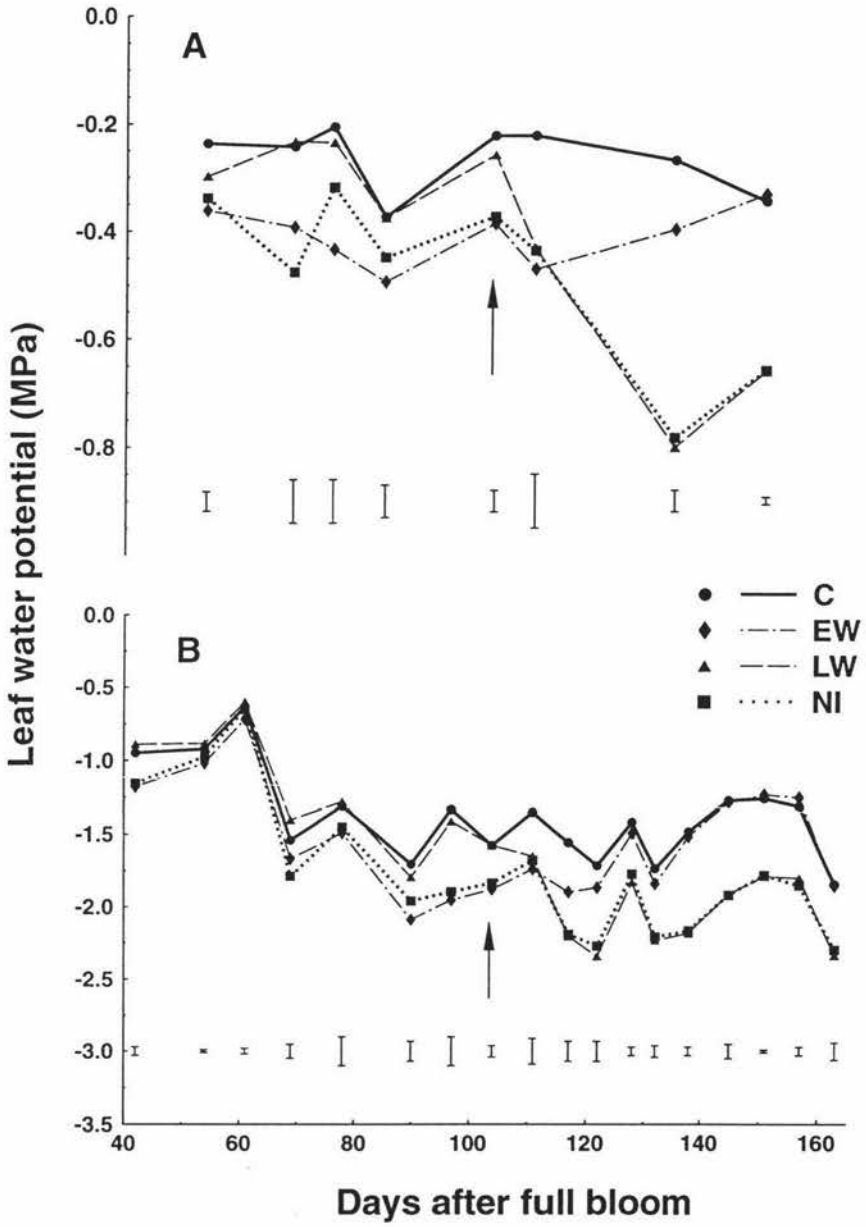

Figure 4.5: Changes in predawn (A) and midday (B) leaf water potential during the season for 'Braeburn' apple trees under different irrigation treatments. Arrows indicate the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

4.2.4 Diurnal Pattern of Leaf Water Potential

The results of diurnal measurements of Ψ made on 96, 111, 132, and 151 DAFB are shown in Fig. 4.6. In all dates of measurement, Ψ followed a parabolic pattern reaching a minimum value in the afternoon after which it started to recover. On 96 DAFB, C and LW had higher Ψ at all times of the day relative to NI and EW both of which experienced very low Ψ at about midday (below -2.0 MPa) (Fig. 4.6A). On this day, a mean difference of 0.6 MPa was maintained between C and NI throughout the day. At 111 DAFB, C had higher Ψ than NI, LW and EW during most of the day (Fig. 4.6B). On this date of measurement, irrigation had been resumed for EW only a few days earlier (104 DAFB) and the trees had not recovered from the early season stress. On the other two days of diurnal Ψ measurements (132 and 151 DAFB), Ψ was higher in C and EW as compared to NI and LW throughout the day (Fig. 4.6C and D) with a mean difference of 0.5 MPa and 0.4 MPa respectively between C and NI.

4.2.5 Photosynthesis and Stomatal Conductance

During the early season (before 104 DAFB), the rate of photosynthesis was not affected by the treatments (Fig. 4.7A). A reduction in *Pn* in LW and NI was first observed at 123 DAFB relative to C. However, this difference disappeared until 159 DAFB when there was a significant reduction in *Pn* in LW and NI relative to C and EW. On this day, there was a 19% reduction in *Pn* for NI. At the last date of measurement, 170 DAFB, there was a reduction in *Pn* of 22% and 12% in NI and LW respectively, as compared to C. At this time, NI and LW were not significantly different. The rate of photosynthesis was not reduced in EW at any time during the season (Fig. 4.7A). Stomatal conductance remained unaffected by the treatments until 138 DAFB when it was significantly reduced in NI compared with C (Fig. 4.7B). Thereafter, g_s was always lower in NI and LW compared with C. On the last

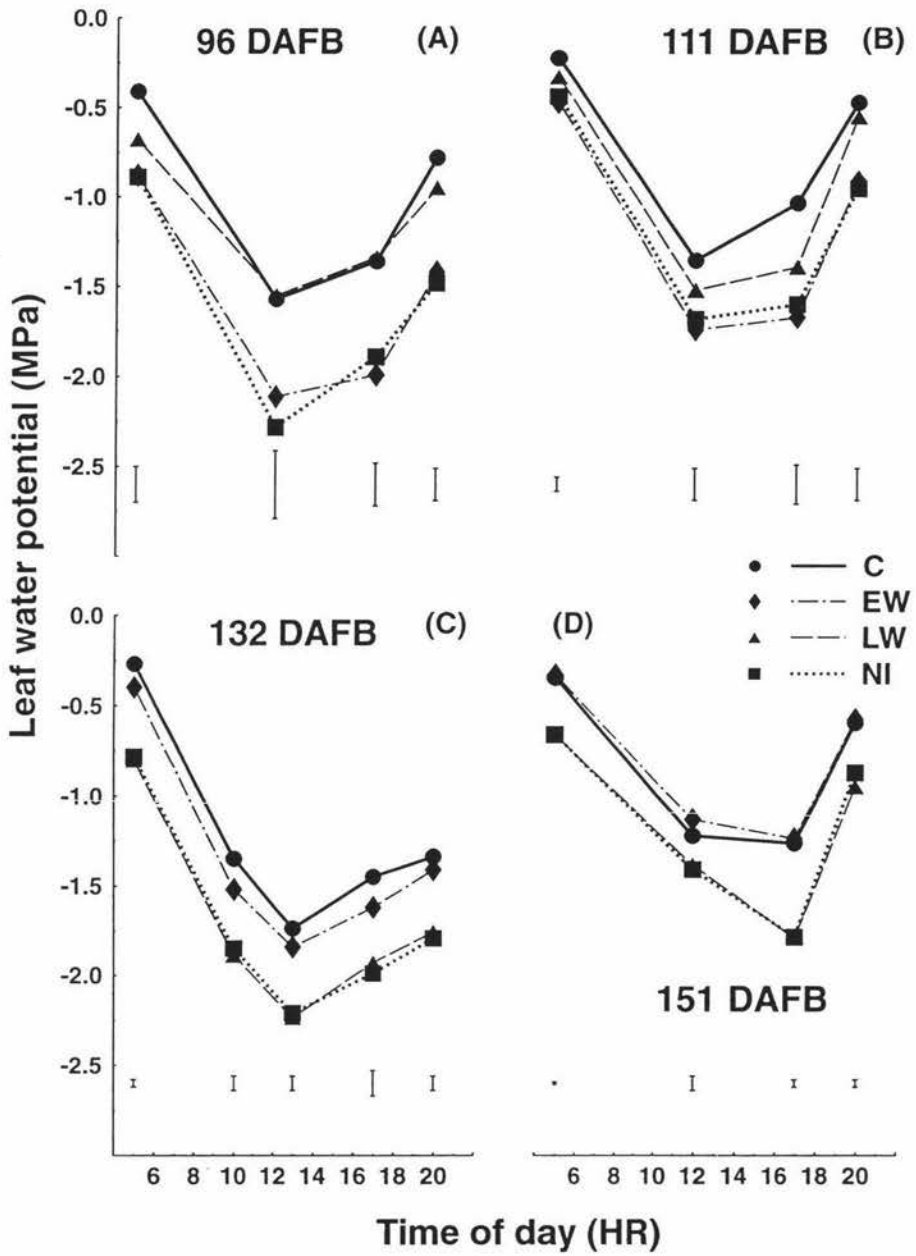

Figure 4.6: Diurnal changes in leaf water potential at 96 (A), 111 (B), 132 (C), and 151 (D) DAFB for 'Braeburn' apples under different irrigation treatments; C = control, EW = early withholding, LW = late withholding of irrigation, and NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

date of measurement, 170 DAFB, g_s was reduced by 21% in NI compared with C.

The diurnal pattern of *Pn* and g_s determined on 156 DAFB for NI and C is shown in Fig. 4.8A and B. Stomatal conductance was lowest at 0800 HR for both treatments with no significant differences between the treatments (Fig. 4.8A). At 1100 HR, the control plants had a higher g_s than the stressed plants. A difference in g_s of 0.061 mol CO_2 m^{-2} s^{-1} was recorded at this time. The difference in g_s was not significant at the time of the highest g_s (1400 HR) but was again significant at 1800 HR.

The rate of photosynthesis at 156 DAFB was similar between both treatments in the early morning (Fig. 4.8B). At about 1400 HR, C had a significantly higher rate of photosynthesis than NI. The rate of photosynthesis was lowest at 0800 HR for both treatments and increased as the day progressed to a maximum at 1400 HR with C having a *Pn* of 15.1 µmol CO_2 m^{-2} s^{-1} and NI having 11.6 µmol CO_2 m^{-2} s^{-1} at an ambient CO_2 concentration of 354 µmol mol^{-1}. Thereafter, *Pn* declined toward the late afternoon (Fig. 4.8B) as PAR declined (Fig. 4.8D).

4.2.6 Rate of Transpiration

Data for the rates of transpiration at midday closely followed changes in g_s. There was no significant difference in the rate of transpiration between the treatments for most of the growing season. The earliest differences in the rates of transpiration between the treatments were observed 133 DAFB (Fig. 4.10) when C and EW had higher rates of transpiration compared to NI and LW. On this day, the rate of transpiration was reduced by about 1.17 mmol m^{-2} s^{-1} in NI relative to C. These differences were maintained until harvest. At 170 DAFB, there was a 20% reduction in the rate of transpiration in NI relative to C.

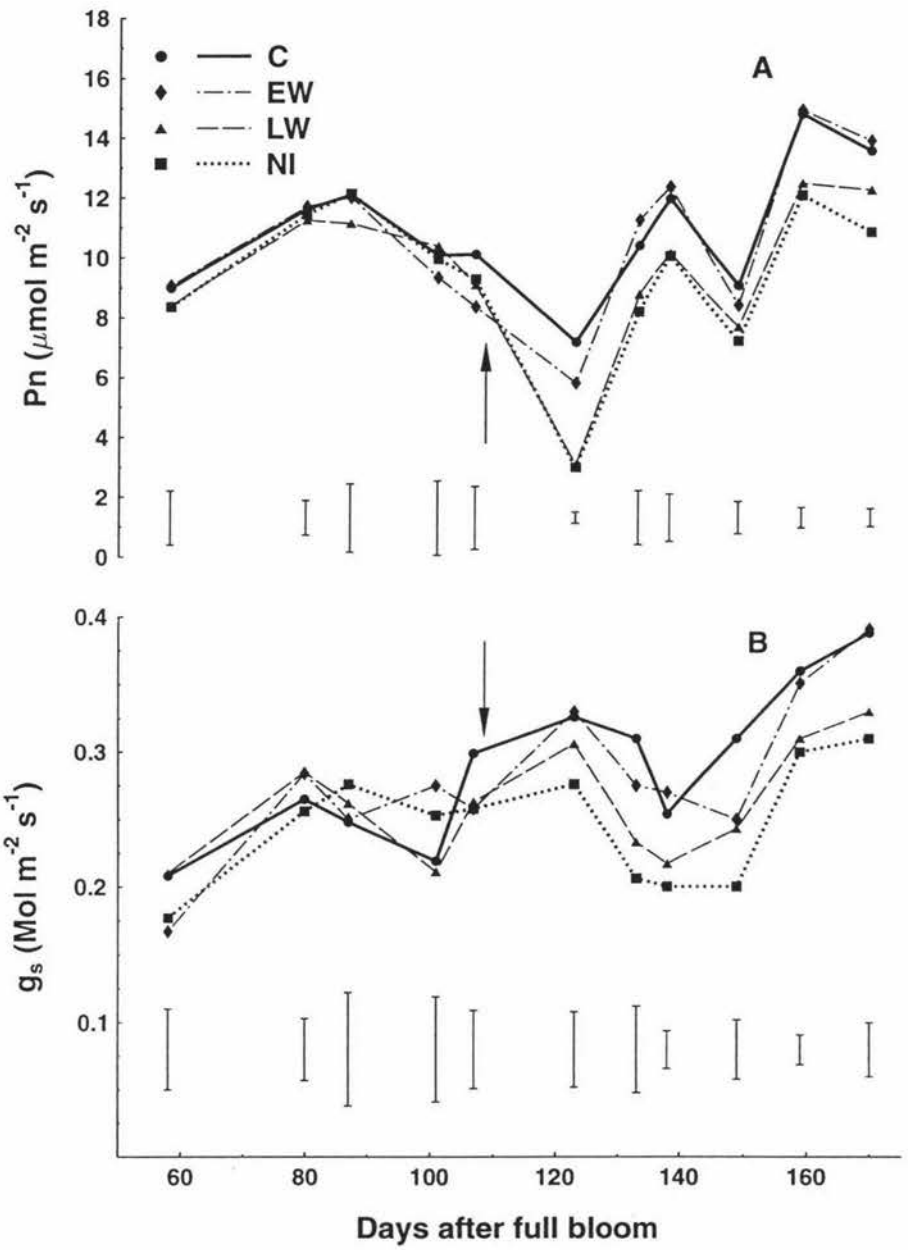

Figure 4.7: Changes in A) rate of photosynthesis (Pn) and B) stomatal conductance (g_s) during the season for 'Braeburn' apple trees under different irrigation treatments. Arrows indicate the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent SEM based on three replicates per treatment.

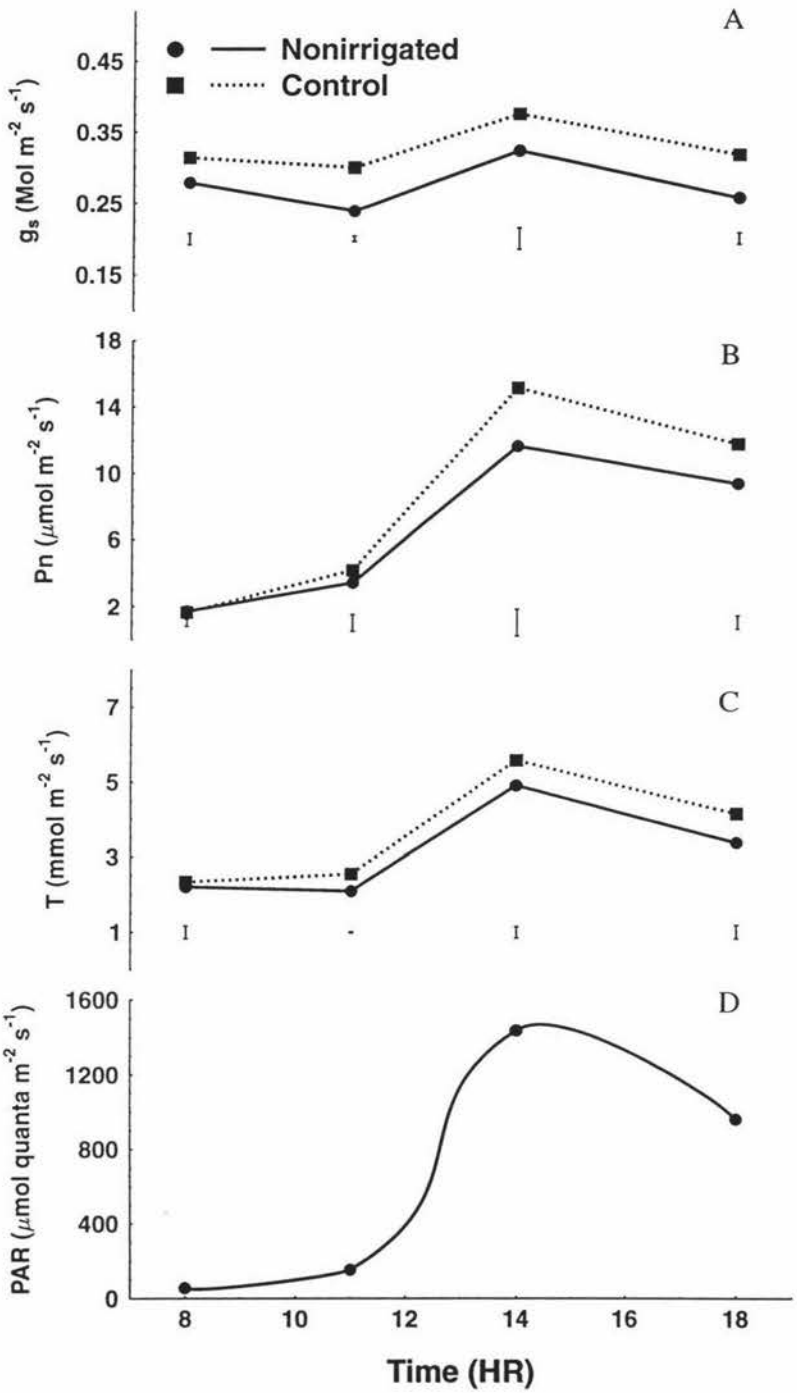

Figure 4.8: Diurnal changes in stomatal conductance (g_s) (A), rate of photosynthesis (Pn) (B), rate of transpiration (T) (C), and photosynthetically active radiation (PAR) (D) for well-watered and nonirrigated 'Braeburn' apple trees at 156 DAFB. Vertical bars represent pooled SEM based on three replicates per treatment.

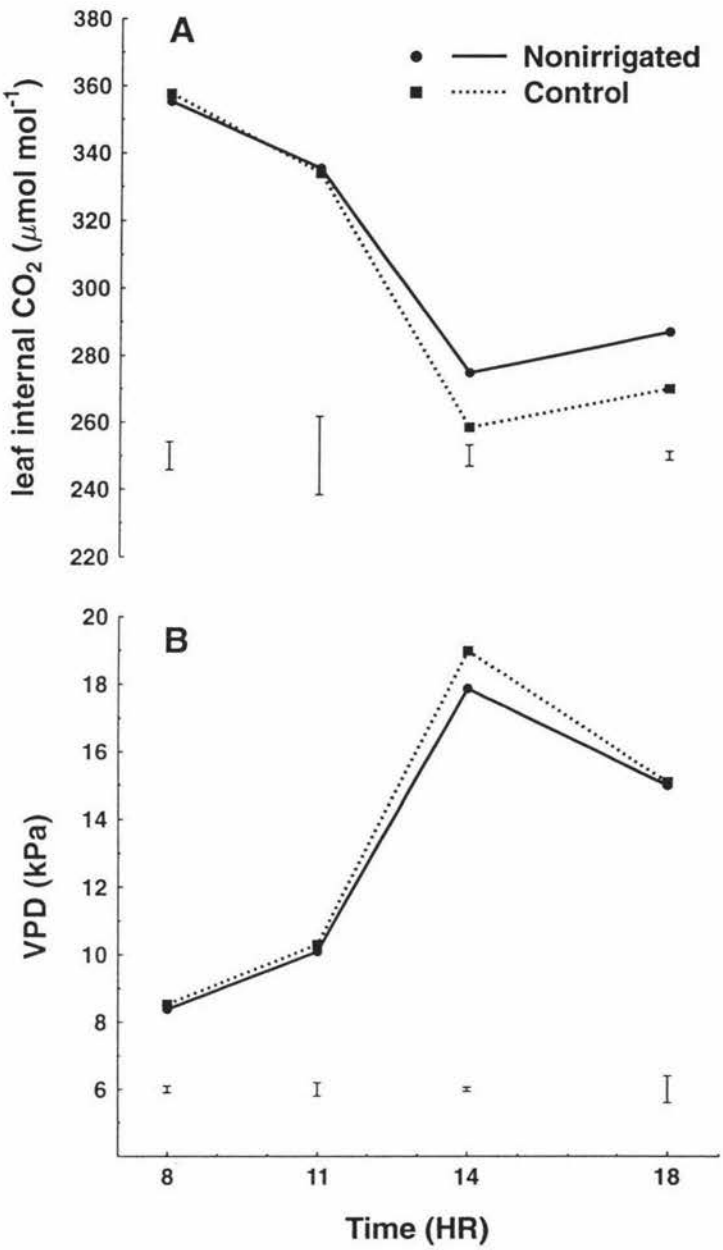

Figure 4.9: Diurnal changes in leaf internal CO_2 concentration (A) and water vapour pressure deficit (VPD) (B) for well-watered and nonirrigated 'Braeburn' apple trees at 156 DAFB. Vertical bars represent pooled SEM based on three replicates per treatment.

Diurnal changes in the rate of transpiration determined on 156 DAFB for C and NI increased in the early morning to a peak at about 1400 HR after which they declined (Fig. 4.8C). These closely followed the trends observed for g_s, PAR and VPD (Fig. 4.8A, D and Fig. 4.9B). The rate of transpiration on this day tended to be higher in C than in NI throughout the day with the differences being significant ($P \leq 0.05$) at midday.

4.2.7 Canopy Temperature and Canopy-Air Temperature Difference

The treatments had no effect on T_c during the early season (Fig. 4.11). At 135 DAFB, NI had a higher T_c than EW and C by 2 °C. There was no significant difference between LW and C although T_c in LW tended to be higher than that of C at 135 DAFB. Thereafter, treatments NI and LW maintained higher T_c than C and EW up to harvest.

Differences in T_c-T_a were observed earlier than those of T_c (Fig. 4.11B). At 120 DAFB, NI and LW had higher T_c-T_a than C. Furthermore, the values for NI and LW were positive while those for EW and C were negative on this day. Positive values mean that the canopy is warmer than the surrounding air. Positive values for NI an LW were maintained up to the last day of measurement, 171 DAFB, except on 154 DAFB when values for NI fell below 0. However, there was still a significant difference in T_c-T_a between NI and C.

Diurnal changes in T_c and T_c-T_a were determined on several occasions. At 111 DAFB (Fig. 4.12), there were no significant differences between the treatments in both T_c and T_c-T_a at all times of the day although there was a tendency for lower values in C relative to the other treatments from 1100 HR. On 171 DAFB, T_c was similar for all the treatments at 0900 HR (Fig. 4.13). As the temperature increased with the time of day, so did differences in T_c such that at 1100 and 1300 HR, both LW and NI had higher T_c compared to C and EW (Fig. 4.13A). The difference however disappeared in the evening.

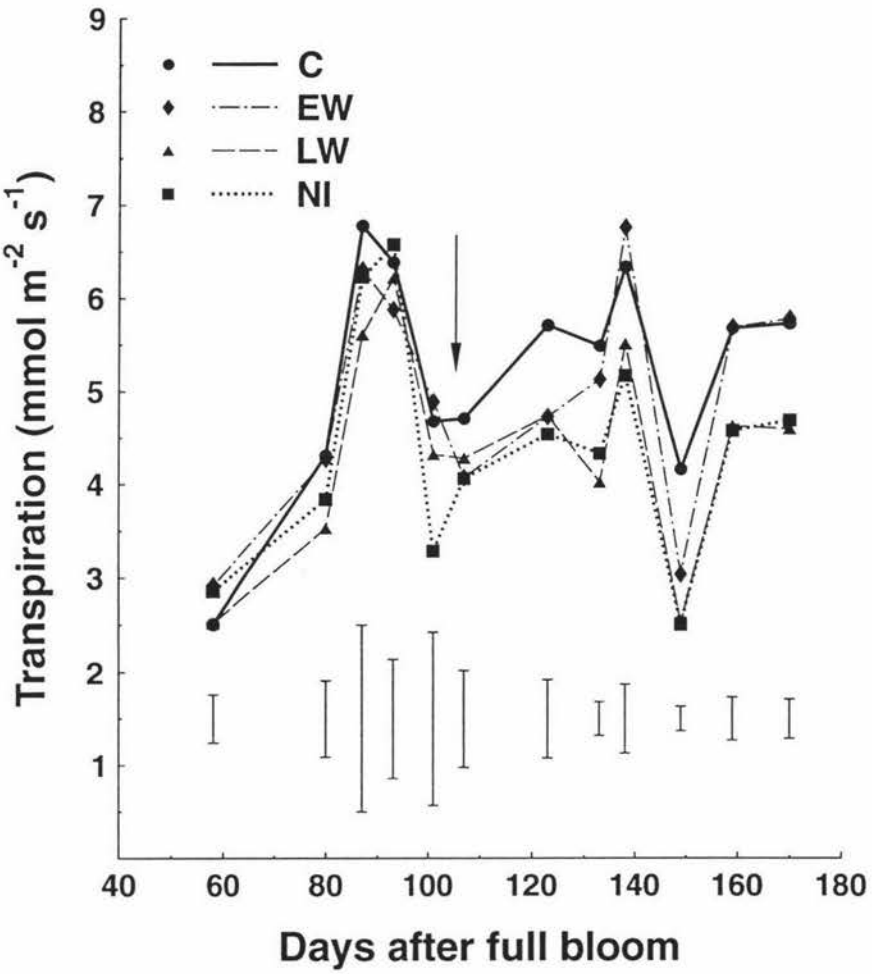

Figure 4.10: Changes in the rate of transpiration during the season for 'Braeburn' apple trees under different irrigation treatments. Arrow indicates the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

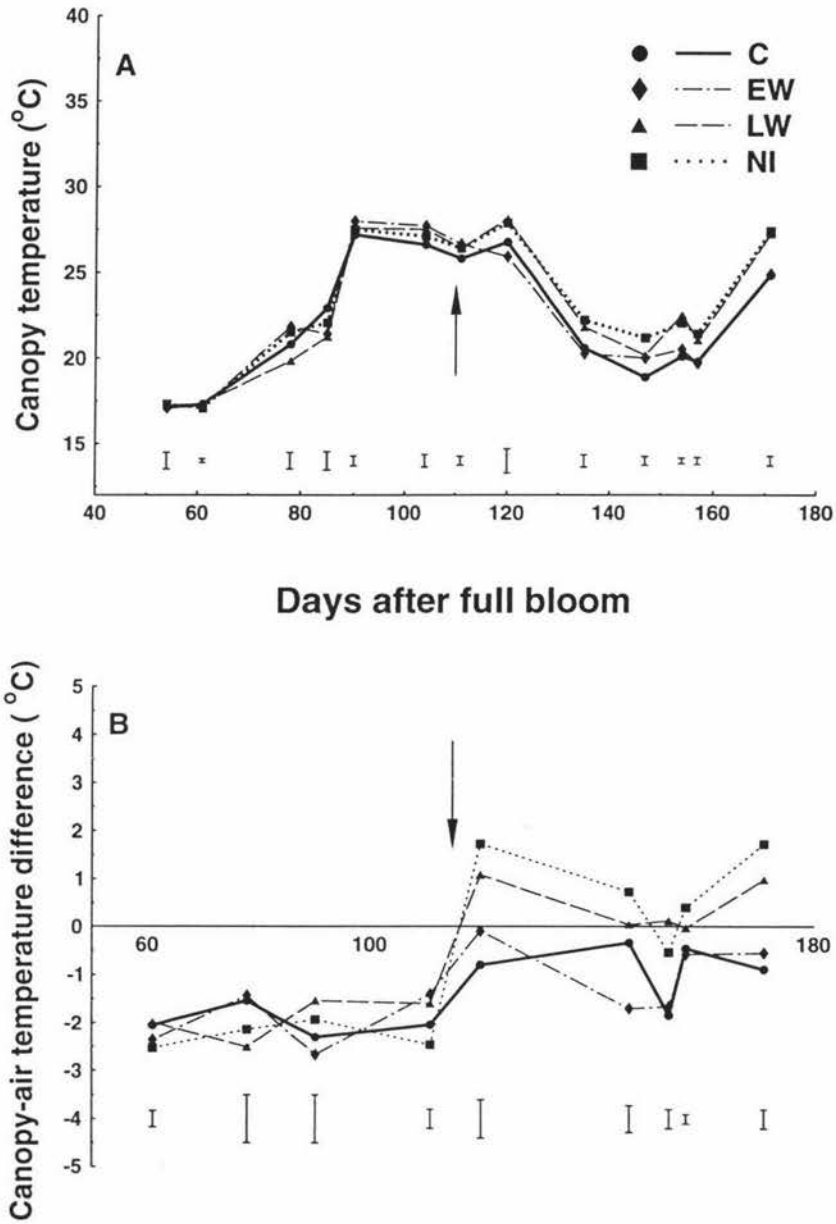

Figure 4.11: Changes in canopy temperature (A) and canopy-air temperature differences (B) during the season for 'Braeburn' apple trees under different irrigation treatments. Arrows indicate the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. The zero line in (B) represents air temperature. Vertical bars represent pooled SEM based on three replicates per treatment.

Treatments NI and LW had higher T_c-T_a at 0900 HR than C and EW (Fig. 4.13B). At this time, all the treatments had negative T_c-T_a. As the air temperatures increased, T_c-T_a increased such that at 1100 HR there was a large difference in T_c-T_a between both the stressed (NI and LW) and irrigated (C and EW) treatments. Furthermore, NI and LW had positive values whereas EW and C had negative values (Fig. 4.13B). Differences in T_c-T_a disappeared at about 1300 HR when T_c began to decline and at 1700 HR, T_c-T_a was similar among the treatments.

4.2.8 Vegetative Growth

The largest increase in trunk circumference was observed in C while the lowest was in NI (Fig. 4.14). Trunk circumference was decreased by 50% by withholding irrigation throughout the season. Withholding irrigation during the late season had no effect on the increase in trunk circumference whereas EW decreased it.

Generally, shoot growth was rapid up to 100 DAFB, thereafter, shoot extension was slower (Fig. 4.15). However, there was a higher cumulative shoot growth in C and LW than in NI and EW (Fig. 4.15A). Clear differences in shoot growth between the two sets of treatments were observed from about 70 DAFB. On average, total shoot length was reduced by about 25% in NI relative to C.

Shoot extension rate was highest from the first day of measurement to about 100 DAFB at which time it declined rapidly in all the treatments (Fig. 4.15B). In general, shoot growth rate was higher in C and LW relative to EW and NI for most of the period of measurement. For instance, at 56 DAFB, shoot extension rate was about twice as high in C and LW compared to NI and EW. Shoot extension evidently ceased at about 138 DAFB and no further measurements were taken after this day.

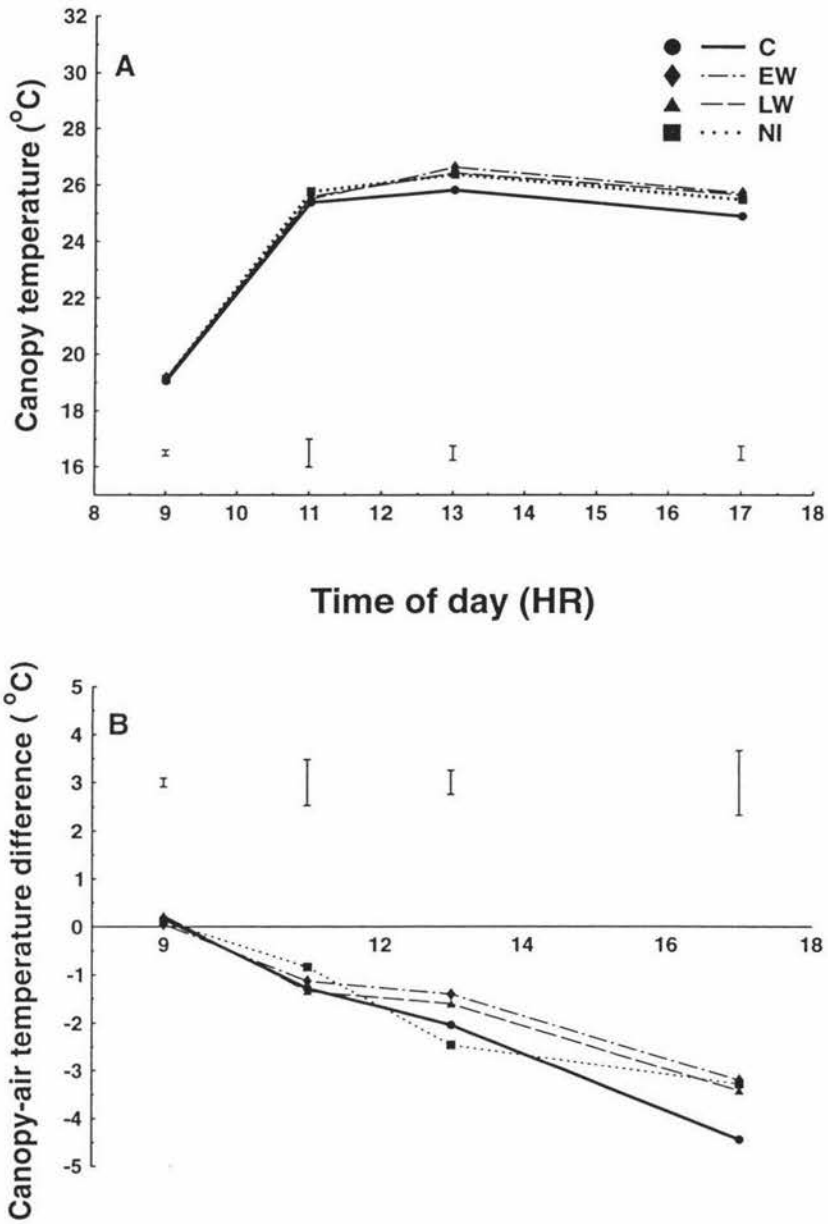

Figure 4.12: Diurnal changes in canopy temperature (A) and canopy-air temperature differences (B) at 111 DAFB for 'Braeburn' apple trees under different irrigation treatments. EW = early withholding, LW = late withholding of irrigation, C = control, NI = nonirrigated. The zero line in (B) represents air temperature. Vertical bars represent pooled SEM based on three replicates per treatment.

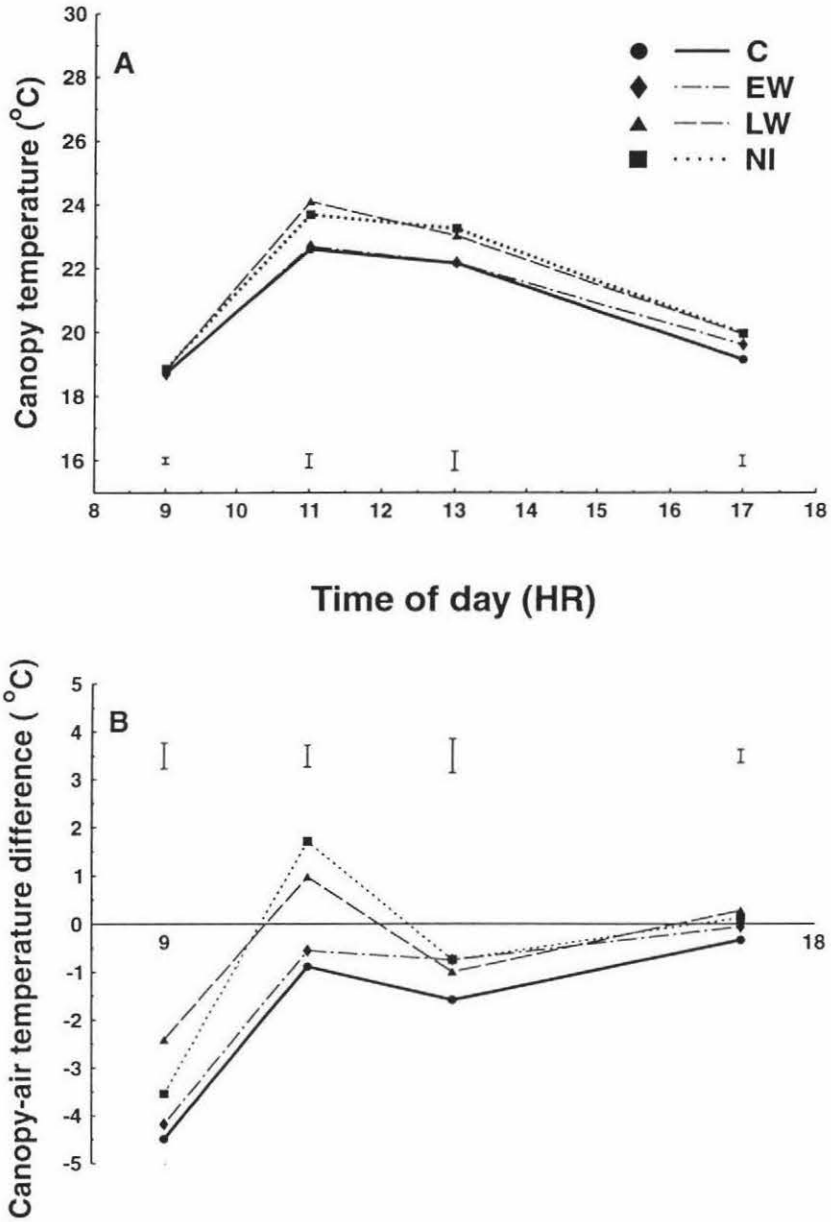

Figure 4.13: Diurnal changes in canopy temperature (A) and canopy-air temperature differences (B) at 171 DAFB for 'Braeburn' apple trees under different irrigation treatments. EW = early withholding, LW = late withholding of irrigation, C = control, NI = nonirrigated. The zero line in (B) represents air temperature. Vertical bars represent pooled SEM based on three replicates per treatment.

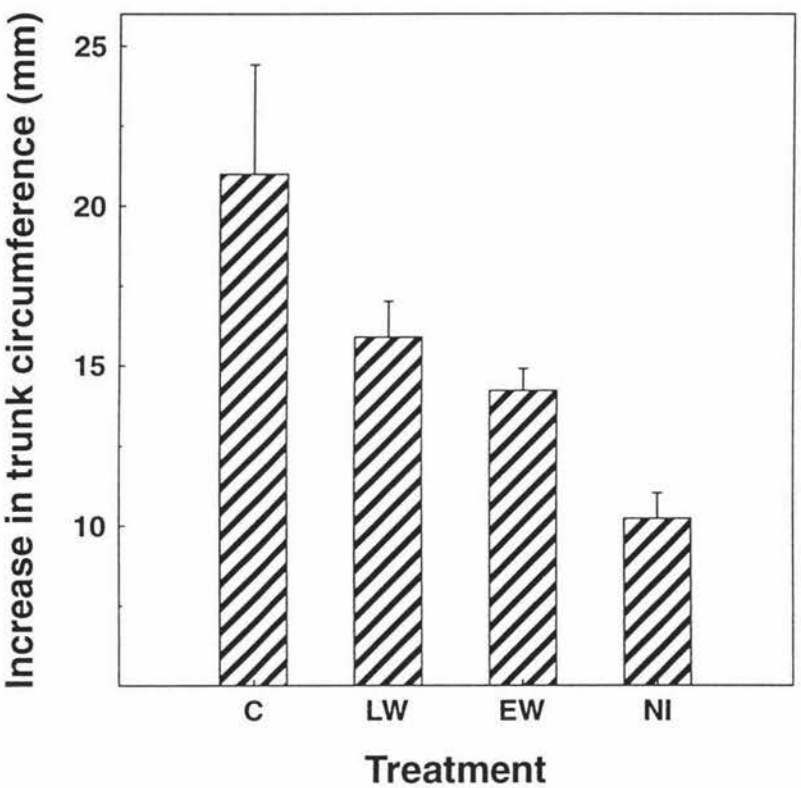

Figure 4.14: The effect of different irrigation treatments on the increase in trunk circumference for 'Braeburn' apple trees. C = control, LW = late withholding of irrigation, EW = early withholding of irrigation, NI = nonirrigated. Vertical bars represent SEM based on three replicates per treatment.

4.2.9 Fruit Growth

Cumulative fruit growth as determined by changes in volume (cm^3) during the season is shown in Fig. 4.16A. Fruit volume was first determined on 42 DAFB. From this date, at which time the selected fruit were approximately 13 cm^3 in volume, there was no difference in fruit growth in any of the treatments until final harvest. At harvest, the mean fruit volume across the treatments was 170 cm^3. Treatment C tended to have larger cumulative fruit volume although this was not significant.

Fruit growth rates are presented in terms of cm^3 day^{-1} (Fig. 4.16B). The growth rates were not significantly different at any time during the measurement period (42 to 170 DAFB).

4.2.10 Yield and Yield Components

Gross yield per tree, yield efficiency and crop density were not affected by the treatments (Fig. 4.17B,C,D). However, there were trends for LW to carry a higher crop load than the rest of the treatments (Fig. 4.17B). Mean fruit weight (g) at harvest was reduced by 11.4% in NI and by 10.6% in EW relative to the control (Fig. 4.17A). There was no significant reduction in mean fruit weight in LW.

Return bloom was significantly reduced in EW and NI relative to C. Withholding irrigation during the late season did not affect return bloom. In spring 1995, the flower density (no. of flowers per branch cross-sectional area (cm^2 ± SEM) for the various treatments were: 40.62 ± 4.19, 26.69 ± 3.14, 38.02 ± 1.53, and 19.36 ± 1.81 for C, EW, LW, and NI respectively.

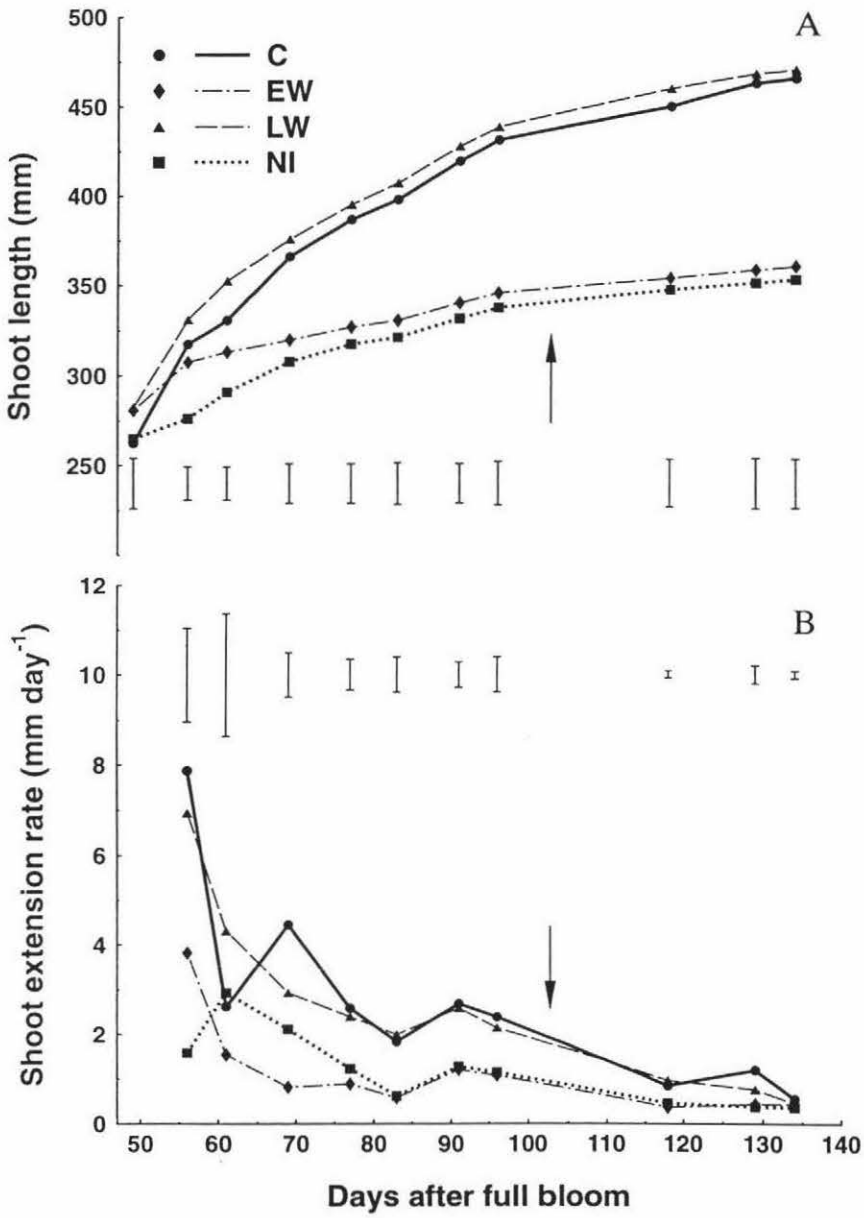

Figure 4.15: Changes in shoot length (A) and shoot extension rates (B) for 'Braeburn' apple trees under different irrigation treatments. Arrows indicate the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

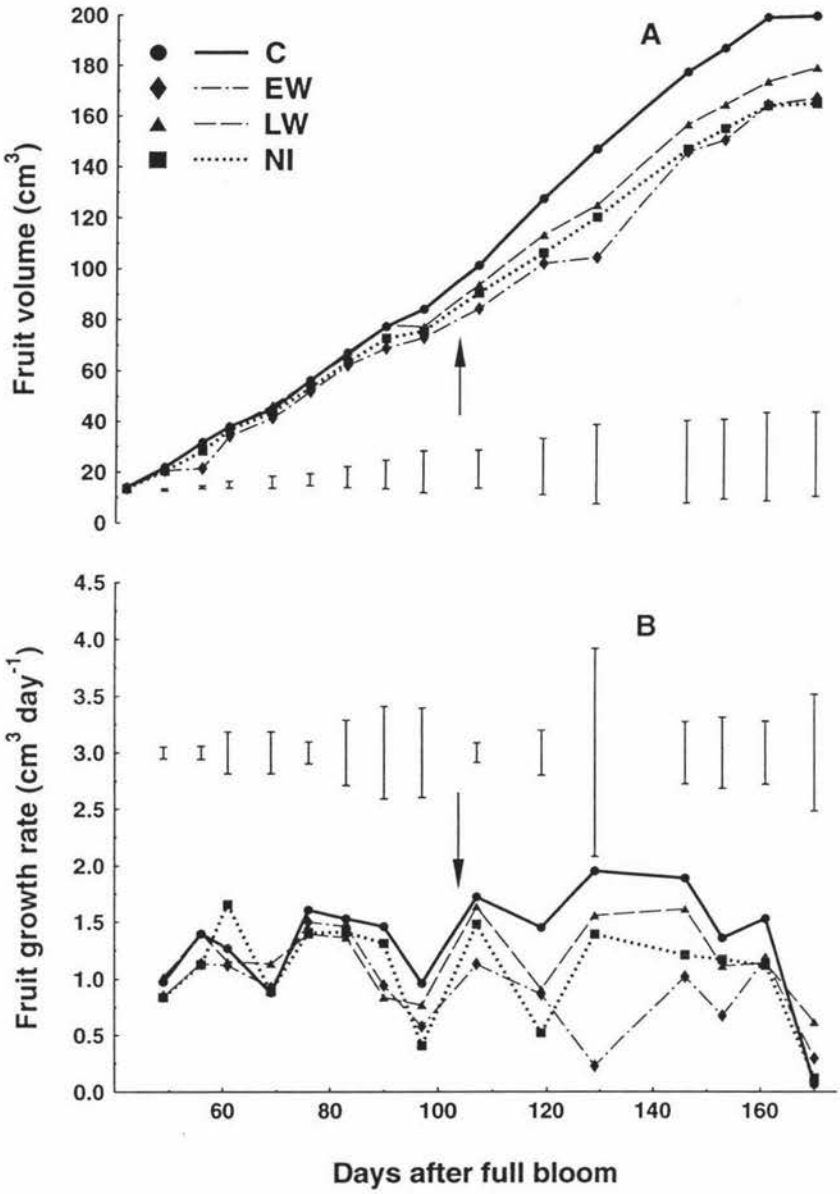

Figure 4.16: Cumulative fruit growth (A) and changes in fruit growth rate (B) of 'Braeburn' apples grown under different irrigation treatments. Arrows indicate the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

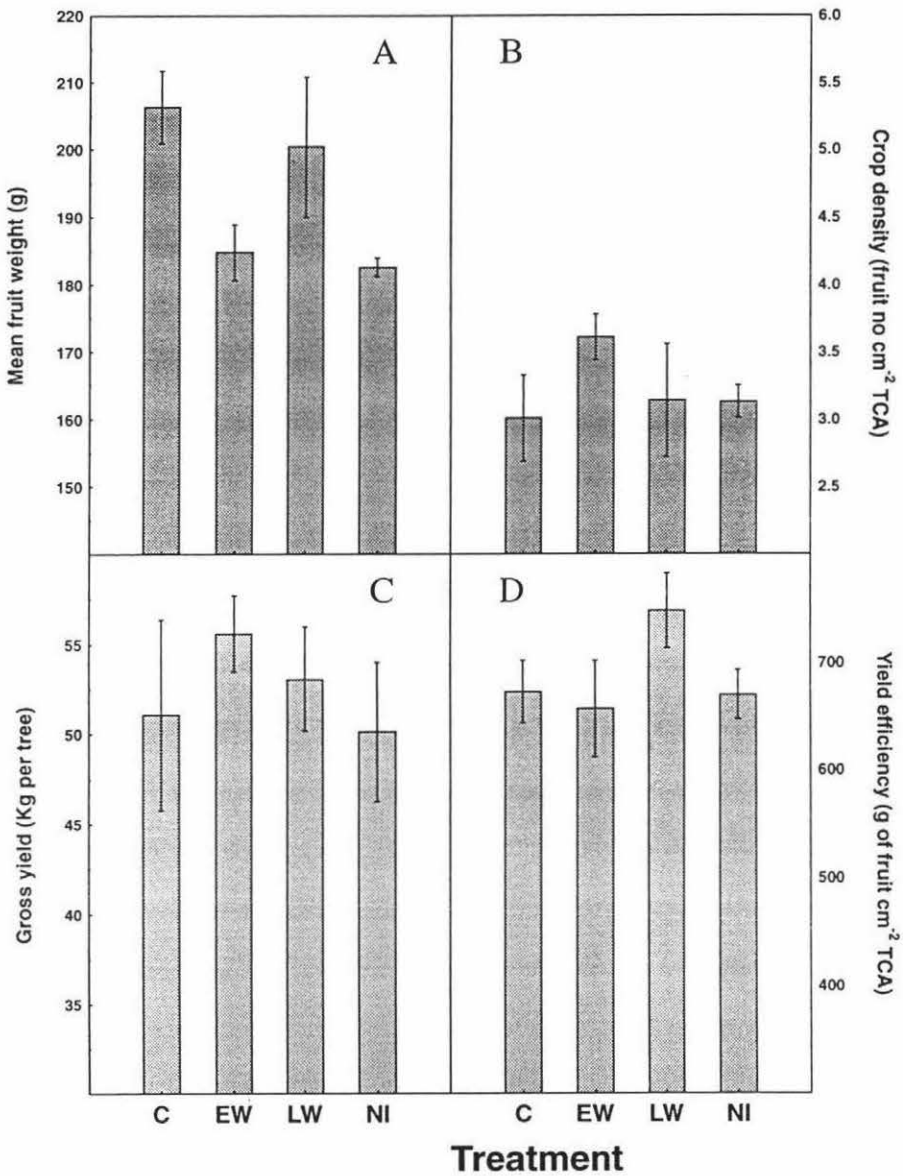

Figure 4.17: The effect of different irrigation treatments on yield and yield components of 'Braeburn' apple trees. C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, NI = nonirrigated. Vertical bars represent SEM.

4.3 DISCUSSION

4.3.1 Plant Water Status

According to Erf and Proctor (1987), midday Ψ is a sensitive measure of plant water status in apple. The experimental trees in the current study did not experience severe water stress at any stage. During the early season (before 104 DAFB), the lowest midday Ψ recorded was -2.1 MPa for EW and NI trees. During the late season, the lowest Ψ was -2.3 MPa for LW and NI with differences of about 0.8 MPa being recorded between C and the stressed trees. Mills et al. (1994) reported differences of about 0.7 MPa between irrigated and nonirrigated 'Braeburn' apple trees and this was effective in causing differences in various fruit and plant characteristics. The results from the current study are also similar to those of Irving and Drost (1987), whereby Ψ values were in the range of -1.3 MPa to -1.8 MPa for control trees and -1.7 MPa to -2.3 MPa for deficit treatments.

Predawn Ψ was also a clear plant-based indicator of the treatment effects, and the data indicate that the reduced irrigation treatments had significant effects on the plant water status. Previous studies have shown that predawn Ψ is closely correlated with soil moisture content since it closely represents soil water availability after equilibration of soil-plant potentials at the end of the night (Xiloyannis et al., 1980). The lowest predawn Ψ was -0.78 MPa for the stressed trees compared to -0.51 MPa for C which indicates that the trees developed an internal water deficit. Seasonal predawn Ψ differed between the four treatments in a pattern similar to mean θ and there was a clear relationship between predawn Ψ and θ during the course of the experiment. Linear regression analysis indicated a significant ($P \leq 0.0001$) relationship between both predawn and midday leaf water potential and θ measured at 1000 mm depth. There was a better relationship between between predawn Ψ and θ than between midday Ψ and θ (Fig. 4.18).

Plant water status is a function of soil water availability, hydraulic resistance along the flow path, plant water capacitance, and meteorological conditions that determine evaporative demand (Hsiao, 1990). The observed parabolic pattern at 96, 111, 132, and 151 may be due to diurnal changes in evaporative demand (Jones et al., 1985) with a midday minimum Ψ corresponding to the period of highest evaporative demand. According to Jones et al. (1985), there are marked diurnal changes in Ψ for apple trees, with minimum values of between -1.0 MPa and -2.5 MPa which usually occur in the early afternoon at the time of the highest transpiration rates. In the current study, the lowest Ψ was usually observed at midday to early afternoon with recovery toward evening. The stressed trees maintained lower Ψ during most of the day than C and also recovered more slowly (Fig. 4.6).

Although NI plants were subjected to the longest period of nonirrigation, their Ψ was similar to that of LW which only had a short period without irrigation in the late season. This might be due to Ψ adaptation under prolonged stress in NI and/or the effects of the humid climatic conditions and the limited degree of soil drying. The soil in the experimental block is deep and has a good water retention capacity (Clothier et al., 1977).

There were practical limitations to achieving significant stress during the early season. Due to heavy rainfall in winter and high relative humidity, it was difficult to achieve any more than minor levels of stress in the trees before January. Therefore, in terms of the degree of water stress, we may consider treatment EW as mild whereas LW and NI are moderate water stress treatments relative to C. In view of this, it is not possible to compare equivalent stress levels at all fruit growth stages studied.

4.3.2 Photosynthesis and Stomatal Conductance

As seen from the θ and Ψ measurements, the trees under reduced

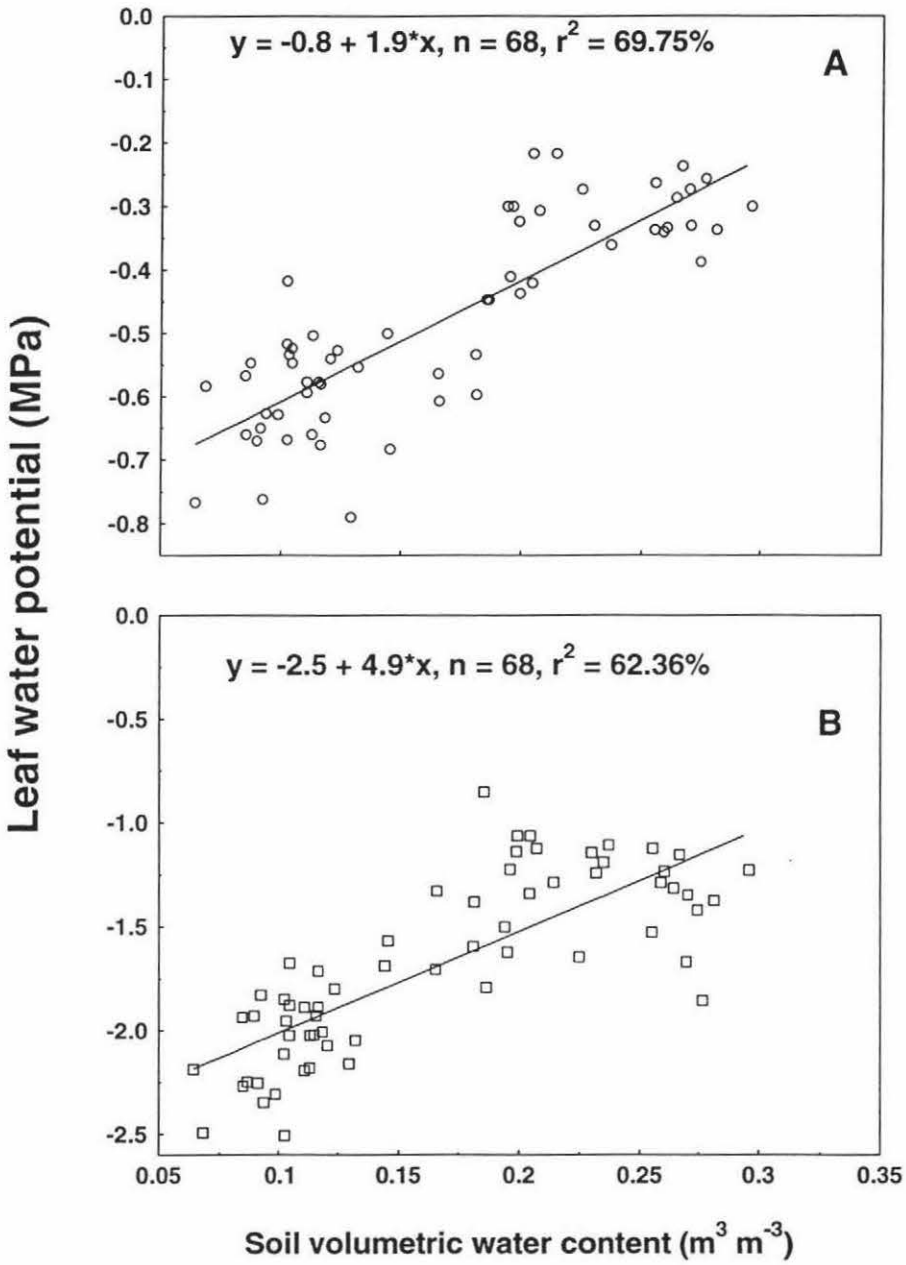

Figure 4.18: Relationship between soil volumetric water content at 1000 mm depth and predawn (A) and midday (B) leaf water potential for 'Braeburn' apple trees.

irrigation and nonirrigation were stressed significantly compared to the control trees. It is also clear that the limited water availability caused significant decreases in g_s and *Pn* which was observed in the late season towards harvest. Stomata are sensitive to plant water status, tending to close as Ψ declines (Jones et al., 1985). In the current study, a reduction in Ψ led to decreased g_s. This is consistent with the idea that stomata function to reduce excessive water loss when evapotranspiration is higher than water supply (Bradford and Hsiao, 1982). In the current study, reduction in Ψ and θ did not affect g_s until 138 DAFB. These results are similar to those obtained by Mills et al. (1994) who observed a reduction in g_s from 140 DAFB in nonirrigated 'Braeburn' apple trees. West and Gaff (1976) found that stomatal resistance in apple leaves was independent of Ψ until Ψ fell below -1.9 MPa after which stomatal resistance increased dramatically. This is in agreement with the results obtained in the current study whereby midday Ψ had declined to less than -2.0 MPa for LW and NI at 138 DAFB when a reduction in g_s was first observed.

Plant water deficits result in low *Pn* rates in leaves (Sritharan and Lenz, 1989). In this study, reduced irrigation caused a reduction in *Pn* by as much as 20% in the water-stressed plants relative to the control. Reduction in *Pn* in response to a reduced plant water status has been attributed, in part, to stomatal closure. Farquhar and Sharkey (1982) reported that water stress causes stomatal closure which thus restricts the uptake of CO_2 leading to a reduction in the rate of photosynthesis. Regression analysis showed a significant ($P \leq 0.001$) linear relationship between the rate of photosynthesis and stomatal conductance for both the stressed and control plants (Fig. 4.19). This shows a close dependence of photosynthesis on the extent of stomatal opening. Indeed, on 156 DAFB, *Pn* followed a course of change very similar to that of g_s (Fig. 4.8). However, a comparison of the two lines showed that although the slopes of the straight lines fitted were not significantly different

at $P \leq 0.05$ from each other, a common line does not fit the dataset as well as two separate lines. Thus there must have been other factors that contributed to the reduction in photosynthesis in the stressed plants apart from the degree of stomatal opening. Moreover, although a significant reduction in g_s was observed from 138 DAFB in the stressed plants, it was not until 156 DAFB that a consistent reduction in *Pn* was observed.

Recent studies on water stress have often indicated that *Pn* is also reduced for reasons other than increased stomatal resistance (Berkowitz and Gibbs, 1983; Hsiao, 1993; Janoudi et al., 1993). Further evidence of non-stomatal inhibition of *Pn* in the stressed plants is the fact that the leaf internal CO_2 (C_i) and the ratio of air CO_2 concentration to leaf internal CO_2 concentration (C_a:C_i) remained unchanged under water stress, although *Pn* was reduced (Fig. 4.20A and B). If stomatal closure were the only cause for the reduction in *Pn*, one would expect C_i to be reduced under water stress, because a normal rate of *Pn* metabolism with the restricted CO_2 transport to the intercellular space would lead to a depletion of intercellular CO_2. The non-stomatal factors which have been implicated as the possible causes of reduced *Pn* under water stress conditions include accumulation of assimilates in the photosynthetic sites leading to a feedback inhibition of the process (Azcon-Bieto, 1983) and decreased activity of photosynthetic enzymes particularly ribulose-1,5-biphosphate carboxylase oxygenase (RUBISCO) which is involved in the carboxylation reaction that fixes CO_2 into organic compounds (Vu and Yelenosky, 1988).

In summary, these results indicate that the effects of reduced irrigation on *Pn* in apples cannot be explained solely by the observed decrease in g_s in water-stressed 'Braeburn' apple plants and that there were non-stomatal factors reducing *Pn* under water stress whose investigation was beyond the scope of this study.

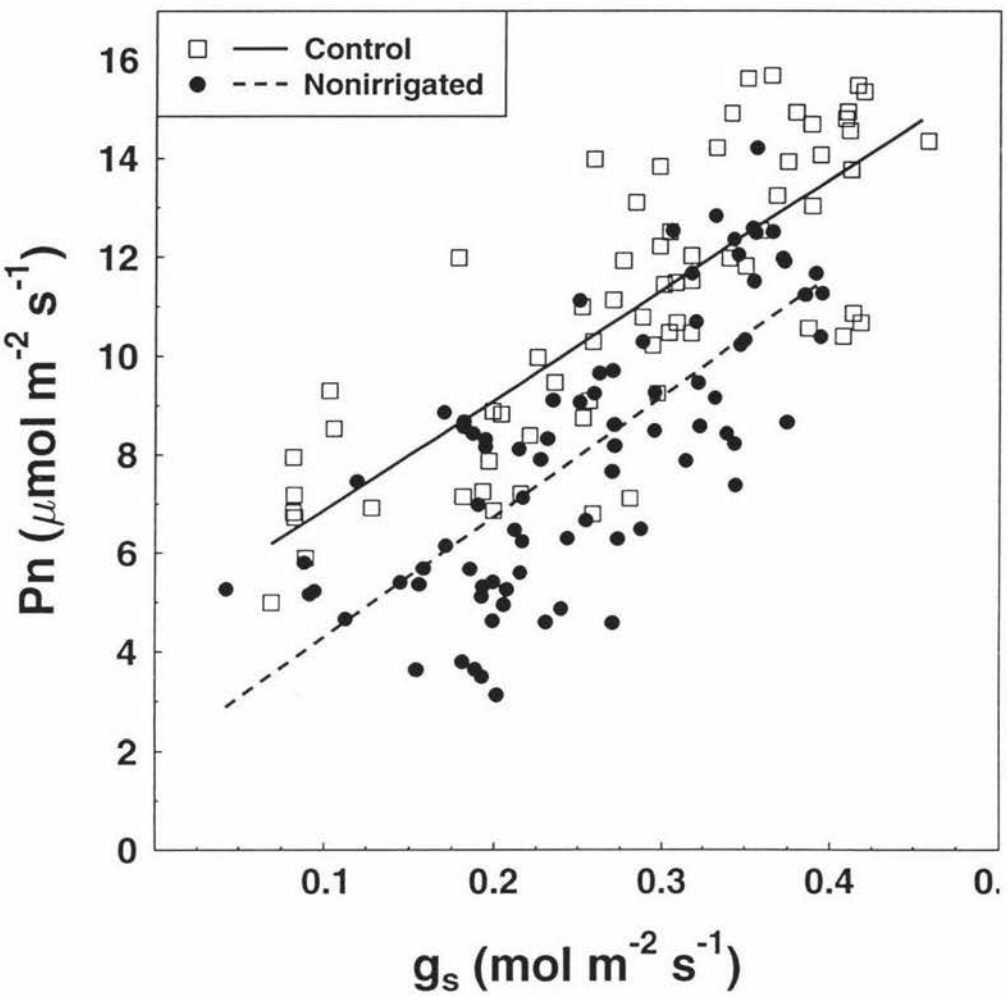

Figure 4.19: Relationship between stomatal conductance (g_s) and the rate of photosynthesis (Pn) in control and nonirrigated 'Braeburn' apple trees. The linear equations are Pn = 4.635 + 22.349*g_s, n = 67, r^2 = 64.37% and Pn = 1.84 + 24.49*g_s, n = 67, r^2 = 56.31% for control and nonirrigated plants respectively.

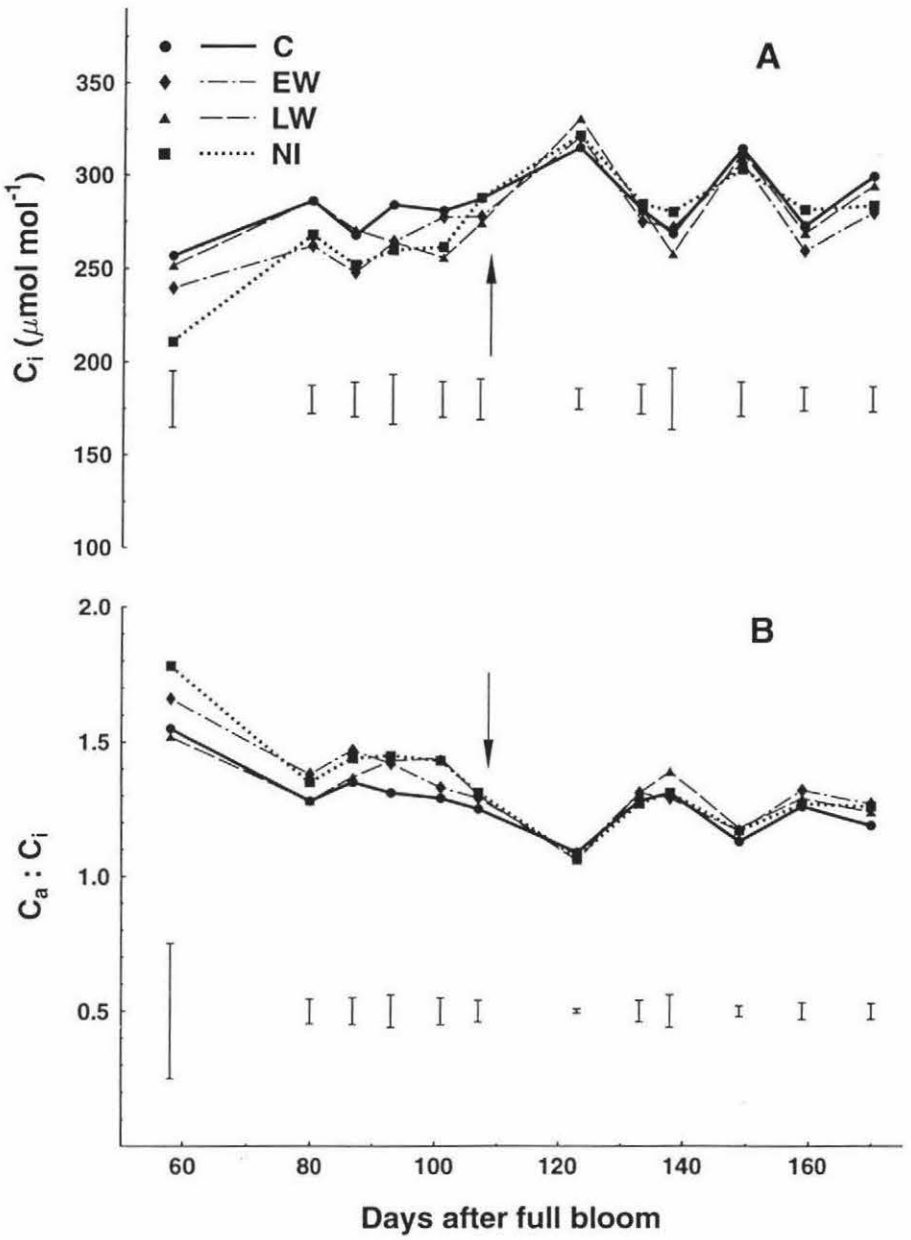

Figure 4.20: Changes in A) leaf internal CO_2 concentration (C_i) and B) air CO_2 : internal CO_2 ratio (C_a:C_i) during the season for 'Braeburn' apple trees under different irrigation treatments. Arrows indicate the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent SEM based on three replicates per treatment.

4.3.3 Canopy Temperature and Canopy-Air Temperature Difference

Seasonal and diurnal canopy temperatures (T_c) increased in the stressed plants from about 138 DAFB (Fig. 4.11 to 4.13). This closely corresponds to the decrease in g_s and the subsequent decrease in the rate of transpiration for the water-stressed plants. Canopy-air temperature difference (T_c-T_a) results showed differences between the treatments from about 110 DAFB after which the values were generally higher in the stressed plants than in the well-watered plants. This means that the canopy for the well-watered plants was generally cooler than that for the stressed plants. On several days, the canopy in the stressed plants was warmer than the surrounding air but that of the control plants was always cooler than the surrounding air.

Diurnal T_c and T_c-T_a results followed similar trends as the diurnal changes in the rate of transpiration with usually no differences between the treatments in the early morning and the largest differences at the time of the highest light intensity and rate of transpiration.

These results are consistent with the idea that a well-watered plant transpires at its maximum potential rate resulting in leaf temperatures lower than the air temperature and that as water deficits increase, transpiration declines and the leaf temperature rises relative to the air temperature (Jackson, 1982).

Since plant water potential has gained wide acceptance as a fundamental measure of plant water status, it is of interest to compare such measurements with canopy temperature data. Regression analysis of Ψ on both T_c and T_c-T_a indicated a significant ($P \leq 0.01$) quadratic relationship between the canopy temperature data and Ψ (Fig. 4.21). As water stress increased (increasing Ψ), both the T_c-T_a and T_c increased in a quadratic manner. However, there was considerable amount of scatter in the data and the models accounted for less than 50% of the variation.

4.3.4 Vegetative Growth

Withholding irrigation in the early season and throughout the season caused substantial decreases in shoot growth and trunk growth. However, withholding irrigation in the late season had no effect on shoot and trunk growth.

Trunk growth is related to the above ground weight of the tree (Westwood and Roberts, 1970) and the TCA increase is consequently related to the annual growth of the tree. The length of shoots also relates to the amount of tree growth (Higgs and Jones, 1991). Therefore, in this study, vegetative growth of the trees was significantly reduced in EW and NI but not in LW.

Reduction in vegetative growth as a result of reduced plant water status has been reported previously in apples (Ebel et al., 1995; Failla et al., 1990; Goode and Ingram, 1971; Higgs and Jones, 1991). Higgs and Jones (1991) found a reduction of as much as 62% in the weight of shoots removed by summer pruning following RDI on apple trees. Goode and Ingram (1971) recorded a reduction in trunk increment of as high as 38% in unwatered Cox's Orange Pippin apple trees. The results obtained in the current study agree with those of Failla et al. (1990) who found that water deficit in 'Granny Smith' apples affected shoot growth only in the early season, during which the shoots were still actively growing. Similar results have been obtained in other fruit crops as well. In peaches, vegetative growth was reduced by 80% and 70% when their daily water replacement was reduced to 1/8 and 1/4 respectively, of the evapotranspiration from a class A pan during the early part of the growing season (Chalmers et al., 1984). In pears, RDI applied during the early season reduced vegetative growth in proportion to the water deficit (Mitchell et al., 1984).

Although the reduction in growth by water stress has been well documented, different physiological processes have been put forward to

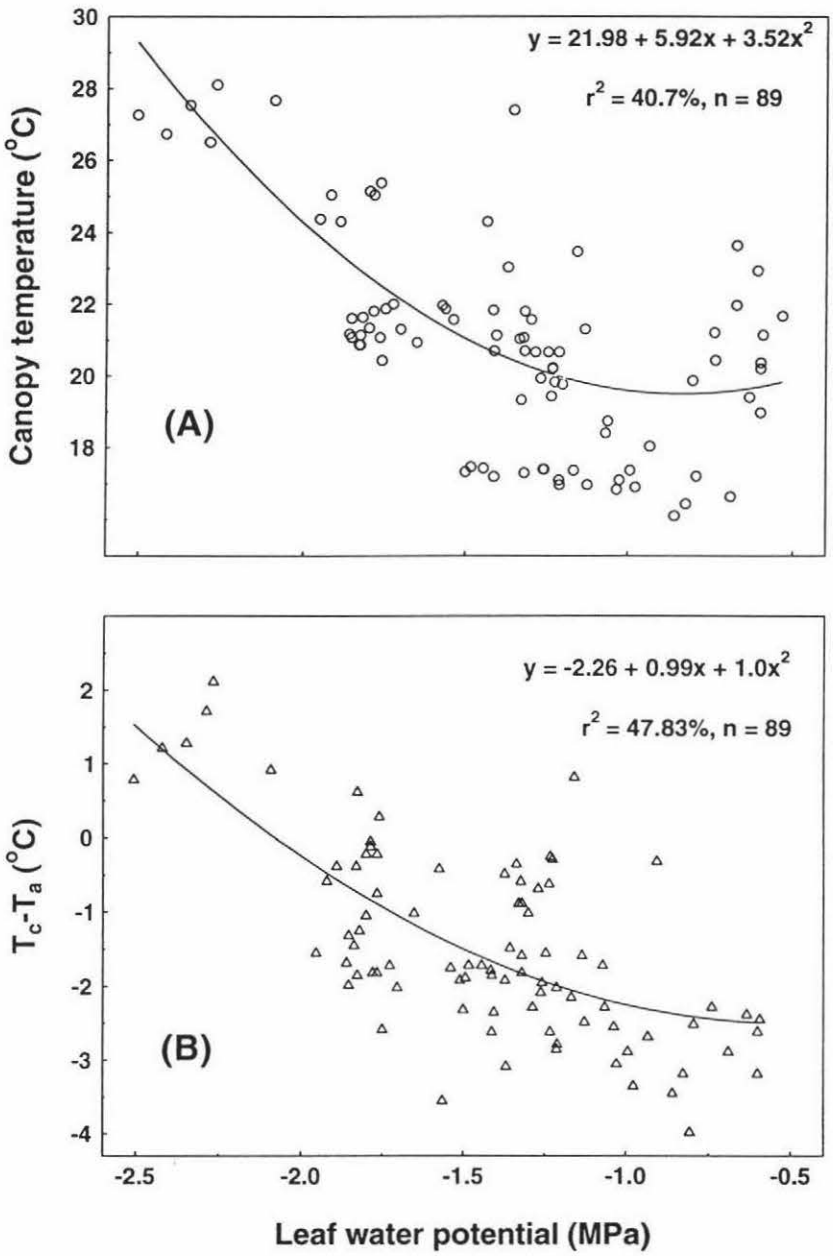

Figure 4.21: Relationship between leaf water potential and A) canopy temperature and B) canopy-air temperature difference (T_c-T_a) for 'Braeburn' apple trees.

account for this reduction in different species. Chartzoulakis et al. (1993b) found a reduction in plant height of 78% to 84% by severe water stress in kiwifruit. These authors attributed this decrease to a reduction in photosynthesis, leaf area development, and photosynthate partitioning. In the current study, it is unlikely that reduced vegetative growth in EW and NI was a consequence of reduced photosynthesis because *Pn* was not reduced until much later in the season (156 DAFB) by which time shoot growth had ceased. Indeed *Pn* was not affected at all by EW, yet a reduced shoot and trunk growth was recorded in this treatment.

Several suggestions have been put forward to explain growth control due to water stress. Kriedemann (1986) indicated that cell division could be inhibited by low water potentials as a result of reduced supply of photoassimilates while cell enlargement is hampered by low osmotic potentials. Under water stress, several metabolic processes such as carbohydrate and protein synthesis are affected which are required for tissue growth (Kozlowski et al., 1991). An alternative explanation is that plant growth regulators such as auxins, abscisic acid, and cytokinin or the ratio between these are influenced by low moisture content in the soil (Cleland, 1986). These growth regulators may be involved in growth either directly or through their influence on the hydraulic conductivity of cell mebranes and cell wall loosening (Turner, 1986).

My results suggest that for vigour control in the apple orchard, it is preferable to develop the soil water deficit during the early season when shoot growth is most rapid than during the late season when shoot growth is very slow (lag phase) or has ceased.

4.3.5 Reproductive Growth

The withholding of irrigation early in the season and throughout the growing season caused a significant reduction in mean fruit weight relative

to the control. However, fruit growth rates as determined after 42 DAFB until harvest were not affected by treatment. Furthermore, cummulative fruit growth during this period (42 to 170 DAFB) was also not affected by treatment (Fig. 4.15). Therefore, the reduction in fruit size in NI and EW could have been established prior to 42 DAFB and maintained until harvest. In this study, a significant reduction in Ψ was observed as early as 42 DAFB. In apples, cell division occurs from full bloom up to about 40 DAFB (Westwood, 1993, p.258). This period may be important in determining final fruit size. Our results agree with those obtained by Failla et al. (1990) who found that fruit growth rate was reduced during the first 15 days of stage I of fruit growth as a result of water deficit. During the second period (stage II) and up to harvest, the fruit growth rate in water-deprived trees was analogous to that of the fully watered trees. These authors found that the differences induced by water deficit in fruit size at the cell division phase were maintained until harvest. Similarly, Ebel et al. (1993) reported reduced fruit size in 'Delicious' apple subjected to deficit irrigation during the early stages of the growing season. In another study Failla et al. (1992), recorded a decrease in the size of 'Granny Smith' apples that received deficit irrigation from 23 DAFB to 53 DAFB which coincided with the period of cell division (stage I). According to these authors, water deficit imposed on fruit growing by cell division reduces fruit growth by decreasing water uptake by the fruit. This invariably leads to increased dry matter concentration.

Although reduced plant water status, severe enough to reduce photosynthesis, was imposed on LW, no reduction in fruit growth was recorded. This is in agreement with data on Asian pears (Behboudian et al., 1994) and apple (Irving and Drost, 1987) who showed no reduction in fruit size when water stress was imposed late in the growing season. In the current study, LW was started at 104 DAFB at which time the fruit were almost at the end of stage II and the growth rates had decreased.

Return bloom was decreased by withholding irrigation during the early and entire growing season but not during the late season. In apples, floral initiation for next year's crop occurs in early summer (Westwood, 1993, p. 219). This corresponds to late December and early January in the southern hemisphere. During this time, EW and NI trees were not receiving irrigation and water stress may have affected floral bud development and hence return bloom. Faust (1989, p. 134) cites flower bud differentiation as one of the processes adversely affected by water deficit. In this study, the reduction in return bloom was not so severe as to affect subsequent year's yield because further thinning was still required for EW and NI trees to attain commercially desirable crop loads. Therefore the reduction in return bloom may be potentially beneficial in terms of reduced costs of hand and chemical thinning.

4.3.6 Shoot Vs Fruit Growth

From the data obtained in the current study, shoot extension in 'Braeburn' apples is clearly more sensitive to water stress than fruit growth. At the intensity of stress imposed during the early season, shoot growth was markedly reduced whilst fruit growth continued unimpeded (Figs. 4.16 and 4.17). According to Forshey and Elfving (1989), fruit growth is less sensitive to water stress than any other above ground portion of the tree. This phenomenon is the basis for some of the benefits obtained by RDI. Regulated deficit irrigation reduces vegetative growth with increases in fruit yield (Chalmers et al., 1986). The mechanism is based on the phenomenon that different tissues and organs have different sensitivities to reduced plant Ψ. For example, peach and pear fruit growth was not inhibited by the water deficit induced by RDI, although vegetative growth occurring at the same time was reduced by 52% (Mitchell and Chalmers, 1982; Mitchell et al., 1986). Different plant processes also have different sensitivities to reduced Ψ. According to Hsiao (1973), cell expansion, which depends upon turgor,

is most sensitive, while photosynthesis and translocation needed to get assimilate from leaf to fruit are less sensitive. Thus fruit may continue accumulating solutes although plant Ψ may be too low to allow cells to expand.

This study has shown that reduced irrigation can be successfully applied to 'Braeburn' apple as a means of vigour control without significantly reducing crop density and yield. Benefit in terms of reduced vegetative growth was only obtained when irrigation was withheld in the early season (before 104 DAFB), rather than later in the season. The implications of the treatments on fruit quality are discussed in Chapter 5.

4.4 SUMMARY

The effects of the water status of the soil were investigated with respect to the plant water status, *Pn*, g_s, T_c and T_c-T_a, vegetative and reproductive growth in 'Braeburn' apples. The main conclusions from this chapter are as follows:

~ The use of under-tree polythene covers combined with the withholding of irrigation was effective in reducing the soil moisture content.

~ Trees not receiving irrigation at any time of the season developed a lower predawn and midday leaf water potential relative to the well-watered controls. Also, the diurnal leaf water potential followed a parabolic pattern with a rapid decrease during the morning and recovery in the afternoon. This pattern shows the influence of evaporative demand on the leaf water potential.

~ Water stress affected various physiological processes such as stomatal conductance, the rate of photosynthesis, and the rate of transpiration. The effect of water stress on the above mentioned processes generally occurred late in the season.

~ Although there was a strong relationship between stomatal conductance and the rate of photosynthesis, there was evidence that the

decrease in the stomatal conductance was not the sole factor responsible for decreased rate of photosynthesis. Leaf internal CO_2 during the season was not affected by the treatments at any stage suggesting that there could have been an impairment of the carbon fixation mechanism hence the observed reduction in the rate of photosynthesis.

~ Fruit growth may have been affected by water-stress during the cell division phase. After the cell division phase, fruit growth was not inhibited by water stress at any time of irrigation withholding.

~ Shoot growth and increase in trunk circumference were greatly reduced by water-stress during the early growing season. Shoot extension is very sensitive to water stress especially if the water stress is imposed at the time when shoot growth is most rapid.

~ Withholding irrigation during the early and entire growing season caused a significant reduction in fruit weight at harvest and a substantial decrease in return bloom. However, the treatments had no effect on the total yield, yield efficiency, or crop density.

CHAPTER FIVE

EFFECT OF IRRIGATION TREATMENT ON FRUIT QUALITY AND COMPOSITION

5.1 INTRODUCTION

The main benefits of reduced irrigation applied in the form of RDI strategy as elucidated by Chalmers and his colleagues (e.g., Chalmers et al., 1981) relate to the control of vegetative growth of the fruit trees. Although Considerable amount of work has been done on the water relations of apples (e.g., Higgs and Jones, 1991), there is limited information regarding the effects of reduced irrigation on fruit quality. The hypothesis was that reduced irrigation modifies fruit quality attributes depending on the stage at which irrigation is withheld. The objective of this part of the study was to compare the effect of withholding irrigation at different times of the season on the quality and composition of 'Braeburn' apples.

5.2 RESULTS

5.2.1 Fruit Carbohydrates

Total sugar concentration was significantly higher in NI than in C from 110 DAFB (Fig. 5.1). This difference was maintained until harvest. Up to 110 DAFB, LW had similar total sugar levels as C. Thereafter, total sugar concentration increased rapidly in LW and remained higher than in C up to harvest (Fig. 5.1). At 110 DAFB, EW had a higher total sugar content than C, a difference which was not seen on 129, 171, DAFB and at final harvest. The trends of individual sugars were similar to that observed for the total sugars. In general, the fruit had higher levels of fructose than any of the other sugars while sorbitol was lowest. There was a rapid increase in sucrose in NI and LW after 95 DAFB such that at 129 DAFB, sucrose was significantly higher in LW and NI than in C and EW (Fig. 5.2A). These

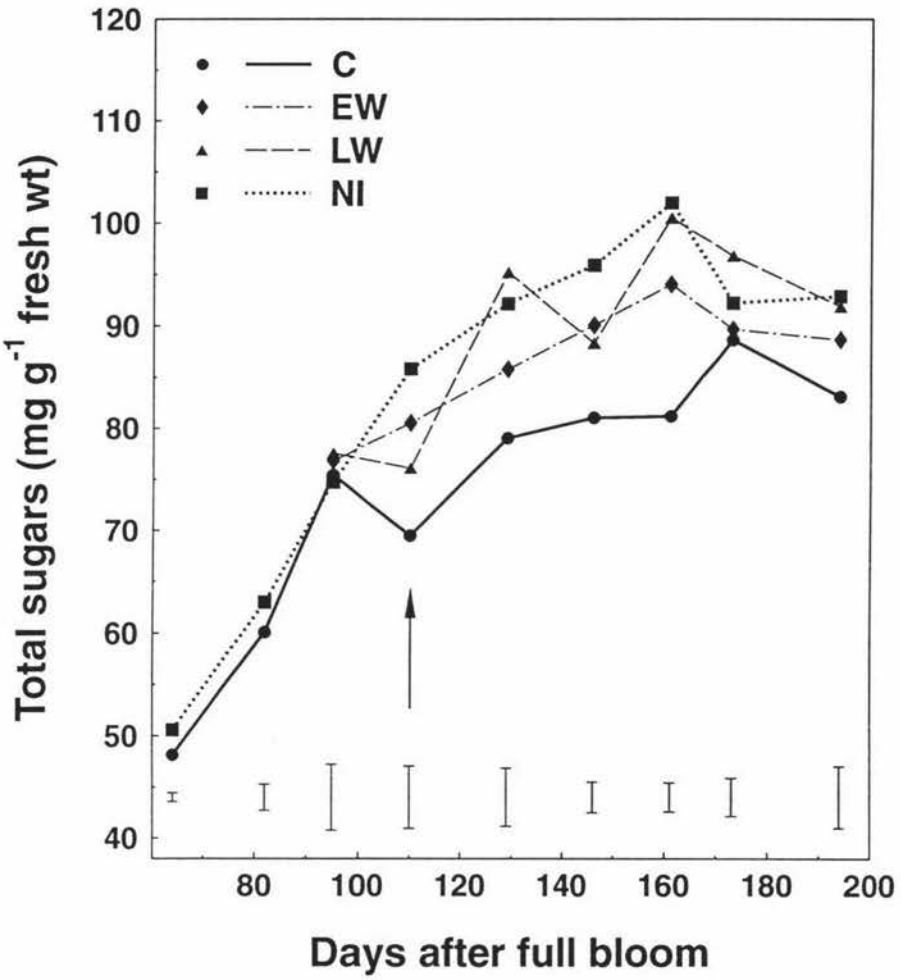

Figure 5.1: Changes in the concentration of total sugars (sucrose+fructose+sorbitol+glucose) in fruit of 'Braeburn' apples under different irrigation treatments. Arrow indicates the end of early withholding (EW) of irrigation and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on nine composite samples per treatment.

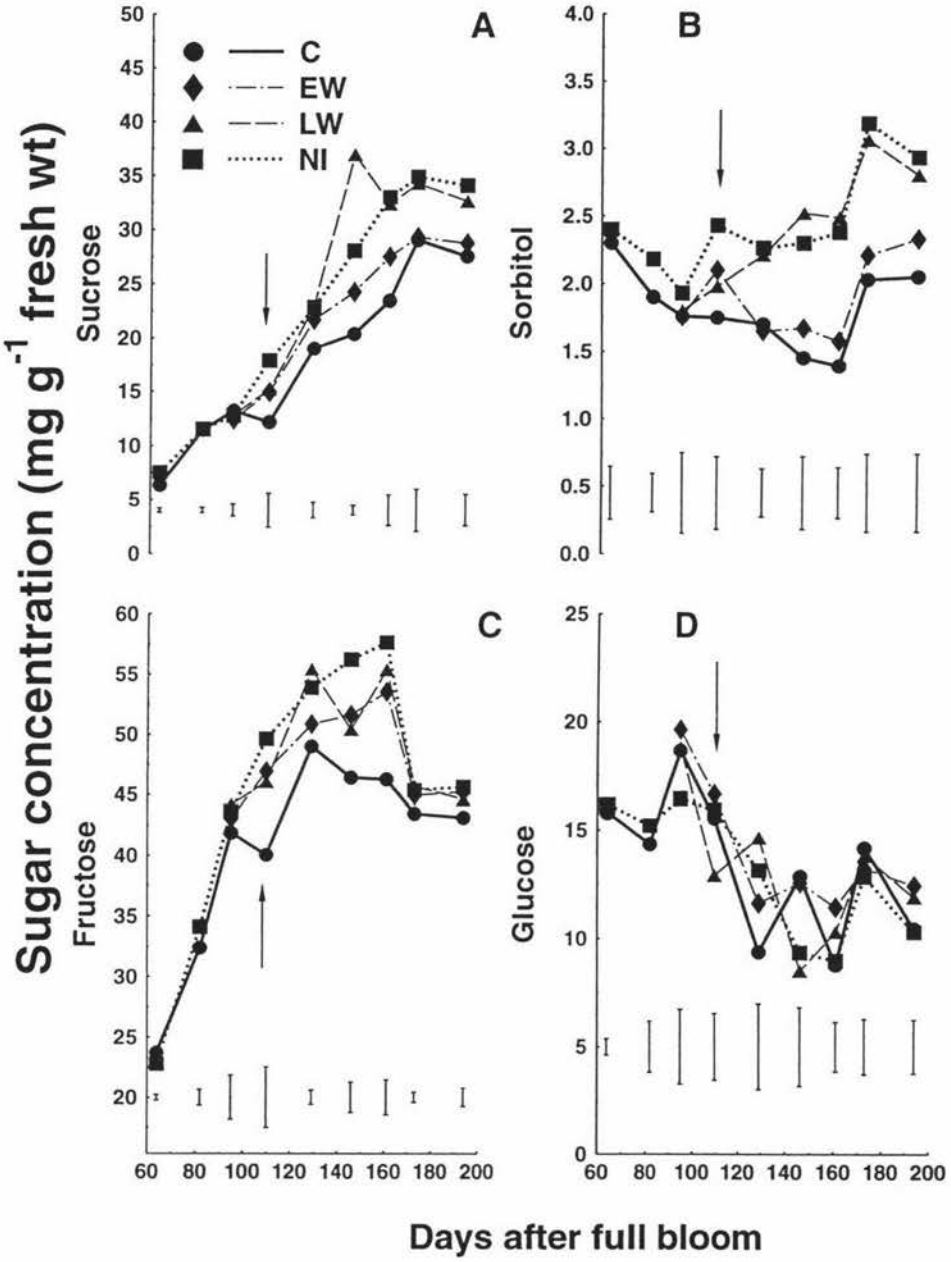

Figure 5.2: Changes in the concentration of fructose, sucrose, sorbitol, and glucose in fruit of 'Braeburn' apples under different irrigation treatments. Arrows indicate the end of early withholding (EW) of irrigation and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on nine composite samples per treatment.

differences were maintained until harvest. Fructose levels increased in NI, EW, and LW after 95 DAFB and remained higher in these treatments than in C until final harvest. No significant differences in fructose were observed at final harvest between NI, LW, and EW (Fig. 5.2B). Sorbitol was higher in LW and NI than in C and EW from about 129 DAFB up to final harvest. The level of sorbitol was consistently lower in C than in all the other treatments (Fig. 5.2C). There were no significant differences between the treatments in the glucose concentration at any time (Fig. 5.2D).

5.2.2 Total Soluble Solids

At 110 DAFB, TSS was higher in NI and EW fruit than in C and LW (Fig. 5.3). Treatment NI maintained a higher TSS than C until final harvest with differences of as much as 1.8 °Brix. There was a rapid increase in TSS in LW after 110 DAFB to a similar level as NI at about 128 DAFB. Thereafter, LW had higher TSS than C until final harvest. A difference of about 1.6 °Brix was observed between LW and C at final harvest. The concentration of total soluble solids in EW changed slowly after 110 DAFB such that the increase noted earlier in the season had disappeared at harvest relative to C. Both NI and LW had higher TSS than C at harvest.

5.2.3 Titratable Acidity

Titratable acidity (% malic acid) before harvest declined in all the treatments as the season progressed (Fig. 5.4). Although titratable acidity tended to be higher in C than in the other treatments for most of the season, the differences were not significant at 5% level of probability (Fig. 5.4).

5.2.4 Mineral Composition

Changes in fruit mineral composition (N, P, K^+, Ca^{2+}, and Mg^{2+}) during the season are shown in Figs. 5.5 and 5.6. From the start of measurements

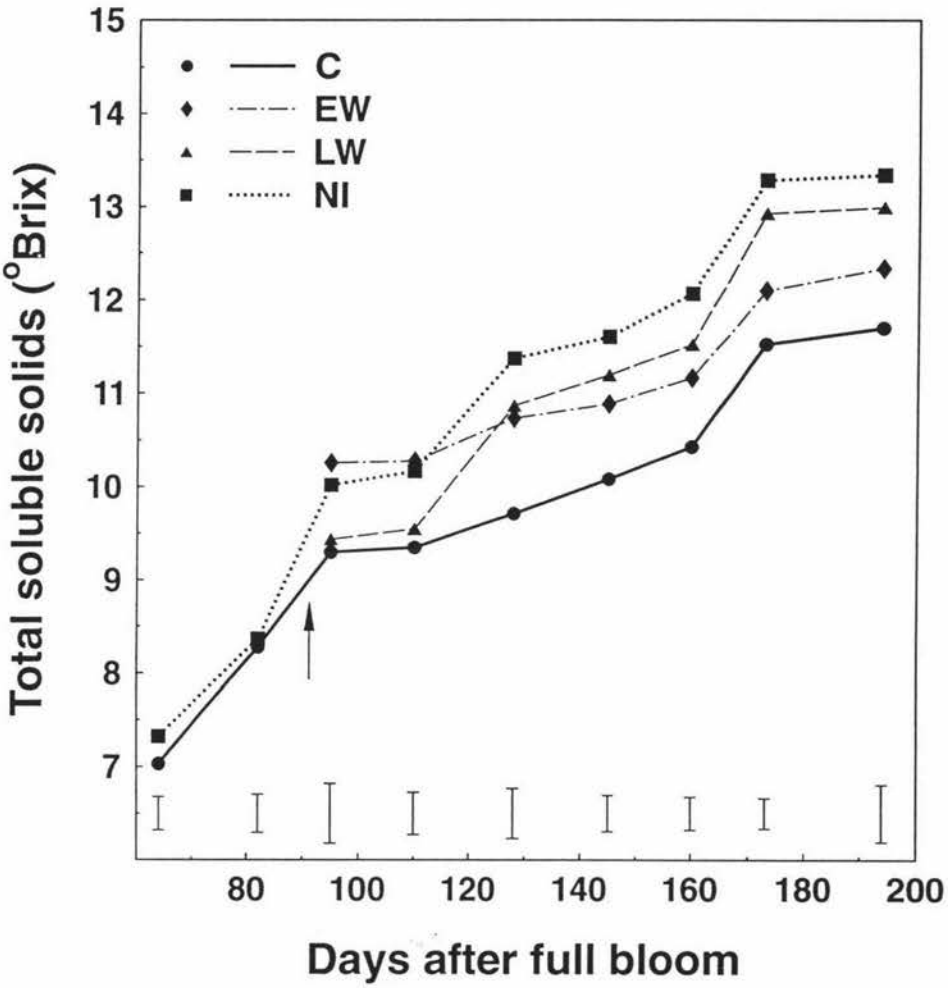

Figure 5.3: Total soluble solids concentration in fruit of 'Braeburn' apples under different irrigation treatments. Arrow indicates the end of early withholding (EW) and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

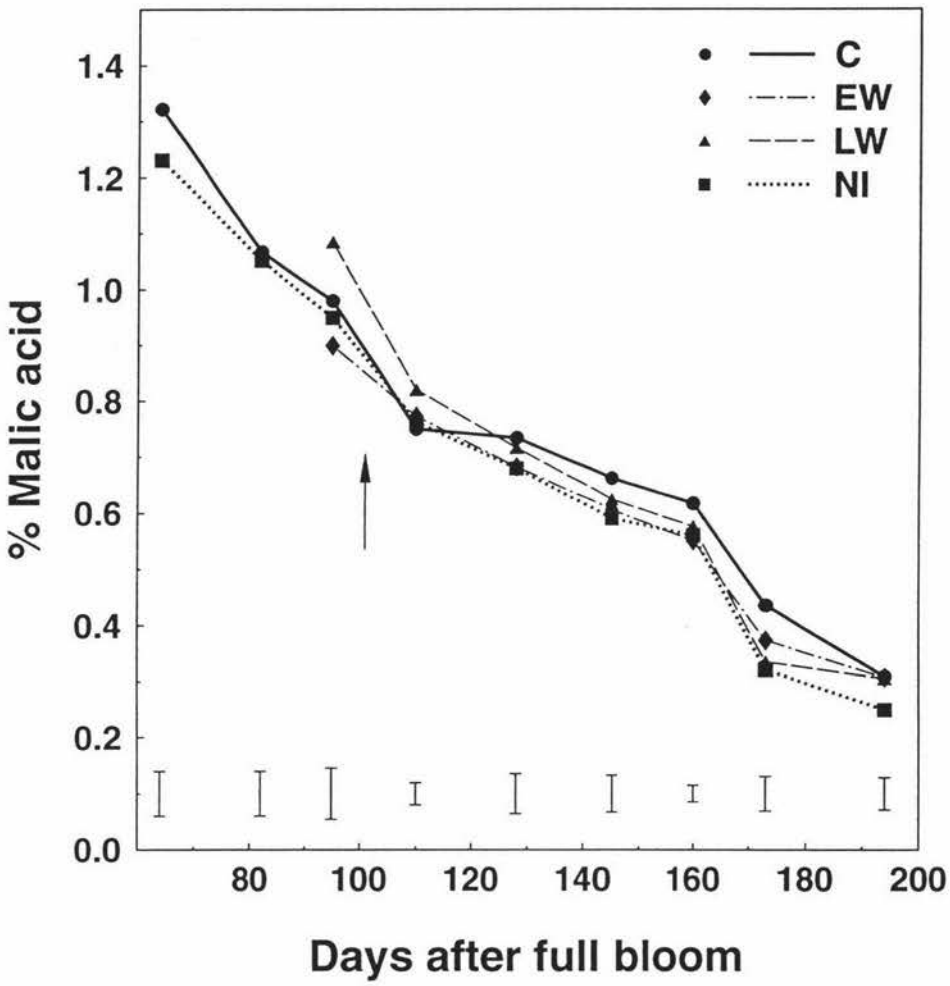

Figure 5.4: Titratable acidity expressed as % malic acid of 'Braeburn' apples under different irrigation treatments. Arrow indicates the end of early withholding (EW) of irrigation and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent SEM based on nine composite samples per treatment.

at 64 DAFB, there was a general decline in mineral concentration for all the treatments as the season progressed. However, no significant differences in concentration were observed between the treatments for any of the mineral elements.

5.2.5 Skin Colour

At the start of colour measurements (128 DAFB), the hue angle (H) and lightness (L) of the blushed surface for NI fruit were significantly lower than those for C ($P \leq 0.05$) (Fig. 5.7). Lightness and H values were always highest in C and lowest in NI for most of the late season. Hue angle and lightness for LW was similar to that of C at 128 DAFB. Thereafter, both H and L values declined rapidly in LW such that at harvest, LW had a lower H value than C. Although EW had lower H and L values than C at the first day of colour measurements, this difference disappeared at about 145 DAFB. At harvest EW and C had similar H and L values.

A similar trend was observed in the background skin colour (Fig. 5.8). At 128 DAFB, H was lower in EW and NI than in C and LW. Hue angle remained high in C up to harvest and was lowest in NI. At harvest, LW had a lower H angle than both C and EW individually.

5.2.6 Dry Matter Concentration

The dry matter concentration (%) of the fruit at 194 DAFB from different treatments is shown in Fig. 5.9. At this time, NI and LW had higher dry matter content than both EW and C. At final harvest fruit dry matter content expressed as mg g^{-1} ± SEM were: 154.36 ± 1.78, 140.10 ± 5.11, 152.11 ± 1.46, and 133.83 ± 0.07 for NI, EW, LW, and C respectively.

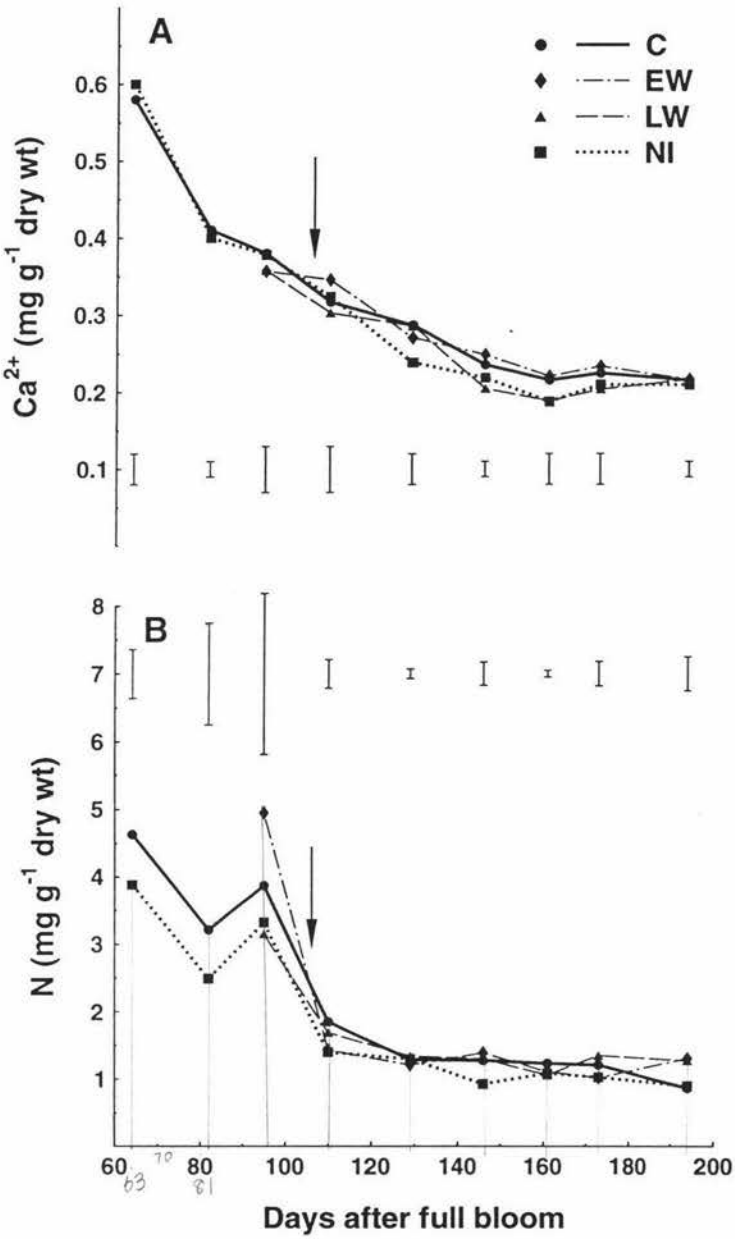

Figure 5.5 Changes in the concentration of Ca^{2+} (A) and N (B) in fruit of 'Braeburn' apples under different irrigation treatments. Arrows indicate the end of early withholding (EW) of irrigation and the start of late withholding (LW) of irrigation. Vertical bars represent pooled SEM based on nine composite samples per treatment.

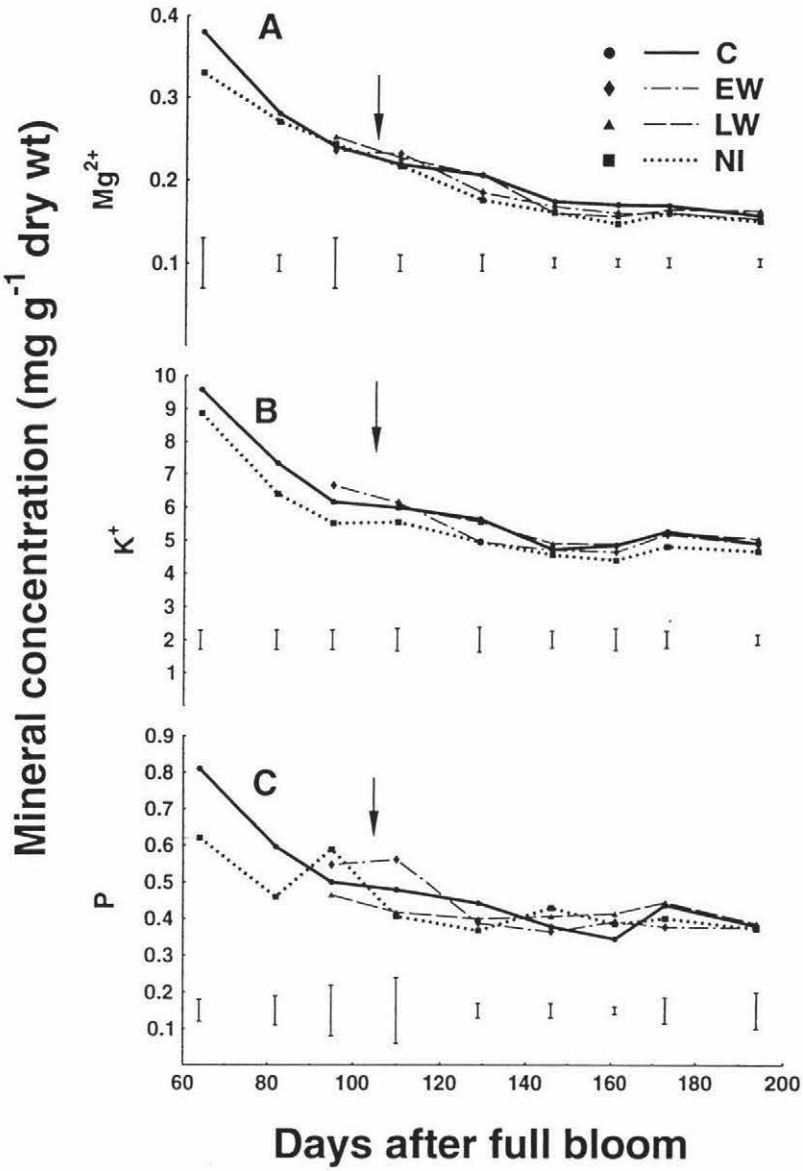

Figure 5.6: Changes in the concentration of Mg^{2+} (A), K^{+} (B), and P (C) in fruit of 'Braeburn' apples under different irrigation treatments. Arrows indicate the end of early withholding (EW) of irrigation and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on nine composite samples per treatment.

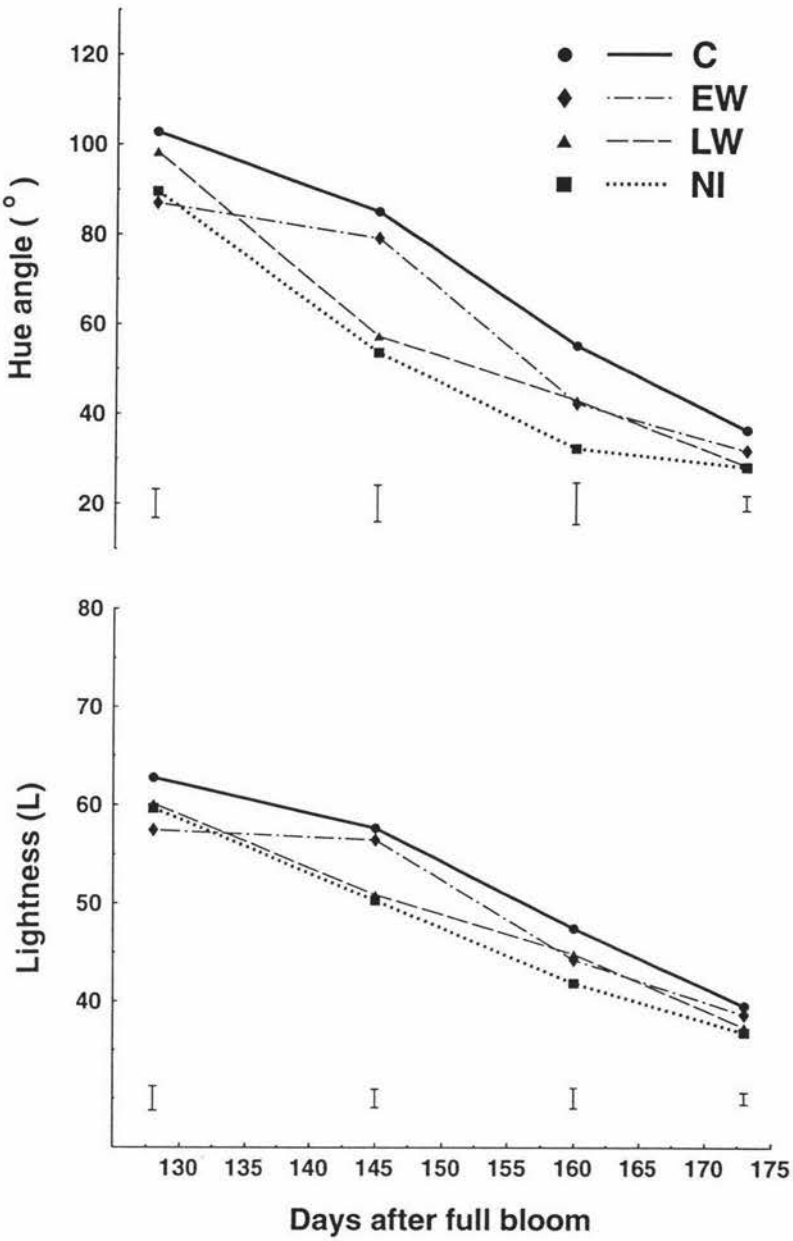

Figure 5.7: Changes in red blush hue angle (H) and lightness (L) during the late season in 'Braeburn' apples under different irrigation treatments. C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

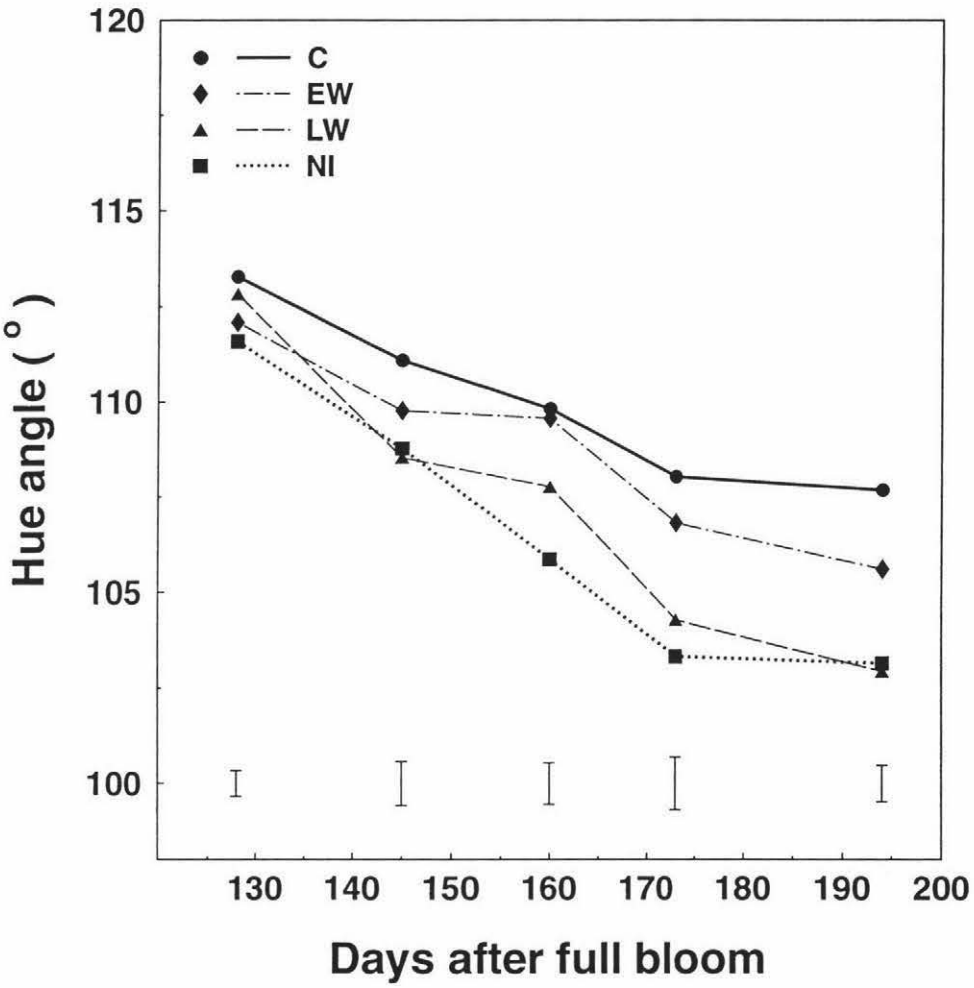

Figure 5.8: Background skin colour hue angle (H) in fruit of 'Braeburn' apples under different irrigation treatments. C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

5.2.7 Flesh Firmness

On the first day of flesh firmness determination, 95 DAFB, NI and EW fruit were firmer than C and LW (Fig. 5.10). Fruit from NI treatment were always firmer than C up to harvest. Diferences in firmness of 12.6 N were observed between these two treatments at harvest. However, flesh firmness for EW decreased rapidly upon rewatering to a similar level as C whereas LW fruit were as firm as NI at harvest. At harvest, firmness in LW fruit was increased by 7.5% relative to C.

5.3 DISCUSSION

5.3.1 Fruit Composition

In general, fruit from the reduced irrigation treatments had higher total soluble solids concentration and higher concentration of simple sugars relative to C. Increased TSS in water-stressed fruit has been reported in previous studies. In a study on 'Braeburn' apples, Mills et al. (1994) found an increase in TSS when irrigation was withheld late in the growing season. Ebel et al. (1993) found an increase in TSS in 'Delicious' apples when they applied deficit irrigation early in the growing season. Proebsting et al. (1984) reported increased TSS when the plants were deficit irrigated during the entire growing season. Various reasons have been suggested for this increase in TSS and simple sugars. Guelfat'Reich et al. (1974) suggested that fruit from water stressed trees may have been more mature at harvest than those from trees receiving ample water hence the differences in TSS. This is based on the fact that as apples mature, starches are converted into simple sugars as a result of the hydrolysis of the carbohydrate reserves within the tissue by β-amylase and α-amylase and/or starch phosphorylase (Biale and Young, 1981). In the current experiment, differences in TSS and sugars could have been a result of differences in fruit maturity. However, there are other more likely reasons. At harvest, there was increased dry matter concentration in NI and LW than

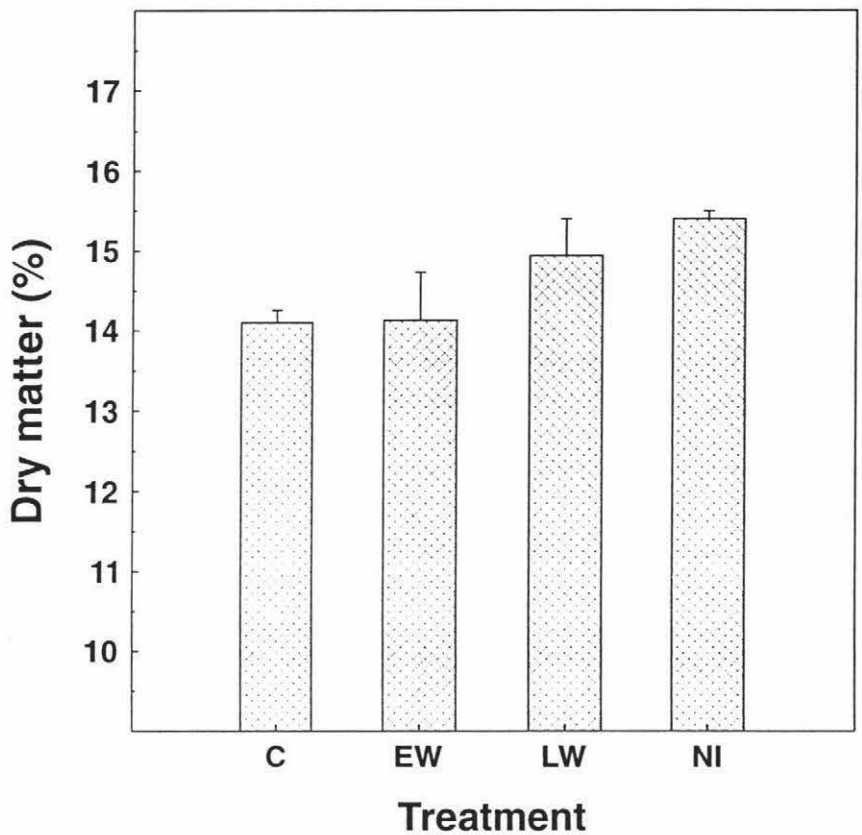

Figure 5.9: Fruit dry matter concentration of 'Braeburn' apples under different irrigation treatments 194 DAFB. C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, NI = nonirrigated. Vertical bars represent SEM based on three replicates per treatment.

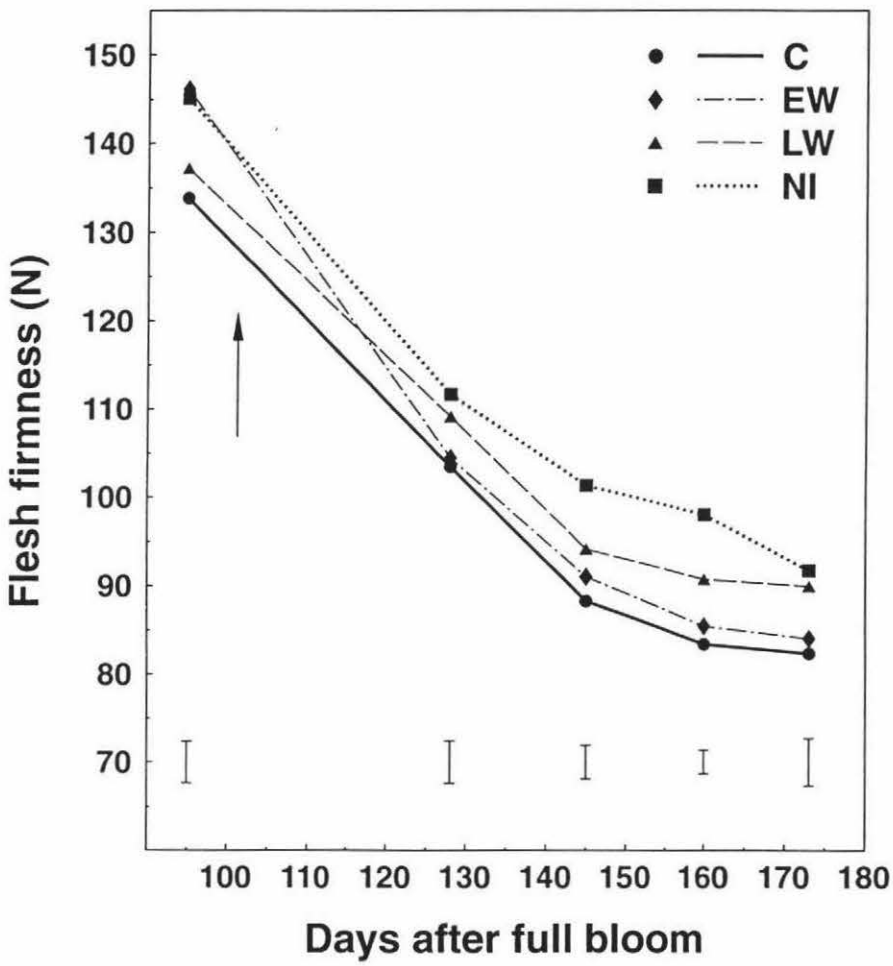

Figure 5.10: Influence of irrigation treatment on flesh firmness of 'Braeburn' apples. Arrow indicates the end of early withholding (EW) of irrigation and the start of late withholding (LW) of irrigation. C = control, NI = nonirrigated. Vertical bars represent pooled SEM based on three replicates per treatment.

in C and EW hence dilution effects could have led to decreased sugar and TSS concentration in C and EW at harvest.

Several authors have attributed the increase in TSS and simple sugars in water stressed fruit to active or passive accumulation of the compounds in osmotic adjustment (Chalmers et al., 1986; Davies and Lakso, 1978). In Asian pears, Behboudian et al. (1994) found a higher TSS in fruit from water stressed trees as early as 35 DAFB. This increase in TSS was involved in osmotic adjustment of the fruit. This study did not investigate fruit osmotic adjustment. Water-stress has a direct effect on the accumulation of sugars in that it increases the conversion of starch to sugars (Kramer, 1983, p. 264). In the current experiment withholding irrigation at any stage had a clear effect on the accumulation of TSS and simple sugars. For instance, whereas TSS was higher in EW than LW at 95 DAFB, rewatering of EW and withholding of irrigation for LW led to a 'changeover' such that at harvest, LW had a higher TSS than EW. A similar trend was observed for the simple soluble sugars.

The level of TA was not affected by the treatments. Titratable acidity declines as the fruit matures due to the utilization of organic acids as respiratory substrates and as carbon skeletons for the synthesis of new compounds during ripening (Biale and Young, 1981). Our results are similar to those obtained by other workers (Drake et al., 1981; Irving and Drost, 1987) who found that reduced irrigation did not affect TA.

The flavour of the fruit results from the combination of acids, sugars and volatiles within the fruit (Kays, 1991). The ratio of soluble solids:titratable acidity (TSS:TA) can therefore be used to predict the eating quality of the fruit. In the current experiment, the TSS:TA ratios at harvest (± SEM) were: 29.51 ± 3.05, 33.34 ± 2.02, 38.85 ± 1.13, and 42.61 ± 2.74 for C, EW, LW, and NI respectively. The increase in TSS:TA in fruit from NI and LW was mainly as a result on increased TSS since the treatments had

no effect on TA. A high TSS:TA ratio could influence the flavour appeal of NI and LW fruit in some markets (Drake et al., 1981). There is need for further studies to investigate the effects of irrigation timing and frequency on the flavour and aroma of the fruit.

The treatments did not affect the concentration of minerals in the fruit (Figs 5.5 and 5.6). These results are in agreement with those obtained by Irving and Drost (1987) who recorded no differences in the concentration of N, P, K^+, Mg^{2+} or Ca^{2+} concentrations with differing irrigation regimes. However, several authors have reported different results. For example, Guelfat'Reich et al. (1974) who found decreased K^+ in fruit from nonirrigated treatments and Mills et al. (1994) who found decreased Ca^{2+} in fruit from nonirrigated trees.

Calcium is one of the most important mineral elements in apples. The postharvest life of the fruit is critically determined by its Ca concentration. A low Ca level in the fruit has been associated with the occurrence of several physiological disorders such as bitter pit (Shear, 1975). Calcium supply to the fruit depends on the very complex regulation of its uptake, transport, distribution and utilization process (Hilmerick and McDuffie, 1983). Calcium uptake and transport are regulated by the transpiration flow and because of its low mobility through the phloem (Hill, 1980). Therefore, it has been suggested that treatments which affect the rate of transpiration such as water stress also reduce Ca uptake by the fruit.

In the current study, transpiration rate was not affected by the treatments until 130 DAFB (Chapter 4). The uptake of Ca by the fruit is thought to be most rapid in the early stages of fruit growth (Wilkinson, 1968), therefore it is likely that by the time transpiration rates were decreased, the fruit had accumulated most of the Ca. Furthermore, recent studies have suggested that in the later stages of fruit growth, there is 'xylem collapse' such that water and nutrients enter the fruit via the phloem as opposed to the

early stages of fruit growth when water mainly enters via the xylem (Ferguson and Watkins, 1989; Lang, 1990). Thus the reduction in the rate of transpiration late in the season has minimal effects on Ca movement into the fruit since it has a very low mobility in the phloem.

5.3.2 Skin Colour

The colour of apples is the result of a blend of various amounts of different pigments. The red colour on the blushed side of some apple strains is produced by anthocyanins and flavonols which are present in the vacuole (Lancaster, 1992). Lower values of H and L indicate a redder and darker skin and these correspond with a higher anthocyanin concentration (Singha et al., 1991). Thus the results obtained in the current study indicate that fruit from trees receiving less water had a higher anthocyanin content than those from the control. The trends observed are clear indication that withholding of irrigation at any stage has a significant and rapid effect on skin colour. The current study did not investigate the physiological basis of the differences observed in skin colour. Nitrogen is an important mineral element that has been implicated in colour development (Magness et al., 1940). A high N content stabilizes chlorophyll and hence reduces the development of red and yellow colour in apples. Reduced irrigation studies that have reported decreased N content in the fruit have associated the low N to increased red skin colour in the fruit (Mills et al., 1994). In this study, N content was not affected by the treatments (Fig. 5.5B) yet there were obvious colour differences between the treatments. It is speculated that increased sugar content in the fruit may have led to an increase in the substrate levels for anthocyanin biosynthesis and hence more intense red colour in fruit from NI, LW, and EW. Anthocyanins are composed of anthocyanidin and sugar (Lancaster, 1992). A laboratory study by Vestrheim (1970) showed that fructose, glucose and sucrose all stimulated anthocyanin production in apple

skin discs.

The background colour of 'Braeburn' apples is a useful index of maturity (Kupferman, 1994). As the fruit matures, the background colour changes from green to yellow. This change in colour occurs as a result of the breakdown of chlorophyll due to chlorophyllase activity (Looney and Peterson, 1967) leading to the unmasking of carotenoids and other pigments (Gorski and Creasy, 1977). The increased yellow background colour as a result of reduced irrigation in the current experiment could have been as a result of more advanced maturity. Several workers have reported that water stress leads to early fruit maturity e.g., Ebel et al. (1993) who found that 'Delicious' apples grown under RDI reached an 'earlier-than-normal' ethylene climacteric peak compared to well-watered controls.

5.3.3 Flesh Firmness

Softening is one of the most significant quality alterations associated with maturity (Ferguson, 1984). Apple fruit softening occurs as a result of the disolution of the middle lamella (Knee, 1982) which is the cementing material between cells (Wills et al., 1989).

In general, fruit from trees receiving reduced irrigation were firmer than the controls. Increased firmness of water stressed fruit has been reported in previous studies (Ebel et al., 1993; Guelfat'Reich et al., 1974; Mills et al., 1994; Powell, 1976). In these studies, the water-stressed fruit were smaller and hence had a higher cellular density than the fruit receiving ample water. When Ebel et al. (1993) adjusted their firmness data for fruit size, they found no differences in firmness between the treatments. In the current study, regression analysis showed a significant relationship between calculated fruit density (g cm^{-3}) and firmness (Firmness(N) = 12.29 + 142.62*Density, r^2=0.56, n=216, $P \leq 0.001$) (Fig. 5.11). Apart from fruit density, decreased cellular hydration as a result of reduced irrigation may also have contributed

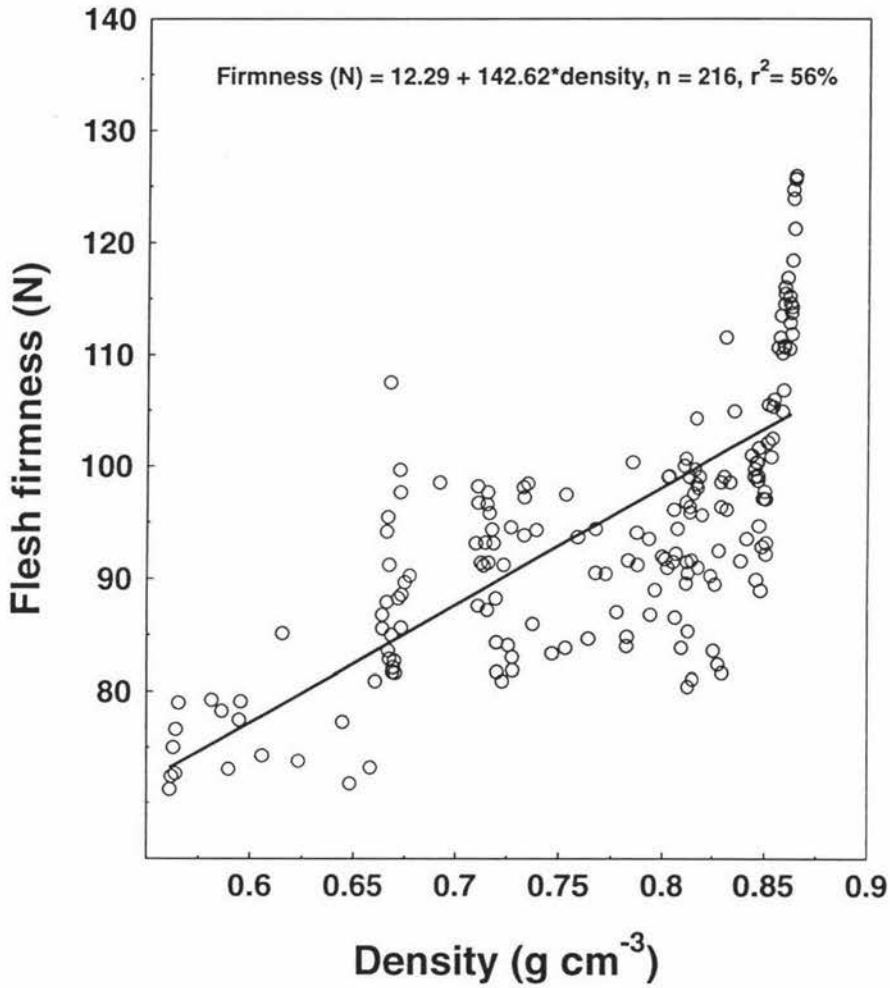

Figure 5.11: Relationship between fruit density and flesh firmness in 'Braeburn' apples.

to increased flesh firmness. This could explain the observed responses in EW fruit upon rewatering and the rapid increase in firmness of LW fruit on withholding irrigation. Increased cellular hydration in apples has been shown to increase their susceptibility to bruising (Banks et al., 1993). A similar mechanism may be in operation in this case whereby increased cellular hydration causes easier rupturing of the cells on application of pressure using a penetrometer.

5.4 SUMMARY

Irrigation was withheld at different times of the growing season in 'Braeburn' apples. Fruit composition and quality attributes were evaluated both during the growing season and at harvest. The main findings and conclusions are summarized below.

~ The time at which irrigation is withheld has important implications on the fruit quality attributes in 'Braeburn' apples.

~ Withholding irrigation in the late season and during the entire growing season led to increased TSS and the concentration of fruit soluble sugars (sucrose, fructose, and sorbitol) but did not affect titratable acidity. This could have important consequences on the flavour of the fruit. There is need for further investigations on the effect of withholding irrigation on the flavour of the fruit.

~ Withholding irrigation had rapid and significant effects on fruit skin colour both on the blushed and the nonblushed skin surfaces. At harvest fruit from LW and NI had intensified red skin colour (blushed side) and more background yellow colour. The increase in red colour could not have been due to differences in N content but may be due to increased sugars and hence increased substrate for anthocyanin biosynthesis. Increased yellow background colour may have been related to more advanced maturity of LW and NI fruit.

~ Withholding irrigation late in the season and during the entire growing season led to increased flesh firmness. Increased firmness was due to increased fruit density and also probably due to a reduction in cellular hydration. Further research in this area is necessary especially to determine the water potential of the fruit and its relationship with flesh firmness.

~ The concentration of K^+, Mg^{2+}, Ca^{2+}, N, and P was not affected by the treatments. Considering the importance of fruit mineral content especially Ca on the keeping quality of the fruit, it is likely that under reduced irrigation treatments the storage life of the fruit is not affected.

CHAPTER SIX

EFFECT OF IRRIGATION TREATMENT ON MATURITY, RIPENING CHANGES, AND WEIGHT LOSS

6.1 INTRODUCTION

The postharvest behaviour of apples is an important factor determining the storage life and marketability of the fruit. However, there is limited information on the postharvest behaviour of apples as affected by irrigation amount and frequency. This chapter evaluates some of the changes that occur during ripening and the weight loss characteristics of fruit from trees subjected to different irrigation treatments.

Ripening has been defined by Dilley (1969) as the process by which physiologically mature fruit are transformed from a relatively unfavourable to a favourable condition with respect to texture, colour, flavour, and aroma. In apples, ripening can occur while the fruit is still attached to the tree or after harvest but in both cases, the fruit has to be physiologically mature. As Dilley (1969) puts it, 'a fruit is physiologically mature when the stage is set for ripening to ensue'. Senescence, on the other hand, has been described as a series of endogenously controlled deteriorative changes that result in the natural death of cells, tissues, organs, and organisms (Brady, 1987). Ripening is therefore a transition phase between maturity and senescence and all the changes that occur during ripening lead to senescence. Ripening is accompanied by both physical and chemical changes which lead to changes in colour, texture, and flavour of the fruit (Kays, 1991, p.269). These alterations include changes in pigmentation due chlorophyll breakdown and/or synthesis of other pigments (Gorski and Creasy, 1977); softening due to the

alteration in the cell wall components and hydrolysis of storage materials (Huber, 1983); changes in carbohydrate composition e.g., starch conversion to sugar (Biale and Young, 1981); and changes in the rate of ethylene synthesis (Beaudry et al., 1993).

In postharvest technology, the aim is to extend the storage life of the commodity to its theoretical maximum by delaying ripening and senescence as much as possible. I hypothesised that withholding irrigation affects fruit maturity and weight loss depending on the stage at which irrigation is withheld. The objective of this part of the study was to determine the effects of withholding irrigation at different times of the growing season on the postharvest behaviour of 'Braeburn' apples in terms of maturity, ripening, and weight loss.

6.2 RESULTS

6.2.1 Internal Ethylene Concentration

The change in internal ethylene concentration after harvest for fruit from the different irrigation treatments is shown in Fig. 6.1. From the third date of measurement i.e. six days after the fruit were harvested up to 14 days after harvest, the treatment effect was significant ($P \leq 0.05$) with LW and NI fruit showing consistently higher levels of internal ethylene concentration as compared to EW and C fruit. There was no significant difference in internal ethylene concentration between the treatments on Day 16. Whereas a rapid rise in the internal ethylene concentration was observed for LW and NI fruit from the first and second day of measurement, respectively, the internal ethylene concentration for EW and C fruit was not measurable until Day 8 when it started rising rapidly. The standard error of the mean was also larger for LW and NI fruit, a result which indicated that a higher proportion of LW

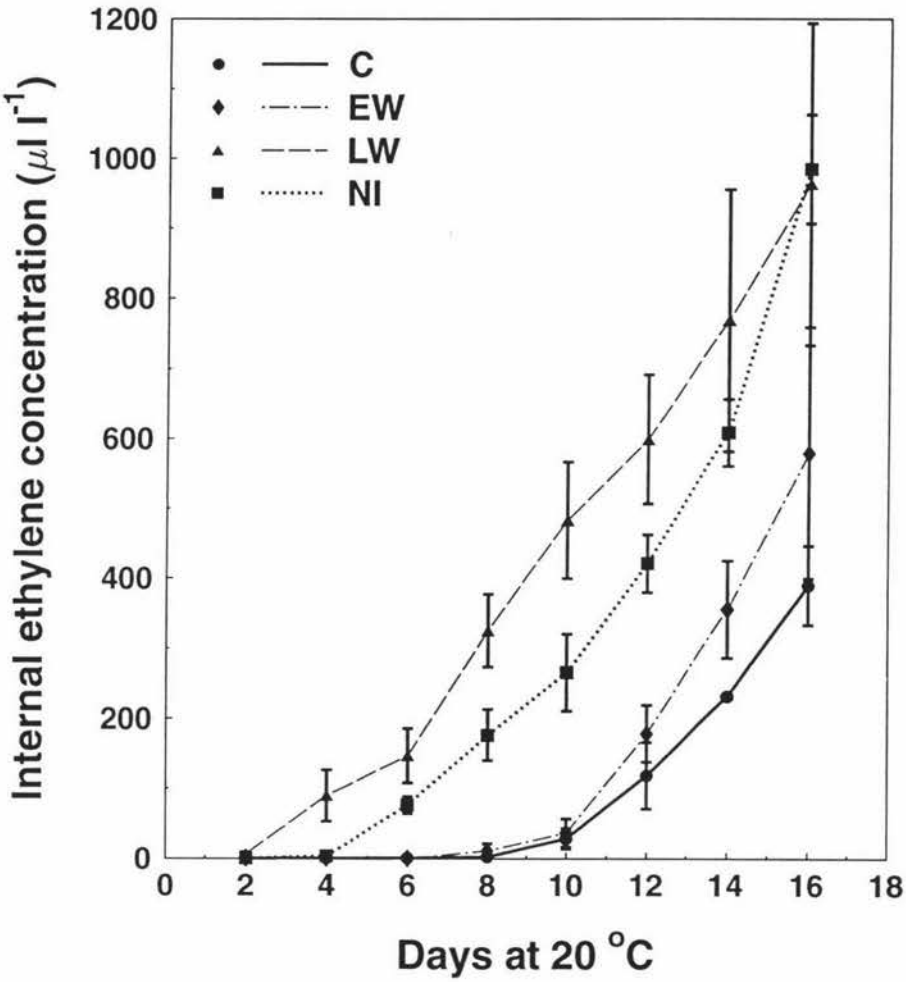

Figure 6.1: Changes in internal ethylene concentration after harvest for 'Braeburn' apples grown under different irrigation treatments. C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, and NI = nonirrigated. Each point is a mean of 15 fruit. Vertical bars represent the SEM.

and NI fruit had entered the logarithmic rise in ethylene evolution before the C and EW fruit.

6.2.2 Background Skin Colour

The changes in the background skin colour measured for fruit kept at approximately 1 °C and 20 °C are shown in Fig. 6.2. There was a general decrease in H with time in storage and also a significant interaction between time in storage and the treatment main effect. Consistently lower H values were observed for LW and NI fruit relative to those of the C and EW fruit throughout the period of evaluation.

6.2.3 Total Soluble Solids

Figure 6.3A shows the change in TSS for fruit from the different treatments during storage at approximately 1 °C. There was a general increase in TSS with time in storage. From the first date of sampling (Week 3), NI and LW had significantly higher TSS than EW and C. This trend was maintained consistently during the 12 weeks of evaluation. Differences of approximately 2°Brix were maintained throughout the storage period between NI and C fruit.

6.2.4 Firmness

At harvest, LW and NI fruit were firmer than EW and C fruit (Chapter 5). During storage, there was a general decrease in firmness with time for all the treatments (Fig. 6.3B). Throughout the 12-week evaluation period, NI and LW remained significantly firmer than EW and C fruit. There were no significant differences between either NI and LW or EW and C at any time during storage. Differences in firmness of approximately 10 N were observed between NI and C throughout the storage period.

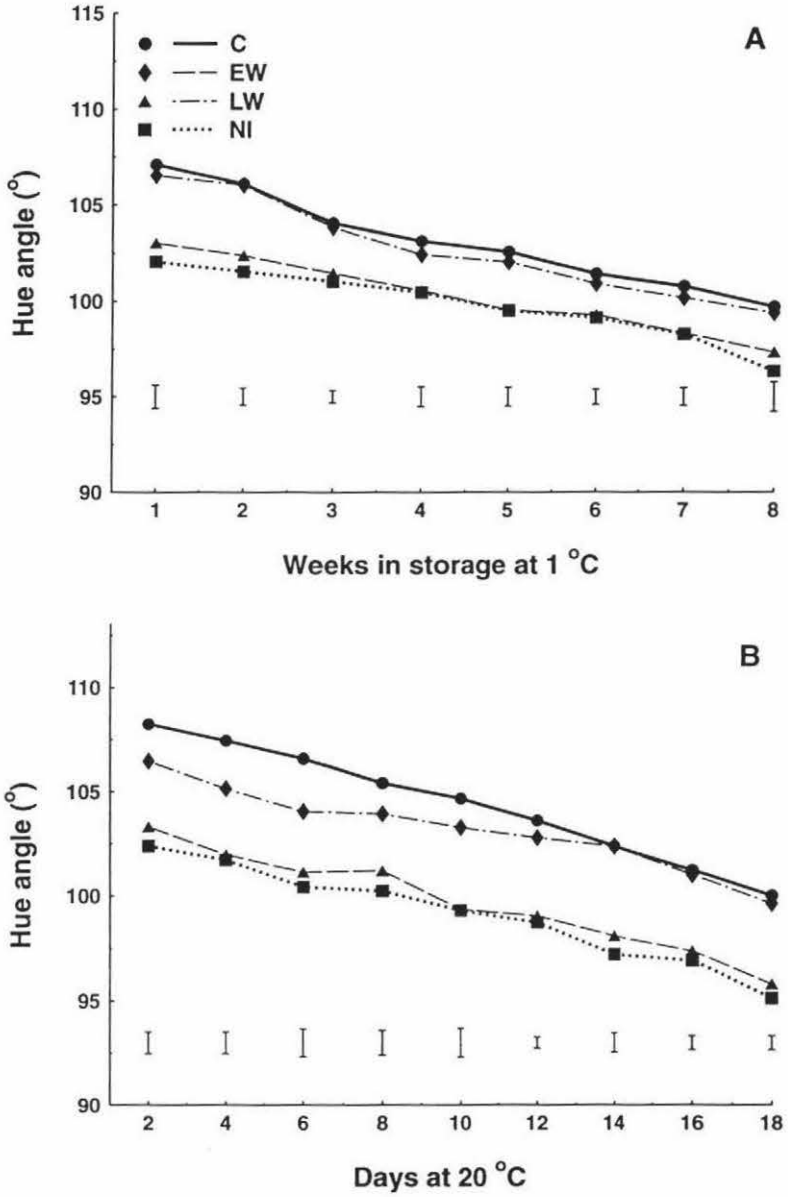

Figure 6.2: Changes in background colour after harvest for 'Braeburn' apples grown under four irrigation treatments: C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, and NI = nonirrigated. The fruit were kept at 1 °C (A) and at 20 °C (B). Each point is a mean of 30 fruit. Vertical bars represent SEM.

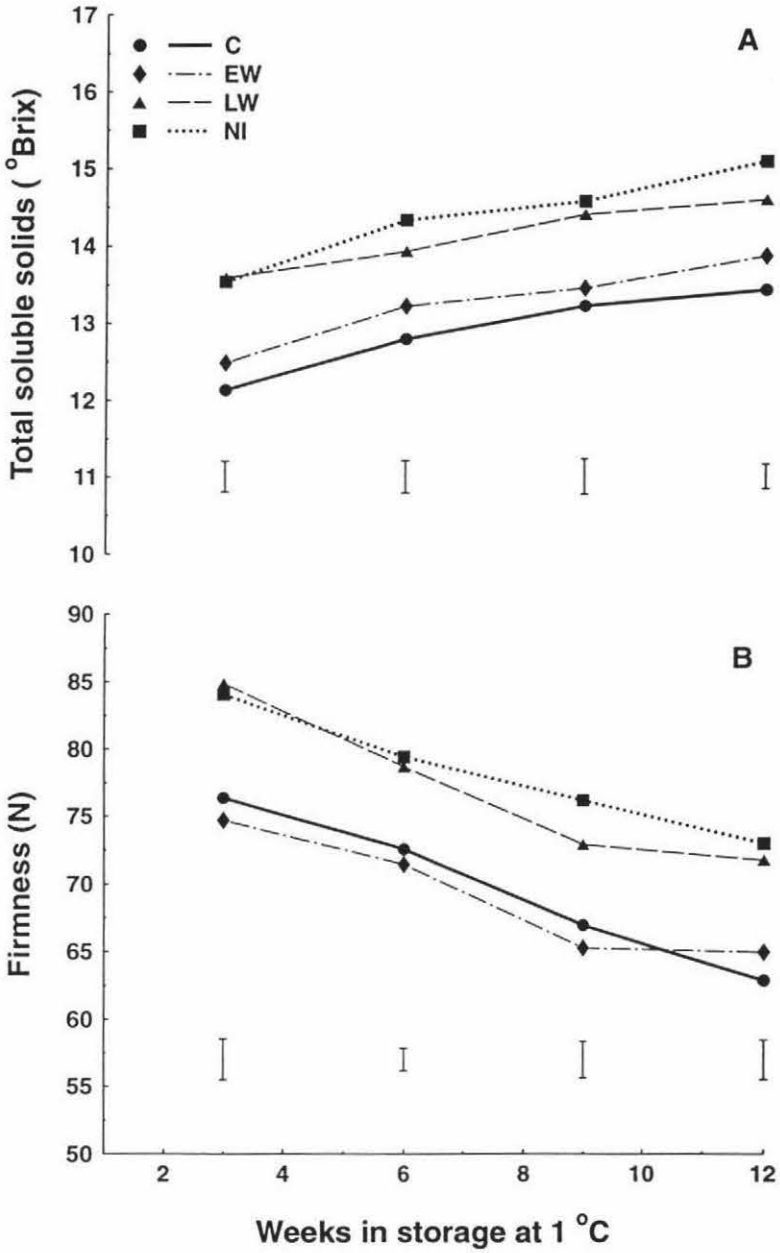

Figure 6.3: Changes in total soluble solids concentration (A) and firmness (B) during storage for 'Braeburn' apples grown under four irrigation treatments: C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, and NI = nonirrigated. Each point is a mean of 15 fruit. Vertical bars represent pooled SEM.

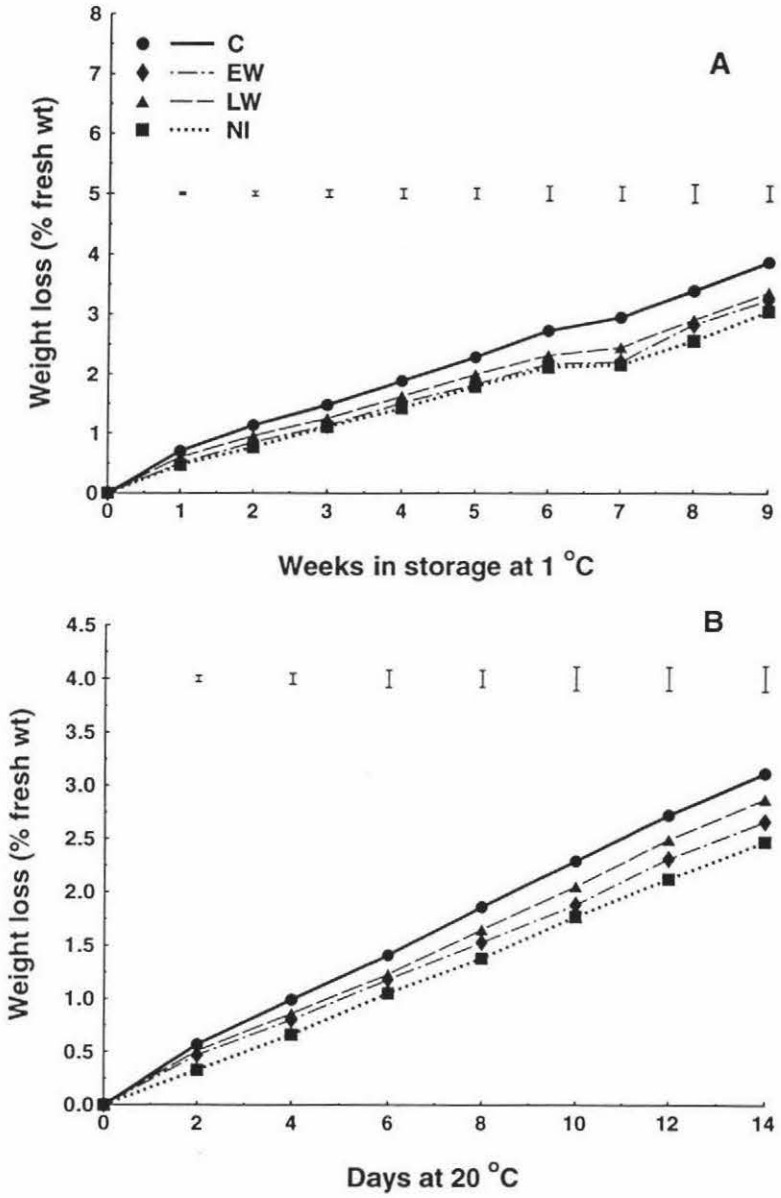

Figure 6.4: Postharvest weight loss (percentage of initial weight) of 'Braeburn' apples grown under four irrigation treatments: C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, and NI = nonirrigated. The fruit were kept at 1 °C (A) and at 20 °C (B). Each point is a mean of 30 fruit. Vertical bars represent pooled SEM.

6.2.5 Weight Loss

Fruit weight loss was dependent on time in storage and was generally higher in fruit from C than in fruit from reduced irrigation treatments (Fig. 6.4). Control fruit had lost nearly 40% more water than NI fruit after one week of storage at 1 °C and about 34% more water than NI after two days at 20 °C. After nine weeks of storage at 20 °C and 10 days at 20 °C, C fruit had lost 21% and 20% more water than NI fruit respectively. There were no significant differences in water loss between LW, EW, and NI fruit at any time of storage at 1 °C.

6.3 DISCUSSION

Apples show greatly differing rates of ethylene production at different stages of their postharvest life increasing to about 1000 fold as the fruit ripen (Biale and Young, 1981; Knee, 1993). Results from the internal ethylene concentration measurements indicate that fruit from LW and NI treatments entered the climacteric phase of ethylene production earlier than those of C and EW. Furthermore, LW and NI fruit had higher concentrations of internal ethylene relative to C and EW. In general, stressed plant tissues produce higher ethylene (Abeles et al., 1992, p. 266). According to Yang (1985), water stress causes plant tissue to increase ethylene production by an induction of ACC synthase which converts S-adenosyl methionine (SAM) to 1-aminocyclopropane-1-carboxylic acid (ACC) (the rate limiting step) in the biosynthesis of ethylene. Previous studies have shown that water stress at different stages of fruit growth not only increases the rate of ethylene production, but also results in the fruit reaching an earlier climacteric phase. Ebel et al. (1993) found that 'Delicious' apples grown under RDI entered an 'earlier-than-normal' climacteric rise while control fruit had lower internal ethylene concentrations and entered the climacteric phase later. In a study by Guelfat'Reich et al. (1974), fruit from the 'dry' treatments had consistently

higher ethylene production rates than those from the 'wet' treatments. Furthermore, the former entered climacteric rise earlier than the latter. In this study, EW fruit did not differ from C in terms of internal ethylene concentration and the time to reach climacteric. Since the autocatalytic production of ethylene in climacteric fruits characterizes the initiation of ripening (Brady, 1987) which occurs after full maturity is attained, these results indicate that water stress during the late and entire growing season may advance fruit maturity as determined by the time required to reach the ethylene climacteric phase.

Softening, colour change from green to yellow, and increased conversion of starch to sugars are some of the processes associated with ethylene and respiratory climacteric (Biale and Young, 1981). The climacteric rise is said to initiate the process of ripening which leads to changes in colour, texture, and fruit composition. In this study, LW and NI fruit maintained a higher background yellow skin colour than C and EW fruit whether the fruit were kept at 1 °C or at 20 °C. The background yellow colour in apples is attributed to the breakdown of chlorophyll which leads to the unmasking of carotenoids and other pigments responsible for the yellow colour (Gorski and Creasy, 1977). Colour is the primary criterion used by consumers in determining ripeness of many fruits (Kays, 1991, p. 275). The background colour is widely used as an index of maturity for 'Braeburn' apples (Kupferman, 1994). Therefore, in this study it may be an indication that LW and NI fruit were more mature and the ripening process occurred earlier than in C and EW fruit after harvest.

During maturation and ripening, there is increased conversion of starch to sugars (Kingston, 1992). This explains the increasing TSS observed for all the treatments after harvest. Total soluble solids concentration was consistently higher in LW and NI fruit during storage than in C and EW fruit.

Similar results were obtained by Proebsting et al. (1984) who attributed the higher TSS in deficit irrigated 'Delicious' and 'Golden Delicious' apples to advanced maturity of the fruit relative to the well-watered control. In the current study, there is evidence of more advanced maturity in LW and NI than in EW and C in terms of changes in the internal ethylene concentration and the background skin colour. Therefore, it is also likely that the higher TSS observed in LW and NI was partially due to advanced maturity in these fruit as well as increased conversion of starch to sugar in the water stressed fruit that occurred before harvest (Chapter 5).

Withholding irrigation during the late and entire growing season maintained a higher flesh firmness during storage than C and EW. Although fruit softening occurs with increased maturity and has been used as an index of maturity (Kingston, 1992), this study found a higher firmness in LW and NI fruit relative to EW and C fruit. The other results discussed previously have indicated that LW and NI fruit were more mature. Therefore the decrease in firmness of the fruit from the C and EW treatments in comparison with the LW and NI fruit was probably not an indicator of their ripeness, but was caused by differences in fruit size and/or cellular hydration as discussed in Chapter 5. Indeed Westwood (1993, p. 304) concludes that firmness is not a good maturity index for apples because it does not relate well to other changes that signify maturity.

Withholding irrigation at any stage of fruit growth decreased the rate of fruit weight loss. Linear regression analysis indicated a strong relationship (r^2 values of at least 0.83) between weight loss and time in storage (days at 20 °C or weeks at 1 °C) for all the treatments with all the regression models being highly significant ($P \leq 0.0001$) (Fig. 6.5). The regression models are given in Table 6.1. Pairwise comparative analysis of the regression lines indicated a significantly ($P \leq 0.05$) greater rate of weight loss for C fruit than for fruit from the reduced irrigation treatments. The differences in weight

loss may in part be attributed to differences in P'_{H2O} (Fig. 6.6). Skin permeance to water vapour was significantly lower in the reduced irrigation treatments relative to the control. There was a reduction in P'_{H2O} by approximately 19% in NI relative to C. The structural properties of the skin that could have caused differences in P'_{H2O} were not investigated. However, it is speculated that differences in P'_{H2O} may be due to differences in the structure and/or composition of the skin or the epicuticular waxes covering the skin. Epicuticular waxes and the cuticle act as a partial barrier to water vapour movement from inside the cuticle to the environment (Gaffney, 1978; Horrocks, 1964). Cuticle modification by deficit irrigation has been observed in peaches by Crisosto et al., 1994 who attributed the less rate of water loss in peaches grown under deficit irrigation to a thicker cuticle and a higher density of trichomes on the skin surface. The reduction in the rate of water loss in fruit from reduced irrigation treatments is an important beneficial effect of this irrigation strategy. There is need for studies to investigate the morphological and physiological basis of the reduction in the rate of weight loss in apple fruit grown under reduced irrigation.

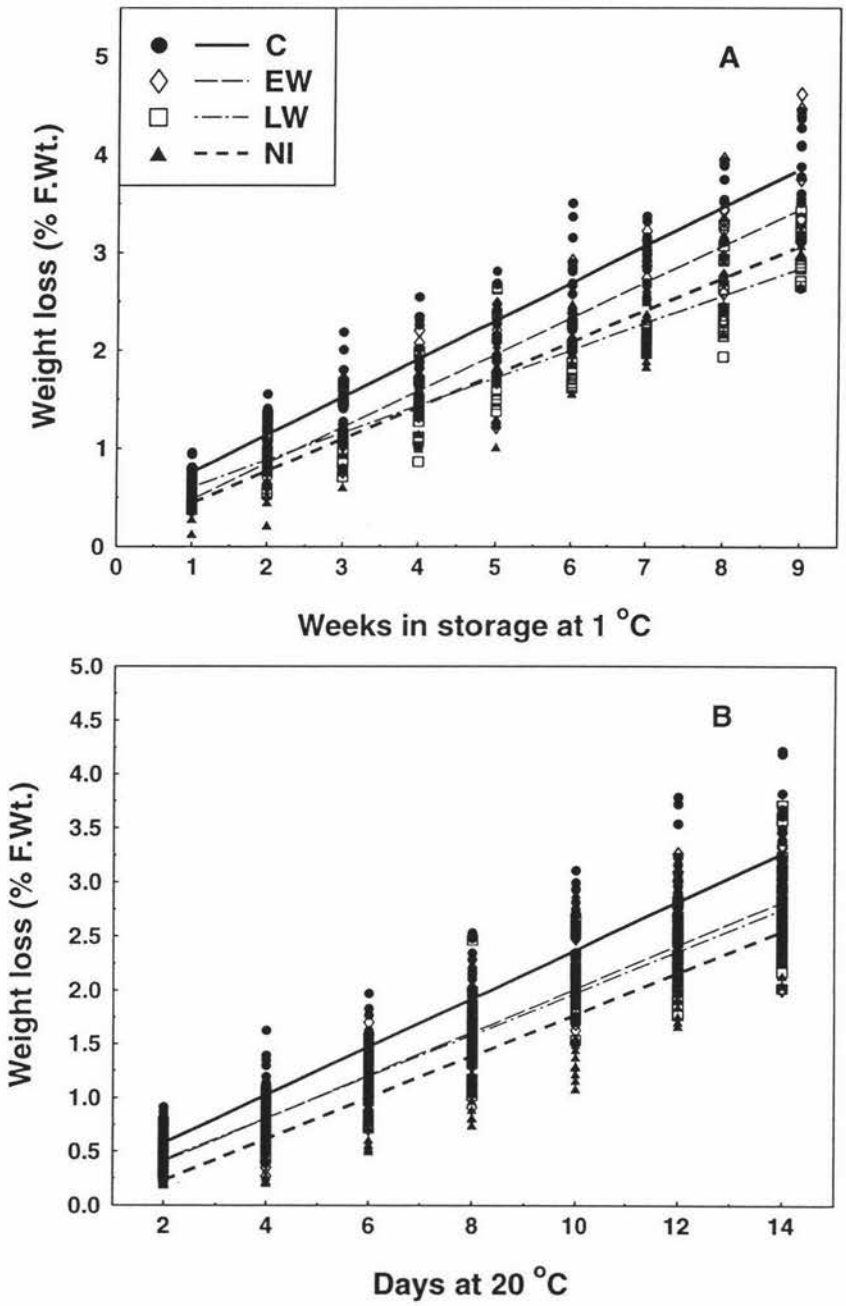

Figure 6.5: The relationship between weight loss (% of initial fresh weight) and weeks at 1 °C (A) and days at 20 °C (B) for 'Braeburn' apples grown under different irrigation treatments. C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, and NI = nonirrigated. The regression equations are given in Table 6.1.

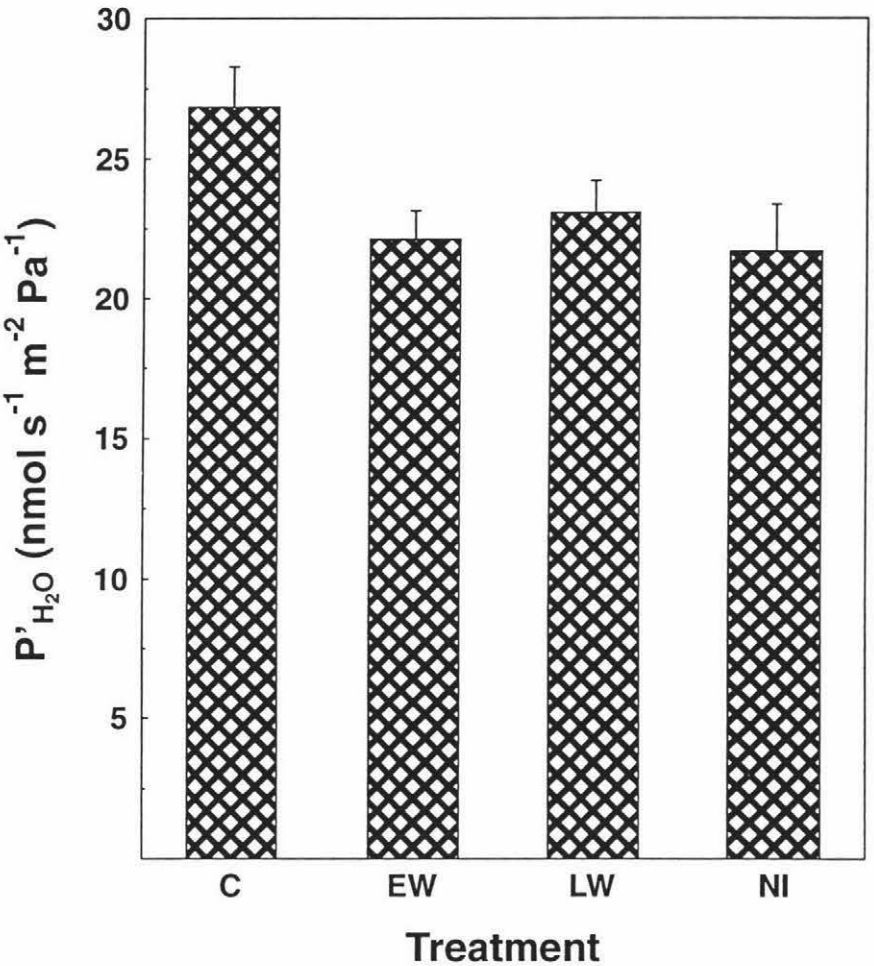

Figure 6.6: Effect of irrigation treatment on the skin permeance to water vapour (P'_{H_2O}) of 'Braeburn' apples. C = control, EW = early withholding of irrigation, LW = late withholding of irrigation, NI = nonirrigated. Vertical bars represent SEM.

Treatment	Equation	r^2
	1 °C	
Control	y = 0.369 + 0.387*x	0.896
Late Withholding	y = 0.326 + 0.279*x	0.833
Early withholding	y = 0.111 + 0.310*x	0.880
Nonirrigated	y = 0.116 + 0.328*x	0.904
	20 °C	
Control	y = 0.130 + 0.22*x	0.881
Late withholding	y = 0.035 + 0.19*x	0.879
Early withholding	y = 0.002 + 0.20*x	0.883
Nonirrigated	y = -0.16 + 0.19*x	0.863

Table 6.1: Regression models of the relationship between weight loss and time in storage at 20 °C and at 1 °C. y = weight loss (expressed as percentage of fresh weight), x = days (at 20 °C) or weeks (at 1 °C) in storage. In all cases $P \leq 0.0001$ and n = 210 for the 20 °C experiment and n = 270 for the 1 °C experiment.

6.4 SUMMARY

The following is a summary of the main findings and conclusions from this part of the study:

~Withholding irrigation during the late season and entire growing season causes advanced maturity and earlier ripening of 'Braeburn' apples as indicated by changes in internal ethylene concentration, total soluble solids concentration, and the background skin colour. This may have important

implications on the ideal harvest time since harvest before climacteric is considered best for apples destined for long-term storage (Abeles et al., 1992, p. 266).

~Withholding irrigation during the late and entire growing season causes increased flesh firmness which is maintained even during storage. This is an important beneficial effect of reduced irrigation.

~'Braeburn' apples grown under reduced irrigation have a lower rate of weight loss probably as a result of skin and/or cuticle modifications.

CHAPTER SEVEN

GENERAL DISCUSSION AND CONCLUSION

'Braeburn' apple trees were subjected to withholding of irrigation at different times of the growing season to evaluate the effects of four irrigation treatments on growth, yield, composition, and quality of the fruit. The working hypothesis was that reduced irrigation modifies fruit quality attributes depending on the stage at which irrigation is withheld. This chapter summarizes and further discusses some of the main points of this thesis.

7.1 WATER RELATIONS, PHOTOSYNTHESIS, GROWTH AND YIELD

In previous studies at Massey University, it has been difficult to achieve a lowered water status in tree crops such as apples (Durand, 1990; Mills et al., 1994) and apricots (Arzani, 1994). This is due to the heavy winter rainfall that leaves a high soil moisture content whose depletion is slow in the spring due to a high humidity and rainfall. In the study by Durand (1990), RDI was supplemented with lucerne cover to increase the rate of moisture depletion while in the study by Arzani (1994), reduced irrigation was supplemented with root pruning. In the current study, the approach was to install under-tree polythene covers long before the start of the growing season for the EW and NI treatments so as to prevent much of the early spring rainfall from reaching the soil and to ensure a water deficit at full bloom. This approach worked well as shown by the soil moisture (θ) and leaf water potential (Ψ) results such that a reduced plant water status in NI and EW was observed as early as 42 DAFB. However, the level of water stress at this time was mild. As the season progressed, there was a gradual soil moisture depletion in EW and NI such that the midday Ψ levels as low as -2.0 MPa

were recorded on some days before 104 DAFB. Under-tree covers were installed for LW in late January 1995 and irrigation was withheld in early February 1995 (104 DAFB). Moisture depletion and decrease in Ψ for LW was more rapid than that observed for NI and EW earlier in the season. This is attributable to the low rainfall and high temperatures experienced in summer. Hence by the end of the growing season, differences of ≥ 0.8 MPa were observed between the treatments not receiving irrigation (NI and LW) and those receiving irrigation (C and EW). The pattern obtained for Ψ indicated that our objective was achieved with decreased Ψ for EW and NI during the early season albeit to only a small extent, and decreased Ψ for LW and NI during the late season. Previous studies on reduced irrigation have obtained similar differences in Ψ between water stressed and well-watered trees. For example, Mills et al. (1994) recorded differences of 0.7 MPa between irrigated and nonirrigated 'Braeburn' apples during the late season. This difference was adequate to cause differences in fruit quality and trunk growth between the treatments.

Reduced water status in plants affects various physiological processes and organs (Kozlowski et al., 1991). However, different tissues, organs, and processes have different sensitivities to water stress (Chalmers, 1989). This phenomenon was well manifested in the current study. For example, fruit growth was not affected by reduced irrigation during the period of measurement from 40 DAFB up to harvest, however, there was a large reduction (as much as 50%) in the shoot growth of 'Braeburn' apples under early and entire season withholding of irrigation. The reduction in shoot growth was caused by an early season water stress when shoot growth was greatest. It is important to note that the level of water stress during this time was quite mild and yet there was a substantial reduction in vegetative growth. A reduction in vegetative growth due to water stress without reduction in yield or fruit size was also observed in 'Delicious' apples by Ebel et al.

(1995). This phenomenon has also been observed in other fruit crops such as peaches (Chalmers et al., 1981) and pears (Mitchell et al., 1986) and is one of the physiological basis for the beneficial effects of RDI (Chalmers, 1989). According to Chalmers (1989), shoot growth is more sensitive to reduced Ψ than fruit growth and therefore irrigation can be reduced to a level of Ψ that affects shoot growth without adversely affecting fruit growth. The reduction in shoot growth may have an added advantage in cases where assimilates no longer being used for shoot growth are diverted to fruit growth leading to increased yields and fruit size as observed by Chalmers et al. (1986). To take advantage of this phenomenon, however, requires the knowledge of how much water stress, i.e the level of Ψ, is necessary to reduce vegetative growth without affecting fruit growth. Improper management may cause a water status that is too low and that reduces fruit growth and yield.

Studies in kiwifruit have indicated that a reduction in the rate of photosynthesis and photoassimilate partitioning are the main reasons of reduced growth under reduced irrigation (Chartzoulakis et al., 1993a and b). This is unlikely in the current study because a reduction in the rate of photosynthesis did not occur until 159 DAFB by which time shoot growth had ceased and differences in shoot extension between the treatments were already evident. A more likely reason is that elucidated by Chalmers (1989) that cell expansion, being very sensitive to reduced Ψ, is adversely affected. Fruit cells expand by a similar mechanism as shoot cells, however the former are stronger assimilate sinks even under reduced Ψ.

A reduction in stomatal conductance was observed in NI and LW from 138 DAFB. Stomatal conductance was not reduced at any time for EW plants. The results from this experiment indicate that g_s does not respond rapidly to a reduction in Ψ. This is shown because although low levels of Ψ were observed in NI from as early as 42 DAFB, g_s was not affected in this treatment until late in the season (138 DAFB). Similar results were obtained

by Mills et al. (1994) who found a reduction in g_s from 140 DAFB in nonirrigated 'Braeburn' apples.

A higher rate of transpiration in the irrigated plants had a 'cooling' effect on the canopy as shown by the infrared thermometry data. There was a significant quadratic relationship between Ψ and the IR thermometry data. This indicates that there is good potential for the use of infrared thermometry to determine the water status of the plant in deciduous fruit crops. Infrared thermometry has hitherto been used mainly in field crops such as wheat (Jackson, 1982) but rarely in tree crops. It offers several advantages such as ease of use and its non-destructive nature. There is need for further research into how IR may be used in irrigation scheduling of deciduous fruit crops.

Although it is widely accepted that water stress causes a reduction in the rate of photosynthesis, the actual mechanism involved is not clear. A reduction in *Pn* has been attributed to stomatal closure (Farquhar and Sharkey, 1982), reduced enzymic activity e.g., RUBISCO (Vu and Yelenosky, 1988), or accumulation of photoassimilate in the leaves (Janoudi et al., 1993). This study has shown that although g_s was closely related to *Pn*, there were other additional factors which led to the reduction in *Pn*. This was shown by the regression analysis of *Pn* and g_s and also by the fact that although g_s was reduced in the stressed plants, C_i did not decrease, indicating an impairment of the photosynthetic machinery. Similar conclusions were reached by Behboudian et al. (1994) who found increased C_i/C_a ratio in water stressed Asian pears and attributed this effect to an impairment in carbon fixation at the chloroplast level. Hence water stress affects *Pn* by other mechanisms in addition to reduced CO_2 diffusion into the leaf.

Water stress adversely affects flower bud initiation and differentiation (Faust, 1989, p. 159). This was manifested in the present study by a reduction in return bloom in EW and NI trees. Water stress in these treatments occurred at the time at which flower initiation and differentiation

occurs i.e late December to January. This affected flower initiation and hence return bloom in the following season. A reduction in return bloom may, to some extent, be horticulturally desirable as it reduces thinning costs.

7.2 FRUIT QUALITY, COMPOSITION, AND POSTHARVEST PERFORMANCE

The second part of the experiment evaluated the quality and composition of 'Braeburn' apples under irrigation withholding at different times of the growing season. Various quality attributes were evaluated before harvest, at harvest and during a 12-week storage period.

In general, fruit from the reduced irrigation treatments developed increased TSS and total sugars during the growing season. Changes in TSS and total sugars closely followed the irrigation treatments. For instance, whereas TSS and total sugars tended to be higher in EW and NI relative to C before 104 DAFB, LW and NI had higher TSS and total sugars than C during the late season. The effect of withholding irrigation on TSS and total sugars was rapid. The increase in sugars and TSS in fruit upon withholding irrigation has been observed in previous studies in apples (e.g., Mills et al., 1994) and in other fruit crops such as Asian pears (Behboudian et al., 1994). Dilution of the sugars may play a role in the changing concentration of TSS and soluble sugars. During a period of mild water stress, the fruit received less water as indicated by increased dry matter content of the fruit relative to unstressed fruit but received similar photoassimilate levels hence the concentration of sugars was increased. On rewatering, these sugars are diluted and hence a low concentration of sugars was measured. This may contribute to the passive osmotic adjustment of the fruit by raising the osmotic potential to maintain turgor. In some instances, however, there may be an active uptake of sugars or increased conversion of starch to sugars as a result of water stress (Kramer, 1983, p. 364). This study did not investigate

the mechanism involved in increasing sugar and TSS by reduced irrigation treatments. At harvest, NI and LW fruit had higher sugars and TSS than C and EW fruit. A higher TSS was maintained in NI and LW relative to C and EW during storage for the entire 12-week period of evaluation.

Withholding irrigation caused an increase in flesh firmness. The trend in flesh firmness was similar to that observed for TSS in that prior to 104 DAFB, NI and EW fruit tended to be firmer than C and LW fruit. During the late season however, i.e. after 104 DAFB, NI and LW fruit were firmer than C. This study showed that increased firmness is strongly related to the density of the fruit. This was also suggested by Ebel et al. (1993) who attributed increased firmness in RDI fruit to their smaller size and hence increased cellular density. Other factors may also have been involved because although NI fruit were generally smaller than C fruit, those of LW were not smaller than C and yet they were firmer. This suggests that fruit size was not a contributing factor to increased firmness in this case. It is therefore speculated that decreased cellular hydration as a result of reduced irrigation may have caused the increased firmness. This would explain the rapid responses observed in EW fruit upon rewatering and LW fruit on withholding irrigation. Increased firmness in LW and NI was maintained throughout the 12-week storage period. In this study, firmness was not a good measure of maturity as it did not relate with other maturity indices such as internal ethylene concentration and background colour.

Reduced irrigation resulted in redder and darker skin colour on the blush side of the fruit. The changes in red skin colour showed that withholding of irrigation at any stage has a significant and rapid effect on skin colour. Mills et al. (1994) also reported increased red skin colour in 'Braeburn' apples that were not irrigated during the late season. In the current study, LW and NI had redder and darker skin colour at harvest than C and EW. These results are consistent with the speculation by Mills et al.

(1994) that increased sugar concentration in the fruit may have led to increased substrate for the synthesis of anthocyanin and hence a more intense red colour in NI and LW fruit. The background surface also showed increased yellow colour in fruit under reduced irrigation. Previous workers have suggested that N, which enhances chlorophyll retention, is reduced under water stress conditions leading to accelerated chlorophyll breakdown and hence increased red and yellow colour development (Magness et al., 1940; Mills et al., 1994). In this study, however, fruit N concentration was not affected by the treatments yet colour differences were observed further enhancing the speculation that increased substrate for anthocyanin biosynthesis may have caused the increase in red colour. The background colour of 'Braeburn' apples is widely used as an index of maturity (Kupferman, 1994). At harvest NI and LW fruit had more yellow background colour than C and EW. Withholding irrigation in the late and entire season led to an earlier ethylene climacteric. These treatments (LW and NI) also had a more yellow background skin colour throughout the storage period compared to C and EW. These results, coupled with increased TSS in LW and NI fruit suggest that these fruit were more advanced in maturity than C and EW fruit. Other workers have also reported that water stress leads to early fruit maturity (Ebel et al., 1993; Guelfat'Reich et al., 1974).

Many physiological disorders which develop during the storage of apples have been attributed to a low Ca^{2+} concentration in the fruit (Shear, 1975). In 'Braeburn' apples one of the most important of these is bitter pit (Kupferman, 1994). In this study, withholding of irrigation at any stage did not affect fruit Ca^{2+} concentration. This implies that there may be no risk of increased Ca^{2+} related disorders in fruit due to reduced irrigation. Indeed, during the 12 weeks of storage, no calcium related physiological disorders were observed in the fruit from any treatment. However, 12 weeks of storage may not have been a sufficient time of storage for the evaluation of

physiological disorders.

Fruit from the reduced irrigation treatments were less susceptible to water loss than the well-watered control. The skin permeance to water vapour was higher in C than in the reduced irrigation treatments. This is an important aspect of fruit storability since a high rate of water loss leads to loss of marketable weight and quality (Hatfield and Knee, 1988; Woods, 1990). This study did not investigate the physiological reason of the differences in skin permeance to water vapour but it is speculated that water stress may have affected the nature and/or amount of epicuticular waxes found on the skin surface of the fruit and which play an important role in the reduction of water passage from the fruit into the atmosphere.

7.3 CONCLUSION

The experiment presented in this thesis reduced plant water status in a humid and high rainfall environment. This was done by withholding irrigation at appropriate times supplemented by the use of under-tree polythene covers that prevent rainwater from reaching the soil. The results present some dilemma as far as recommendations to apple growers are concerned. Shoot extension and trunk growth results suggest that for vigour control, the response is best if irrigation is withheld during the early season. Withholding of irrigation during the early season however has the disadvantage of reducing fruit size although total yield and yield efficiency are not affected. An added advantage of early season withholding of irrigation is the reduction of return bloom which may reduce costs associated with chemical and/or hand thinning. However, severe water stress during this period may also be disadvantageous by reducing return bloom to undesirable levels.

On the other hand, for improved fruit quality in terms of increased TSS, sugars, red skin colour, firmness, and reduced weight loss susceptibility,

the results suggest that withholding irrigation late in the season is more appropriate. Furthermore, these quality attributes are improved without loss of yield or reduction in fruit size. The use of LW would also depend on the postharvest storage requirements. A late withholding of irrigation tends to cause advanced maturation and hence earlier ripening. This may mean that the storage life of the fruit is essentially reduced since the aim of postharvest technology is to delay ripening and senescence as much as possible. A late withholding of irrigation would also affect the optimum time of harvest. Apples for long term storage are best harvested before climacteric (Abeles et al., 1992, p. 266; Knee et al., 1989). Thus LW may advance the harvest dates of the fruit. This may be desirable if fruit are available early in the season and command premium prices. This finding also provides evidence that the potential exists for growers to manipulate the probable harvest time for apples by a manipulation of the water status of the plant through a properly managed irrigation strategy. This would be beneficial in terms of controlling the fruit volumes in the market.

This thesis opens various channels through which future research may be directed. These include:

~ The study of the physiological basis of the skin colour, firmness, and skin permeance to water vapour differences observed in this experiment;

~ the use of infrared thermometry in irrigation scheduling for deciduous orchards;

~ there is need for studies aimed at a more precise recommendation of the best times to withhold irrigation and the threshold levels of plant water status that is beneficial in terms of both improved fruit quality and the control of vigour without adverse effects on yield and fruit size;

~ withholding of irrigation for long periods of time may be detrimental in some environments, there is need for comparative studies in areas with low humidity and rainfall conditions;

~ further studies may also examine the responses of the fruit in terms of flavour and aroma of the fruit by use of chromatography techniques for the analysis of flavour volatiles and sensory evaluation to determine the acceptability of the fruit produced under reduced irrigation in the market.

Overall, this study has demonstrated that there exists great potential for the use of reduced irrigation strategies for apple production.

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APPENDIX ONE

Calculation of Skin Permeance to Water Vapour

Skin permeance to water vapour ($\mathbf{P'_{H2O}}$) may be calculated using the following formula:

$$P'_{H2O} = \frac{r'_{H2O}}{A \cdot VPD} \quad ,$$

where:

$\mathbf{r'_{H2O}}$ = rate of water loss in mol s^{-1} and is calculated as:

$$r'_{H2O} = \frac{(W_1 - W_2)}{Mw \cdot t} \quad ,$$

where:

$\mathbf{W_1}$-$\mathbf{W_2}$ = change in weight of the fruit (g),

Mw = molecular weight of water (g mol^{-1})

t = time interval (s)

A is the surface area of the fruit (m^2) which may be calculated from fruit weight (Clayton et al., 1995) as:

$$A = d\, w^e \quad ,$$

where:

w = Fruit weight (kg)

d,**e** = constants; for 'Braeburn' apples these are 0.0575 and 0.687 respectively.

VPD is the water vapour pressure deficit (Pa) calculated as:

$$VPD = e'_{skin} - e_a \quad ,$$

where:

$$e_a = e'_w - \gamma(T_a - T_w) \quad ,$$

and,

$$e'_{skin} = 611.3\ e^{((19.82-5415)/(T_s+273.15))} \quad ,$$

where:

T_a = dry bulb temperature (°C)

T_w = wet bulb temperature (°C)

e'_w = vapour pressure of air (Pa)

γ = psychrometric constant (60 Pa $°C^{-1}$)

T_s = skin temperature (assumed to be equal to room temperature °C)

e'_{skin} = water vapour pressure at skin (Pa)