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**FRUIT COMPOSITION, GROWTH, AND WATER RELATIONS OF
'BRAEBURN' APPLES UNDER REDUCED
PLANT WATER STATUS**

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the requirements of the degree of
Doctor of Philosophy
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ABSTRACT

Water plays a major role in the physiological processes of plants. Effective irrigation relies on a comprehensive understanding of the impact of water on plant processes. As water becomes an increasingly scarce resource, the impact of reduced plant water status on crop performance (quality and yield) requires investigation. The effects of reduced plant water status on fruit composition, growth, and water relations were therefore studied using both field-grown and container-grown 'Braeburn' apple trees. Vegetative growth and carbon assimilation were also measured. Plant water deficit was imposed at various times during the growing season. The treatments were: control, which was fully irrigated during the experimental period, entire-season deficit, deficit irrigation from 55 days after full bloom (DAFB) until final fruit harvest (183 DAFB), early-season deficit (from 55 - 100 DAFB) followed by rewatering, and late-season deficit (from approximately 105 DAFB until final harvest).

Reduced leaf water potential developed in all deficit irrigated trees during the stress period. Only the entire-season deficit irrigation treatment resulted in a significant reduction in vegetative growth as measured by total leaf area, shoot growth, and trunk growth. Return bloom was reduced under an early-, but not late-season deficit. Photosynthesis was generally reduced in water deficit treatments, as was stomatal conductance.

Only an entire-season deficit irrigation reduced individual fruit weight. Fruit soluble solids and sugar concentration were generally increased under deficit irrigation treatments. However, upon rewatering of the early-season deficit trees, the values again became the same as controls. Fruit mineral concentration did not show consistent differences between treatments and the incidence of storage disorders was low in all

treatments and unaffected by deficit irrigation.

Early-season water deficit lowered both fruit water potential and osmotic potential. Despite turgor maintenance within the fruit during the stress period, growth was reduced at this time. A late-season water deficit did not modify fruit water relations.

It appears that 'Braeburn' fruit are resilient to periodic water deficit during the season, and that water conservation is possible with limited impact on total crop yield. Additionally, a late-season deficit may even enhance some fruit quality attributes, such as increased total soluble solids. An early-season deficit reduced return bloom and must therefore be used with caution. An entire-season water deficit is not recommended due to the reduction in fruit size.

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LIST OF ABBREVIATIONS AND SYMBOLS

Treatment

Control, Expt. 1.	C1
Control, Expt. 2.	C2
Control, Expt. 3.	C3
Control, Expt. 4.	C4
Deficit, Expt. 1.	D1
Deficit, Expt. 2.	D2
Deficit, Expt. 3.	D3
Deficit, Expt. 4.	D4
Deficit Irrigation	DI
Early Deficit, Expt. 4.	ED4
Late Deficit, Expt. 2.	LD2
Late Deficit, Expt. 4.	LD4

Water Relations

Fruit Water Potential (MPa)	Ψ_{fw}
Fruit Osmotic Potential (MPa)	Ψ_{fs}
Fruit Turgor Potential (MPa)	Ψ_{fp}
Leaf Water Potential (MPa)	Ψ_l
Days After Full Bloom	DAFB
Days In Storage	DIS
Experiment	Expt.
Figure	Fig.
Hour	h

Internal CO ₂ Concentration ($\mu\text{mol} \cdot \text{mol}^{-1}$)	C_i
Irradiance ($\text{W} \cdot \text{m}^{-2}$)	I_r
Metre	m
Photosynthetic Rate ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	P_n
Probability	P
Ratio $^{13}\text{C}:^{12}\text{C}$	$\delta^{13}\text{C}$
Regulated Deficit Irrigation	RDI
Seconds	s
Soil volumetric water content ($\text{m}^3 \cdot \text{m}^{-3}$)	θ
Stage 1 harvest	S1
Stage 2 harvest	S2
Standard error	SE
Stomatal Conductance ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	g_s
Time Domain Reflectometry	TDR
Titrateable Acidity (% malic acid)	TA
Total Soluble Solids (% Brix)	TSS
Transpiration ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	T
Treatment	TRT
Vapour Pressure Deficit (KPa)	VPD
Weight (g)	wt

FIGURE CAPTIONS

Fig. 1 Water content of root medium (θ) for Expts. 1 (A), 2 (B), and 4 (C). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21, 18 and 12 experimental units (trees) for A, B, and C respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n \geq 7); D2=deficit, Expt. 2 (n \geq 4); LD2=late deficit, Expt. 2 (n \geq 7); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fig. 2 Midday leaf water potential (Ψ_l) for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21, 18 and 12 experimental units (trees) for A, B, and C respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n \geq 7); D2=deficit, Expt. 2 (n \geq 4); LD2=late deficit, Expt. 2 (n \geq 7); C3=control, Expt. 3 (n=6); D3=deficit, Expt. 3 (n=3); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

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Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 18 and 12 experimental units (trees) for A, and B respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C2=control, Expt. 2 (n≥7); D2=deficit, Expt. 2 (n≥4); LD2=late deficit, Expt. 2 (n≥7); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fig. 4 Pre-dawn leaf water potential (Ψ_1) for Expts. 2 (A) and 4 (B). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 from 120 DAFB) and 12 experimental units (trees) for A and B respectively. C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=late deficit (n=2), Expt. 2; C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

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Fig. 6 Diurnal leaf water potential (Ψ_l) at 61, 81, 135 and 161 days after full bloom during Expt. 4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 12 experimental units (trees). Abbreviations are C4=control (n=4); ED4=early deficit (n=4); and LD4=late deficit (n=4).

Fig. 7 Photosynthetic rate (P_n) for Expts. 1 (A), 2 (B), and 4 (C). Measurements were taken at midday. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21, 18 and 12 experimental units (trees) for A, B, and C respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n≥7); D2=deficit, Expt. 2 (n≥4); LD2=late deficit, Expt. 2 (n≥7); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

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2 ($n \geq 7$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$); and LD4=late deficit, Expt. 4 ($n=4$). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

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Fig. 10 Diurnal Photosynthetic rate (P_n) and irradiance (I_r) at 106, 120 and 148 days after full bloom (DAFB) during Expt. 2. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 at 148 DAFB) experimental units (trees). Abbreviations are C2=control ($n=2$); D2=deficit ($n=2$); LD2=late deficit ($n=2$).

Fig. 11 Diurnal stomatal conductance (g_s) and vapour pressure deficit (VPD) at 106, 120 and 148 days after full bloom (DAFB) during Expt. 2. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 at 148 DAFB) experimental units (trees). Abbreviations are C2=control

(n=2); D2=deficit (n=2); LD2=late deficit (n=2).

Fig. 12 Percent final fruit diameter and shoot length with days after full bloom for control trees of Expt. 1

Fig. 13 Shoot length for Expts. 1 (A), 2 (B), and 4 (C). Separate bars are standard errors of the means. Abbreviations are for C1=control, Expt. 1(n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n=13); D2=deficit, Expt. 2 (n=10); LD2=late deficit, Expt. 2 (n=13); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4).

Fig. 14 Mean fruit diameter for Expts. 1 (A), 2 (B) and 4 (C). Bars indicate standard errors of the means. Abbreviations are for C1=control, Expt. 1 (n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n=7); D2=deficit, Expt. 2 (n=4); LD2=late deficit, Expt. 2 (n=7); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fig. 15 Mean fruit weight for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 18, 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control (n=10 upto 170 DAFB

(stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) when $n=4$), D1=deficit ($n=11$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) where $n=5$); C2=control, Expt. 2 ($n \geq 7$); D2=deficit, Expt. 2 ($n \geq 4$); LD2=late deficit, Expt. 2 ($n \geq 7$); C3=control, Expt. 3 ($n=6$); D3=deficit, Expt. 3 ($n=3$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$); and LD4=late deficit, Expt. 4 ($n=4$). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fig. 16 Fruit firmness for Expt. 1. Bars indicate standard errors of the means. Abbreviations are for C1= control ($n=10$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) when $n=4$), D1=deficit ($n=11$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) where $n=5$).

Fig. 17 Mean total soluble solids for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 ($n=10$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) when $n=4$); D1=deficit, Expt. 1 ($n=11$ upto 170 DAFB (stage 1 harvest) where $n=6$ and 180 DAFB (stage 2 harvest) where $n=5$); C2=control, Expt. 2 ($n=2$); D2=deficit, Expt. 2 ($n=2$); LD2=late deficit, Expt. 2 ($n=2$); C3=control, Expt. 3 ($n=6$); D3=deficit, Expt. 3 ($n=3$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$);

and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fig. 18 Fruit dry matter for Expt. 4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 12 experimental units (trees). Abbreviations are for C4= control (n=4), ED4=early deficit (n=4), and LD4=late deficit (n=4). Arrows indicate rewatering of ED4 treatment, and the beginning of LD4 treatment.

Fig. 19 Fruit titratable acidity for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4); D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=5); C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=late deficit, Expt. 2 (n=2); C3=control, Expt. 3 (n=6); D3=deficit, Expt. 3 (n=3); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fig. 20 Fruit N concentration for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard

error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10 upto 170 DAFB (stage 1 harvest) where n=6 and 180 DAFB (stage 2 harvest) where n=4); D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) where n=6 and 180 DAFB (stage 2 harvest) where n=5); C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=late deficit, Expt. 2 (n=2); C3=control, Expt. 3 (n=6); D3=deficit, Expt. 3 (n=3); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fig. 21 Ethylene evolution for Expts. 1 (A), and 2 (B). Bars indicate standard errors of the means. Abbreviations are for C1= control, Expt. 1 (n=10 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4); D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) where n=6 and 180 DAFB (stage 2 harvest) where n=5); C2=control, Expt. 2 (n=2 upto 180 DAFB where n=7); D2=deficit, Expt. 2 (n=2 upto 180 DAFB where n=4); and LD2=late deficit, Expt. 2 (n=2 upto 180 DAFB where n=7).

Fig. 22 Fruit Ca^{2+} concentration for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from

120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4); D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) where n=6 and 180 DAFB (stage 2 harvest) where n=5); C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=late deficit, Expt. 2 (n=2); C3=control, Expt. 3 (n=6); D3=deficit, Expt. 3 (n=3); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fig. 23 Fruit Mg^{2+} concentration for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4); D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=5); C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=late deficit, Expt. 2 (n=2); C3=control, Expt. 3 (n=6); D3=deficit, Expt. 3 (n=3); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

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1 INTRODUCTION

The ecological significance of water is due to the major roles it plays in the physiological processes of plants. However, of the water absorbed from the soil by the plant, only 5% remains in the plant, the rest is lost to the air via transpiration. If transpiration did not occur, there would be little need for irrigation. The importance of irrigation to plant production can be appreciated by considering the fact that it has made a major contribution to both the creation and destruction of civilisations. As one example of many, the Sumerian empire in Mesopotamia finally collapsed because of irrigation mismanagement that led to waterlogging, salinity, and siltation (Van Schilfgaarde, 1994).

In today's world there is an urgent need to adopt proper irrigation management strategies as water, the most precious environmental resource, is increasingly in demand, mainly because of population growth and increased industrialisation. As reported by Postel (1993a), this dwindling supply of water has prompted the adoption of certain conservation measures by a number of urban centres, for example; Mexico City; Waterloo, Ontario, Canada; Boston metropolitan area; and the city of Bogor in Indonesia. According to Postel (1993a), policies such as effective pricing, setting of regulations, and public outreach have helped in the adoption of 'xeriscape' landscaping on public and private land in many communities in the USA. Problems and conflict with water demands and irrigation procedures are beginning to emerge in New Zealand in horticulturally important regions such as Northland, the Auckland basin, Hawkes Bay, Marlborough, and Canterbury (Ian Cunliffe, Marlborough District Council, pers. comm., 1996). With the Resource Management Act there is powerful legislation to control water use and discharge, and growers will need to adhere to rules concerning levels of

water use and contamination of ground and surface water with nitrates and pesticides (Ministry for the Environment, 1995).

Irrigation of agricultural lands accounts for over 85% of the water usage world wide (Van Schilfgaarde, 1994). Therefore, even a relatively minor reduction in irrigation water use would substantially increase the water available for municipal and industrial purposes. As is the case in urban areas, managing demand rather than trying to develop new supplies seems to be realistic goal for irrigated agriculture. Deficit irrigation (DI) is one such option.

Deficit irrigation involves giving less water to the plant than the prevailing evapotranspiration demand at selected times during the growing season. Economic justification of DI for field crops, whose yield is often decreased under water deficit, has been attempted. For example, Hargreaves and Samani (1984) concluded that deficit irrigation can produce significant benefits under favourable circumstances. These benefits depend upon the interaction of several factors including the management of fertility, rainfall, crop selection, crop value and water costs. For deciduous orchards deficit irrigation, if managed properly, need not decrease yield and may even improve it. As a recent example, Lampinen et al. (1995) reported higher economic returns with DI of 'French' prune in deep soil, and under mild DI in shallow soil.

Besides economic considerations, DI may have a beneficial effect on environmental quality. While well-drained soils are suitable for the establishment of deciduous orchards, they also tend to facilitate the leaching of nutrients and pesticides into ground water. Of primary concern is drainage beyond the rootzone of nitrates, pesticides and dissolved mineral salts (Tanji, 1993). Deficit irrigation, in conjunction with a reduced use of pesticides and nutrients, will therefore help in the prevention of

ground water contamination and it will adhere to the environmental protection legislation which exists in some countries (Tanji, 1993).

Deficit irrigation is a system of managing soil water supply to impose specific periods of plant water deficit which minimises the negative influences of reduced plant water status, while enhancing some facets of crop performance. One specific example of DI is 'regulated deficit irrigation' (RDI), which was initially studied in Australia on peaches and pears (Chalmers et al., 1981; Mitchell and Chalmers, 1982). The term RDI is normally used to denote DI of trees early in the season, before rapid fruit growth starts. Here I will refer to all deficit irrigation treatments as DI and specify the timing of the deficit irrigation in each instance. Early-season DI was developed to control tree vigour in high-density plantings of 'Golden Queen' peaches (Chalmers et al., 1981; Mitchell and Chalmers, 1982) and 'Bartlett' European pears (Mitchell et al., 1984). In these experiments controlled water deficit was established in the plant during rapid shoot, and/or slow fruit growth. The trees were watered at a rate lower than evapotranspiration. Water was then made available to the plant just as the fruit started their rapid growth phase. The application of this early-season DI was found to have no negative effects on fruit growth and final yield.

Most studies have focused on an early-season DI, much less information exists on its impact at later stages of crop development. A late-season DI may be expected to have a greater impact on fruit quality at harvest due to compositional changes that occur in the fruit during the deficit period. Irrigation in New Zealand orchards is predominantly applied during the late summer when rainfall is low. Therefore late-season DI would minimise water use at this time.

This thesis evaluates the impact of early-, late- and entire-season water deficit

on the fruit composition, growth and water relations of 'Braeburn' apples. The cultivar 'Braeburn' was selected due to its importance as a major export cultivar. During 1994 more 'Braeburn' were exported than any other single cultivar, contributing 30% to the total apple exports in that year (New Zealand Apple and Pear Marketing Board Report, 1994). Assessment of fruit quality, yield and plant physiological responses of 'Braeburn' under reduced plant water status is required prior to the adoption of DI as a management tool.

2 LITERATURE REVIEW

2.1 Introduction - The physiology of deficit irrigation

Deciduous orchard trees are complex perennials which respond differently to water deficit depending on the physiological stage (Landsberg and Jones, 1981). Most events in plant development occur periodically during the season and are only sensitive to plant water status during their active periods (Chalmers, 1989). Consequently, identifying these periods allows manipulation of one physiological process with little impact on others. Classically, DI was used during the early stages of the seasonal crop development of deciduous fruit trees as this is when most vegetative growth occurs. The control of vegetative growth being the principle focus of many previous DI studies.

The physiological principles of early-season DI were reviewed by Caspari (1993). These include the functional equilibrium between roots and shoots, the phenological separation of shoot and fruit growth, and the rapid growth that is often observed in DI fruit once irrigation is resumed.

A functional equilibrium exists between the growth of roots and shoots (Richards and Rowe, 1977a). In peach trees, for example, in a given environment, there is a constant relation between the relative growth rates of the top and of the roots. The allocation of dry matter towards the above- and below-ground portions of the tree changes markedly with tree size (Chalmers and van den Ende, 1975). This suggests that a particular ratio of roots to shoots is required for a given environment. Restricting the root development by orchard management techniques can thus be used to reduce vegetative vigour which has the secondary benefit of increased flower production, bloom density, and the allocation of dry matter to the fruit (Richards, 1985). Root volume can be restricted by management techniques such as planting density (Chalmers et al., 1984),

type of rootstock (Chalmers, 1989), and irrigation management (Proebsting et al., 1977; Mitchell and Chalmers, 1983). By assuming that roots in dry soil are physiologically inactive (Proebsting et al., 1989), and will not grow, deficit irrigation can reduce the effective root volume and lead to less vigorous yet more fruitful trees (Richards, 1985). Water deficit in the root zone, once established and maintained until the start of rapid fruit growth, will primarily affect the development of shoots. As fruit in this early growth stage of cell division have a lower assimilate demand, and are less sensitive to water stress than the shoots, water deficit can significantly reduce shoot growth with little or no reduction in fruit growth (Mitchell et al., 1984).

Deficit irrigation is complementary to other management techniques which restrict root system development including planting density. Mitchell et al. (1989) found that increases in fruit yield in response to DI tended to be higher at closer spacing, confirming that DI is more effective where root growth is already suppressed by other mechanisms.

The phenological separation of shoot and fruit growth that occurs in some deciduous fruit crops is an important factor allowing the application of early-season DI (Chalmers et al., 1985). This separation allows the timely application of DI to check undesired vegetative growth. The reduced plant water status has a minimal impact on fruit growth. In addition, different organs, tissues, and processes of the tree can vary in their sensitivity to reduced plant water status (Chalmers, 1989). Processes of photosynthesis and translocation of assimilates are not suppressed at water potentials that inhibit cell expansion which is particularly sensitive to water stress (Hsiao et al., 1976). Fruit are thought to be less affected by water deficit than shoots, because fruit are stronger sinks and accumulate large quantities of soluble solids over the season (Jones

et al., 1985; Chalmers, 1989). This should therefore render feasible DI in species whose shoot and fruit growth show some overlap. Although extensive studies of DI on peach and pear have been published, less information is available on apple, and specifically 'Braeburn' which is an import export cultivar in New Zealand. This thesis evaluates the effects of DI, induced at various times of the season, on both the fruit and vegetative portions of 'Braeburn' apple trees.

Following return to full irrigation at the start of rapid fruit expansion, previously deficit-irrigated peach (Mitchell and Chalmers, 1982) and pear fruit (Mitchell et al., 1984) grew at a faster rate than fruit in a well-watered control treatment. This compensatory growth has been attributed to active osmotic adjustment during the early-season DI (Chalmers, 1989). There is scant evidence of osmotic adjustment in deficit-irrigated fruit in the literature. The work of Behboudian et al. (1994a) showed osmotic adjustment of Asian pear for early-season DI but not for late-season DI. Whatever the mechanism of compensatory growth, whenever it happens it serves to make the final fruit size at least the same as the fully irrigated fruit, providing the deficit is not too long or too severe. Osmotic adjustment of fruit under early-, late-, and entire-season DI is investigated in conjunction with fruit growth in this study.

Most references describe early-season DI, much less is known about DI that is imposed later in the season. Clearly, the imposition of a late-season water deficit will have a minimal impact on vegetative growth as this generally occurs during the early stages of the growing season in deciduous fruit trees. The impact on fruit size and quality will, however, be more marked. Li et al. (1989) observed changes in fruit composition such as increased total soluble solids (TSS) of peach under late-season DI. Irving and Drost (1987) also noted increased TSS in apple under late-season DI. The

incidence of disorders such as bitter pit of apples has also been reported to reduce under late-season water deficit (Lötter et al., 1985). Information as to the influence of late-season DI on apple fruit growth shows some inconsistencies. Irving and Drost (1987) reported no reduction in fruit size whereas Lötter et al. (1985) observed significant fruit size reduction.

There is limited information on the impact of a late-season DI on fruit quality. This is an area well worthy of study. As late-season drought is common in many horticulturally important regions of New Zealand, it has become imperative that effective management strategies are developed in order to minimise production loss during this period. Additionally, a more complete understanding of the physiological basis of fruit tree responses to a late-season water deficit may lead to management techniques which may take advantage of this deficit. The influence of a late-season DI on the fruit qualities of composition and size will be evaluated in this thesis.

2.2 The physiological responses of deciduous fruit crops to reduced plant water status.

Plant water status changes in response to numerous external factors. Plants respond to fluctuating environmental conditions so as to maintain water status at a desirable level. Paramount to the accurate assessment of plant water status is an appreciation for the major factors influencing it. This section outlines the principles of the evaluation of plant water status and responses of plants to water stress.

2.2.1 The evaluation of plant water status

The most frequently-used assessment of plant water status is that of leaf water potential (Ψ_l), and/or its components. It is measured in units of pressure (MPa). Total leaf water potential can be separated into its components as follows :

$$\Psi_l = \Psi_s + \Psi_p + \Psi_g + \Psi_m$$

where Ψ_s represents osmotic potential, Ψ_p pressure or turgor potential, Ψ_g gravitational potential and Ψ_m matric potential. The value of Ψ_g is minimal with a change of 0.01 MPa for each meter increase in height. The value for Ψ_g is limited to a maximum of approximately 0.05 MPa for most deciduous fruit crops, and it is therefore frequently ignored (Jones et al., 1985). The distinction between Ψ_m and Ψ_s is often difficult to make. For this reason estimates of Ψ_m are often included in the evaluation of Ψ_s (Jones, 1983, p. 65). Therefore, in the literature, the value of Ψ_l is taken as the algebraic summation of Ψ_p and Ψ_s .

Plant water status fluctuates rapidly with prevailing environmental conditions both diurnally and seasonally (Jones et al., 1985). The daily Ψ_l is strongly dependent on transpiration of the plant which is dictated to a large extent by the evaporative demand of the atmosphere (Lakso, 1985). As an example, Flore et al. (1985) observed that a high vapour pressure deficit (VPD) can induce water stress symptoms in potted apple trees, even when the soil is near field capacity.

The changes in evaporative demand that occur during the day often cause short periods of plant water deficit to develop (Syvertsen, 1985). With the prevailing environmental conditions playing such an important role in the plant water status the timing of measurement is critical. Pre-dawn measurements of Ψ_l are favoured by many researchers due to the relative stability of environmental conditions at this time (McCutchan and Shackel, 1992). Pre-dawn measurements may also provide an indication of soil water potential. However, the average water potential over the entire rootzone may not be integrated accurately as pre-dawn Ψ_l tends to be biased towards conditions in the wettest part of the rootzone. Midday closure of stomata on hot days

may be a response to high VPD, in order to prevent the development of critically low Ψ_1 (Lakso, 1985). Jones et al. (1985) found that under conditions of lower stomatal conductance (g_s), the Ψ_1 of water-stressed apple trees was higher than that of well watered ones, suggesting that g_s may control Ψ_1 . This indicates that midday measurement of Ψ_1 may not always be appropriate. In this thesis both pre-dawn and midday Ψ_1 are evaluated.

2.2.2 Plant responses to water deficit

Because plants are often exposed to water deficits during growth and development, it is important that they are equipped with mechanisms that allow adaptation to the prevailing conditions so as to avoid serious damage to the plant. Included in the mechanisms of adaptation to water deficit are drought escape, drought tolerance with low plant water potential, and drought tolerance with high plant water potential (Turner, 1986). Drought escape requires that the life cycle of the plant is rapidly completed before significant water deficit can develop so it is therefore not applicable to deciduous fruit crops. Drought tolerance on the other hand is demonstrated by deciduous fruit trees.

2.2.2.1 Osmotic adjustment

Drought tolerance with low plant water potential describes the maintenance of cell turgor through osmotic adjustment, increased cell elasticity and reduced cell size (Turner, 1986). The maintenance of cell turgor is critical for the continuation of many important processes within the plant, including expansion growth, stomatal opening, hydraulic conductivity of membranes, and the synthesis and distribution of hormones (Faust, 1989, p. 146). The occurrence of osmotic adjustment means that as Ψ_1 decreases either diurnally, or during the season, it is paralleled with a similar decline in Ψ_s

resulting in the maintenance of Ψ_p . Turgor maintenance by means of osmotic adjustment is thought to provide a major physiological method for minimising the detrimental effects of water stress in plants (Jones et al., 1985).

Osmotic adjustment may occur actively or passively. Passive osmotic adjustment refers to the reduction in Ψ_s which results from tissue dehydration. This relies on cell elasticity. Active osmotic adjustment on the other hand increases the number of solutes within the tissue. Both active and passive osmotic adjustments have been reported in apple leaves (Jones et al., 1985).

Morgan (1984) reports the occurrence of osmotic adjustment (osmoregulation) in expanding tissue such as roots, leaves, and inflorescence where it contributes to the maintenance of the inflow of water during expansion growth. Additionally Jones et al. (1985) note that the most obvious organ to show osmotic adjustment is fruit. Osmotic adjustment appears to operate in most organs of the apple plant, with some organs being better at it than others. For example, during the onset of water stress the water potential of the root cells can be maintained longer than the water potential of the shoot cells. This in turn results in a discontinuation of growth in the shoot, whilst root growth is maintained. This proves to be an important morphological adaptation by plants to a water stress situation as the root : shoot ratio is increased (Begg and Turner, 1976). Fruit cells are also less sensitive to water deficit than shoots. Fruit cells act as strong sinks which accumulate large amounts of solutes. The accompanying decline in Ψ_s of the fruit due to seasonal solute accumulation may allow water uptake to continue while the Ψ_l of the plant falls in response to water stress (Chalmers et al., 1984). The different sensitivities of various plant organs to reduced plant water status suggests an opportunity to use plant water deficit to manipulate one plant parameter, while others remain

minimally affected (Chalmers et al., 1985).

Age has an influence on the ability of various organs to adjust osmotically. For example, young expanding leaves of apple have a higher Ψ_s than mature fully expanded leaves. So they lose turgor during water deficit more rapidly than mature leaves (Lakso et al., 1984). The loss of turgor in young expanding leaves acts to reduce leaf expansion, and may therefore have consequences on the leaf area of the whole tree (Davies and Lakso, 1979).

The rate of development of water stress is also reported to influence the ability of organs to show osmotic adjustment, with a gradual imposition of stress favouring its development (Morgan, 1984). Fully expanded leaves of apple showed osmotic adjustment in both field grown and potted glasshouse trees (Fanjul and Rosher, 1984) over a 17 day stress imposition. Additionally Wang and Stutte (1992) reported active adjustment of 0.6 MPa in potted apple trees within one week of water stress being initiated. These results suggest apple leaves may show rapid osmotic adjustment under water deficit.

Stress preconditioning also plays an important role in plant responses to reduced water status. Solutes, accumulated during a pre-conditioning stress, are not fully dissipated immediately upon rewatering and may therefore act to favour the water relations of that organ during subsequent stress periods (Morgan, 1984).

Osmotic adjustment of leaves has been extensively studied in a diverse range of plants (Jones and Turner, 1980; Zhang and Archbold, 1993; Morgan, 1980) including apple (Goode and Higgs, 1973; Fanjul and Rosher, 1984; Wang and Stutte, 1992). Much less information exists on osmotic adjustment of fruit. Fruit composition and growth is central in this study, and it is likely to be influenced by fruit osmotic

adjustment. The occurrence of fruit osmotic adjustment under DI is investigated.

2.2.2.2 Stomatal conductance

Drought tolerance with high plant water potential also plays a key role in the adaptation of deciduous fruit trees to water stress. Stomatal control plays an important role in the maintenance of plant water potential as transpiration accounts for most of the water loss through the plant. Initially it was believed that decreasing Ψ_1 caused loss of guard cell turgor and resulted in stomatal closure. However, it now appears that the mechanism behind stomatal closure maybe somewhat more complex. The involvement of hormones such as ABA (Tallman, 1992; Tardieu and Davies, 1993) and cytokinins (Gollan et al., 1986) that are produced under conditions of water deficit may also play a role. Stomata provide the dominant short term control over transpiration (Jones et al., 1985) and hence plant water status. Stomatal conductance in conjunction with Photosynthesis (P_n) under DI is investigated in this thesis.

2.2.2.3 Carbon assimilation

Photosynthesis is reduced in many plant species as water deficit is imposed, but the mechanisms by which this reduction takes place are not fully resolved (Flore and Lakso, 1989). General statements about the influence of water deficit on P_n are difficult to make, as the sensitivity of P_n to reduced plant water status varies between species, and within species depending on the pre-treatment that the plants have received (Flore and Lakso, 1989). Environmental parameters such as VPD, air temperature, and irradiance (I_r) must also be considered when interpreting P_n data. They are known to have an influence on both P_n and g_s (Jones, 1983, p. 117-121 and 155-157; Flore and Lakso, 1989; Brakke and Allan, 1995). Stomatal closure is commonly reported in fruit crops under DI (eg. Flore et al., 1985; Brun et al., 1985; Caspari et al., 1994). The

inhibition of CO_2 assimilation by water stress is thought to be closely linked to the extent of stomatal closure. Often a linear relationship exists between assimilation rate and g_s (Hsiao, 1993). In recent years, however, it has become apparent that stomatal closure is not the only cause of reduced CO_2 assimilation under water deficit conditions (Quick et al., 1992). The metabolic capacity of the cells in the leaf for Pn is usually also reduced (Hsiao, 1993). Boyer and Younis (1983) reported a reduction in photophosphorylation in chloroplasts of water-stressed spinach leaves. Mesophyll resistance may also be increased under water deficit conditions (Jones and Fanjul, 1983; Brakke and Allen, 1995). It has been postulated that an accumulation of carbohydrates, when growth is suppressed by water stress, causes a reduction in CO_2 fixation due to the buildup of photosynthetic product in the leaf. However, Bunce (1982) found no evidence of this. Hsiao (1993) also reports that stomatal closure appears to have a limited influence on leaf Pn as a reduction in g_s under water deficit conditions does not necessarily result in a reduction in leaf internal CO_2 concentration. Additionally, Berkowitz and Whalen (1985) observed that under conditions of low leaf K^+ , water deficit reduced the Pn of spinach leaves more than if leaf K^+ was not deficient. This may be associated with the role K^+ is reported to play as a solute accumulated during osmotic adjustment. This is in agreement with the observation that plants having suffered a previous stress, have to a certain degree, become preconditioned to water deficit. They show less reduction in Pn during subsequent stress periods (Kramer and Boyer, 1995, p. 319). Alternatively, deficiency of K^+ may adversely affect Pn in stressed tomato plants independent of a stomatal response (Behboudian and Anderson, 1990).

In studying the effects of DI it is therefore important to investigate the

parameters of carbon assimilation such as P_n , g_s , and respiration. Information relating DI to P_n upon the removal of water deficit is limited. Additionally, comparisons between the influence of DI imposed at different times of the season on P_n rate is also limited. These are explored in order to give an indication of the recovery of P_n upon rewatering following DI, and to evaluate whether or not P_n is more sensitive to DI at particular times of the season.

Net CO_2 assimilation is the sum of CO_2 assimilated during the day minus the CO_2 lost during the night as respiration. Under conditions of water deficit the level of respiration may be reduced (Bergamini and Jones, 1988; Kramer and Boyer, 1995, p. 321). However, Jones and Fanjul (1983) showed that respiration was minimally affected by water stress in apple. The influence of DI on respiration will also be investigated.

During CO_2 fixation, C_3 plants discriminate against the naturally occurring stable isotope $^{13}CO_2$ (Farquhar et al., 1989). The ratio of $^{13}C : ^{12}C$ ($\delta^{13}C$) in plants is therefore lower than that found in the atmosphere. Organic matter is often depleted in ^{13}C relative to the standard against which it is compared. Therefore values of $\delta^{13}C$ are negative as $\delta^{13}C = ((R_{\text{sample}} / R_{\text{standard}}) - 1) \times 1000$ where R is the ratio of ^{13}C to ^{12}C . A less negative figure represents less discrimination against ^{13}C during photosynthesis. The extent of discrimination may be a useful screening tool to evaluate yield and water use efficiency, as it is an integrated measure of internal physiological and environmental parameters influencing the performance of the plant throughout the season (Meinzer et al., 1991). The Measurement of P_n is transient and is therefore subject to fluctuations in environmental conditions at the time of evaluation. This may mean that a difference in P_n at the time of measurement may not be apparent between treatments due to the overriding influences of environmental conditions other than water

deficit. Determination of $\delta^{13}\text{C}$ has the advantage of integrating the performance of the plant over a longer period of time and therefore could be a more informative, albeit retrospective, measure of the influence of stress on carbon assimilation during the entire stress period. For this reason $\delta^{13}\text{C}$ has been evaluated during this study.

2.2.2.4 Tree growth.

The response of vegetative growth constitutes one of the underlying focuses of DI studies (eg. Chalmers et al., 1981; Mitchell and Chalmers, 1982). Although not a key aim of this study, the total tree growth components of leaf area, root growth, shoot growth and trunk growth were investigated in this thesis for completeness and are reviewed in the following.

2.2.2.4.1 Leaf area

The regulation of leaf area plays an important role in the adaptation of fruit crops to water deficit (Jones et al., 1985; Lakso, 1985). Reduced leaf area can be due to several factors, including a reduction in shoot growth (Lötter et al., 1985; Chalmers, 1989; Durand, 1990) as leaves produced on shoots contribute more to leaf area than do the spur leaves of most apple varieties (Forshey and Elfving, 1989). Total leaf number may also be reduced. Lakso (1983) observed a reduction in total leaf number in water stressed apple trees due to a determinate terminal bud being set on stressed extension shoots. In general, leaf area expansion is sensitive to reduced plant water status (Hsiao, 1993) due to the sensitivity of cell growth, namely cell division and cell expansion, to reduced plant water status (Hsiao, 1973; Kramer and Boyer, 1995, p. 18). Despite some controversy, it is generally accepted that one of the prerequisites for cell expansion is the existence of turgor (Kramer, 1988). This may be lost under reduced plant water status. To illustrate this, Davies and Lakso (1979) showed that the leaf expansion rate

of apple is increased with increasing leaf turgor. Leaf area index (LAI) is a measure of the total leaf area of a plant, or plants, divided by the land area covered (Westwood, 1988, p. 220). A reduction in LAI was observed in peach under early-season DI (Boland et al., 1993). A decrease in LAI may result in a reduction in the interception of photosynthetically active radiation (PAR). This in turn may reduce total carbon assimilation and total dry matter production (Hsiao, 1993). Aside from reduced leaf area expansion, leaf area may also be reduced due to the adaptive responses of the plant to reduced water status. Adaptations include leaf folding about the midrib in apple (Lakso, 1983), and, in extreme cases of water deficit, leaf abscission can occur (Hsiao, 1993; Behboudian et al., 1994a). Water stress has also been reported to advance leaf drop on peaches in autumn (George and Nissen, 1992). The influence of DI, imposed at various times of the season, on leaf area is reported in this thesis.

2.2.2.4.2 Root growth

Water stress generally increases the proportion of new dry matter consigned to the roots, in preference to the shoots, with soil water deficit reducing growth of the shoots before that of the roots (Kramer and Boyer, 1995, p. 146). This is possibly because roots are exposed to less severe water stress than shoots (Kramer, 1988). The absolute amount of root growth may however be decreased under water deficit (Landsberg and Jones, 1981). A reduction in the root growth of apple trees under deficit irrigation was reported by Cripps (1971) who also indicated a general change in the configuration of the root system. Studies by Goode and Hyrycz (1964) on mature apple trees indicated that although the total weight of roots was not different between soil moisture treatments, significantly more roots existed in the top 15 cm of soil around trees that were fully watered. An increase in rooting depth and length density in

response to water deficit is considered a major adaptive mechanism for improving water uptake (Turner, 1986). Under water deficit conditions, an increase in the root to shoot ratio may also occur, as shoot growth is generally reduced more than root growth (Kramer and Boyer, 1995, p. 146). The practical limitations of root studies on field grown trees limits evaluation of root responses to DI. Consequently, here, root growth of potted apple trees was investigated and is reported in this thesis for completeness.

2.2.2.4.3 Shoot growth

A reduction in plant water status during the times of active shoot growth will result in a reduction of vegetative growth in most trees. The practical importance of controlling tree vigour in perennial fruit crops is well established (Chalmers, 1989). During the growing season, fruit growth follows shoot growth in peach, pear (Chalmers, 1989), and apple (Lötter et al., 1985). The reduction in shoot growth under early-season DI is predominantly due to its earlier cessation (Mitchell et al., 1986; Irving and Drost, 1987). Controlling tree vigour by DI reduced the summer pruning requirements in peach (Chalmers et al., 1981; Mitchell and Chalmers, 1982), pear (Chalmers, 1989) and apple (Durand, 1990). Aside from the economic benefit of reduced pruning costs, a reduction in vegetative growth may reduce the competition for photoassimilates between fruit and vegetative parts, and may therefore enhance fruit size (Chalmers, 1989). Less vegetative growth also allows better light penetration into the canopy thereby improving fruit colour development (Westwood, 1988; Lancaster, 1992), and it may also ensure more effective spray coverage. Shoot growth has been a major focus of many DI investigations. The impact of DI on shoot growth is also reported in this study.

2.2.2.4.4 Trunk growth

Water deficit tends to reduce trunk growth in apples (Iancu, 1985; Irving and

Drost, 1987), peach (Chalmers et al., 1985; Boland et al., 1993) and pear (Mitchell et al., 1989). This would result in reduced total tree size, as trunk cross-sectional area is linearly related to the above ground weight of the tree (Westwood and Roberts, 1970) unless complicated by major pruning or training. The annual increment in cross-sectional area will therefore be directly proportional to the annual increment of secondary growth, or to the growth of the tree frame. Unlike shoot growth, trunk growth continues throughout the season, albeit at a slower rate (Johnson et al., 1992). Therefore water deficit at any time throughout the season may reduce trunk growth.

As with most organs in the plant, the trunk shows diurnal fluctuations in size (Landsberg and Jones, 1981; Li and Huguet, 1990). Water deficit increases the diurnal contractions in the stem diameter (Li and Huguet, 1990). Measurement of these diurnal contractions can provide information on the water status of the plant, and irrigation may be scheduled accordingly. Some researchers have used radial trunk growth as an indicator of irrigation requirements (Taerum, 1964). Trunk circumference growth is evaluated in this thesis as an indicator of total tree growth.

2.2.3 Effects of plant water deficit on crop yield and fruit quality

Most DI studies have focused on the control of vegetative growth under early season DI with total fruit yield as a key focus. Fruit quality aspects have been studied less. The following sections indicate the current state of knowledge on the influences of DI on yield and quality and identifies areas that warrant further investigation.

2.2.3.1 Crop yield

Fruit number and fruit size are the important components of total yield.

2.2.3.1.1 Fruit number

Fruit number is dependent on the number of initiated flowers, and on final fruit

set. Findings concerning the effect of water deficit on these processes are contradictory. Mitchell et al. (1984) and Raese et al. (1982) reported an increase in pear flowering in the season subsequent to early-season DI treatments. Chalmers et al. (1985) showed similar increases in peach flowering. Degman et al. (1932) showed an increase in bloom for apple following the development of plant water deficit during the middle of the previous season. However, Caspari (1994) reported a reduction in return bloom of Asian pears if water deficit was induced rapidly during an early-season DI. Water deficit late in the season was found to have no influence on return bloom of Asian pear (Caspari, 1994). Additionally, Brun et al. (1985) reported a reduction in return bloom and fruit set of pears following a low seasonal irrigation treatment during the previous season. It appears that the timing of the water deficit affects the impact that it has on fruit tree flowering. Proebsting et al. (1977) investigated the use of different irrigation methods for apple tree establishment and growth. They reported that under trickle irrigation which provided young 'Delicious' apple trees with significantly less water than sprinkler irrigation, the flower number and fruit set was increased when compared to sprinkler irrigated trees. Improved fruit set after post-bloom drop was also recorded in peach exposed to water stress during flower bud development the previous season (Li et al., 1989). Powell (1974) however recorded reduced fruit set and increased fruitlet abscission (June drop) in droughted compared to irrigated apple trees. Severe water stress at the time of pollination is also likely to inhibit fertilization (Hsiao, 1993).

Another important consideration with many perennial fruit crops is the tendency for biennial bearing. A stimulation of flowering following DI treatments can help counteract the biennial bearing tendencies of some peach and pear cultivars by increasing yield in an off-year (Chalmers et al., 1985). It is clear that, although fruit

number may be influenced by deficit irrigation, the outcome is strongly dependent on the level and timing of the deficit imposed and on tree species. A conclusion as to the influence of deficit irrigation on return bloom is difficult to make and has therefore been investigated in this research.

2.2.3.1.2 Fruit size

Fruit size under early-season DI was initially reduced in peach (Mitchell and Chalmers, 1982) and pear (Chalmers et al., 1986). But once full irrigation was resumed, fruit growth was stimulated and the final yield equalled that of fully irrigated treatments. In some cases the final yield was actually increased (Chalmers et al., 1986; Mitchell et al., 1986; Mitchell et al., 1989). Similar responses of apple under early DI treatments were also reported by Durand (1990). Osmotic adjustment may play a part in the accelerated resumption of fruit growth after the alleviation of stress (Chalmers et al., 1986). Behboudian et al. (1994a) showed osmotic adjustment in Asian pear fruit for early-season, but not for late-season DI. Fruit from the early-season DI resumed growth after rewatering, while growth of the late-season DI fruit was not affected.

Water deficit late in the season may be expected to reduce fruit size more markedly than an early-season DI treatment, as fruit growth predominantly occurs during the later stages of the season (Chalmers et al., 1985; Lötter et al., 1985). The literature, however, provides a record of variation in this response. Irving and Drost (1987) reported no significant reduction in size of apple fruit under a late-season DI treatment, whereas Lötter et al. (1985) reported a reduction in size under similar conditions. Explanation for these discrepancies may be differences in the level of water stress developed.

It is important to note that a reduction in fruit size, as a result of DI, may not

always be a disadvantage. For example, in peach cultivars with extra large fruit, a slight reduction of fruit size does not diminish their market value, and these fruit may in fact be sold more readily (Li et al., 1989). In pear, sensory evaluation by supermarket consumers showed some fruit were too large to be acceptable to the consumer (Kappel et al., 1995). In addition, large apple fruit are often more prone to mineral imbalances and the development of storage disorders (Guelfat'Reich et al., 1974). The influence of early-, late-, and entire-season DI on fruit growth and final fruit size is evaluated in this research as fruit size influences economic yield and financial return.

2.2.3.2 Fruit quality under deficit irrigation

The production of high quality fruit is critical to maximise returns to the grower with premium prices being paid for export quality fruit. Any management strategy must therefore address the impact it may have on the quality of produce. Consumer preference defines fruit quality (Kingston, 1991). In most fruits, flavour, texture and appearance play important roles. Of paramount importance in the determination of fruit quality is the maturity of fruit for eating, commonly termed commercial maturity (Kingston, 1991). Deficit irrigation may advance fruit maturity in apple (Guelfat'Reich et al., 1974; Ebel et al., 1993) and pear (Raese et al., 1982). Thus fruit quality changes are expected under deficit irrigation. The limited information concerning the effects of DI on fruit quality serves to identify this as a key area requiring investigation. The influence of early-, late- and entire-season DI is therefore addressed in this thesis.

2.2.3.2.1 Fruit firmness

Fruit firmness or texture is important in apples and is strongly influenced by fruit maturity, with firmness decreasing in apples and pears as the fruit ripen (Kingston, 1991). Fruit firmness is also influenced by fruit size (Ebel et al., 1993), with smaller

fruit being generally firmer than large fruit, due to a higher cellular density. Treatments that alter fruit size may, therefore, also alter firmness. Information on the influence of soil water content on fruit firmness is conflicting. Drake et al. (1981) indicated that apple slices were softer from trees supplied with less water and Raese et al. (1982) reported that pears grown under reduced irrigation have softer fruit. These findings indicate an increased maturity in fruit from drier treatments, possibly due to low turgor in these fruit cells. In contrast, other researchers have shown that apples from non-irrigated plots were firmer than those from irrigated plots (Haller and Harding, 1937; Guelfat'Reich et al., 1974; Guelfat'Reich and Ben-Arie, 1979; Assaf et al., 1975). In these studies, fruit from trees under water deficit were smaller than those from well watered trees which may account for the observed increase in fruit firmness. Reduced firmness of fruit from well-irrigated trees may be the result of an inflation of cell size and an increase in the fragility of cell walls (Guelfat'Reich and Ben-Arie, 1979). The influence of irrigation on fruit firmness is unclear and appears dependent on many factors. In many studies the relationship between fruit firmness and fruit size has not been sufficiently considered. A comprehensive search for the physiological basis of the influence of water deficit on fruit firmness is outside the scope of this study. However, changes in fruit firmness under DI was evaluated in one experiment and the data are presented.

2.2.3.2.2 Total soluble solids

Total soluble solids (TSS), in conjunction with acidity, have a marked influence on the sensory quality of apple fruit (Ackermann et al., 1992). Numerous authors have reported a significant increase in TSS under DI in apple (Ebel et al., 1993; Rumayor-Rodriguez and Bravo-Lozano, 1991), peach (Li et al., 1989), and pear (Raese et al.,

1982). In contrast, DI applied early in the season reduced TSS levels in European pear (Chalmers et al., 1985) at harvest, but had no effect on Asian pear (Behboudian and Lawes, 1994), or peach (Li et al., 1989). It was suggested by Chalmers et al. (1985) that when full irrigation is supplied to trees during the later stages of growth following early-season DI, the increased water content of previously-stressed fruit may dilute soluble solids, thereby giving a lower TSS value. Because TSS is an important indicator of fruit maturity and sensory quality, the impact of DI at different times of the season has been investigated in this study.

2.2.3.2.3 Titratable acidity

As indicated above, titratable acidity (TA) has an influence on the sensory quality of apple fruit (Ackermann et al., 1992). Layne et al. (1981) reported no change in the acidity of peach under DI, but information on TA in apple is conflicting. Marangoni and Rossi Pisa (1985) found an increase in acidity with no irrigation, whereas Drake et al. (1981) showed a reduction in TA under reduced plant water status. Irving and Drost (1987) showed no change in TA between irrigated and DI treatments. The impact of TA in conjunction with TSS has important implications for fruit quality. Conflicting information regarding the influence of DI on TA levels of apple indicates the need for further investigation of changes in this parameter under water deficit conditions. This was investigated here.

2.2.3.2.4 Fruit colour

Fruit colour is dependent on various pigments present in the skin of fruit. Red colouration is due to anthocyanins and flavonols (Lancaster, 1992) and is stimulated by light and cool temperatures. Factors increasing carbohydrate levels of apple fruit preharvest also tend to increase anthocyanin development (Magness, 1928; Westwood,

1988, p. 238). Marangoni and Rossi Pisa (1985) observed an increase in soluble carbohydrate content in fruit from non-irrigated trees. Apple cultivars that ripen to a green or yellow colour, such as 'Granny Smith' and 'Golden Delicious', have chlorophyll and carotenoids as the predominant skin pigments. Drake et al. (1981) reported that 'Golden Delicious' fruit colour at harvest was enhanced under reduced plant water status. The colour development of both red and yellow apple cultivars is dependent on light reaching the fruit (Lancaster, 1992), and a reduction in vegetative growth under DI will allow better light penetration into the canopy. Deficit irrigation of grapes resulted in greater concentrations of anthocyanins in the fruit which enhanced wine quality, specifically colour (Freeman, 1983; Mathews and Anderson, 1988).

Fruit nitrogen concentration may also influence colour development with high fruit nitrogen levels being associated with poor fruit colour (Saure, 1990; Bramlage, 1993). This may be due to delayed chlorophyll breakdown in fruit high in nitrogen (Magness et al., 1940). As an example Ruiz et al. (1986) used N fertilizer to suppress the development of anthocyanins in 'Granny Smith'. Deficit irrigation is known to reduce the level of N in pear fruit (Raese et al., 1982) and in apple (Goode and Ingram, 1971; Ericsson, 1993). Thus a reduction in fruit N concentration may play an important role in the development of desirable colour attributes in deficit irrigated fruit. However, direct experimental data are not available to substantiate this. Fruit colour development under DI has been minimally studied in apple. This is investigated here as colour is an important quality attribute.

2.2.3.2.5 Fruit soluble sugar concentration

Behboudian and Lawes (1994) showed that soluble sugar concentrations were increased in Asian pear fruit exposed to an early-season water deficit. However, if

water deficit was induced late in the season no such change in soluble sugars was observed. It appears that sorbitol was most affected by a water deficit in Asian pears. An increase in the level of sorbitol in apple leaves has been reported under DI (Wang and Stutte, 1992). Marangoni and Rossi Pisa (1985) observed an increase in soluble carbohydrates in apple fruit from non-irrigated treatments.

Fruit soluble sugars are important in the development of anthocyanins, and therefore fruit colour (Saure, 1990; Lancaster, 1992). Minimal information is available on changes in fruit soluble sugars under deficit irrigation which indicates the need for further investigation of this parameter. Additionally, soluble sugars are likely to influence the water relations of fruit as they constitute the major component of solutes within fruit tissue. Fruit soluble sugar concentrations under DI are evaluated in this study.

2.2.3.2.6 Fruit ethylene evolution

Ethylene evolution in apple fruit has been associated with the respiratory rise of the climacteric. It is, therefore, a good indicator of optimum harvest time (Watkins et al., 1989). Aside from being an indicator of fruit maturity, ethylene production is also encouraged in higher plants under stress situations. Narayana et al. (1991) report that water deficit is one of the more commonly reported stresses to cause an over production in ethylene. Guelfat'Reich et al. (1974) observed that in apple fruit exposed to water deficit during development, ethylene production was greater after harvest than it was in fruit from the well-watered treatment. Additionally, Ebel et al. (1993) observed an increase in ethylene production in fruit from the water deficit treatment throughout the harvesting period, further indicating that water deficit encourages ethylene production of apple fruit and thus influences the physiological maturity of the fruit.

The importance of fruit maturity on overall fruit quality indicates the need for an accurate evaluation of fruit maturity changes under DI. For this reason ethylene evolution under DI has been investigated in this thesis.

2.2.3.2.7 Fruit storage disorders as affected by deficit irrigation

An important aspect that controls fruit quality is the occurrence of disorders at harvest and those that develop during storage. Apple fruit grown under water deficit have been found to have a lower incidence of bitter pit (Guelfat'Reich et al., 1974; Lötter et al., 1985; Irving and Drost, 1987; Failla et al., 1990), scald (Guelfat'Reich et al., 1974; Lötter et al., 1985), and water core (Lötter et al., 1985). In contrast Goode et al. (1975) observed increased cracking and russetting in apple fruit grown under reduced irrigation. Irving and Drost (1987) also report a greater incidence of apple fruit cracking if water deficit was imposed early in the season. Opara et al. (1996) reviewed the effect of soil moisture, rainfall, and irrigation on fruit skin splitting and cracking. They indicated that fluctuations in soil moisture, and especially a sudden increase late in the season following a dry period, may encourage splitting in some fruit. Non-physiological disorders such as the incidence of fungal rot may also be modified by reduced irrigation as was reported for peach (Li et al., 1989). In pear, Raese et al. (1982) reported a reduction in the incidence of alfalfa greening and corkspot in fruit grown under DI, as did Brun et al. (1985). The importance of good storage quality of exported fruit is critical. The implications of DI on fruit storage attributes are discussed in this thesis.

2.2.3.2.8 Fruit mineral concentration

The mineral concentration of fruit has been linked to the development of physiological disorders, with fruit requiring a certain nutrient concentration for good

storability (Faust, 1989, p. 55). For example, low calcium levels in apple fruit may result in the development of bitter pit and water core (Faust, 1989, p. 93). Cork spot, a disorder of both apples (Miller, 1980) and pears (Raese et al., 1982), is also a calcium-related disorder (Faust, 1989, p. 93). Nitrogen also plays an important role in the quality of stored fruit. An increase in the N concentration of fruit may increase the incidence of rot in apple (Ericsson, 1993). As reported above, water deficit reduces N in apple fruit (Goode and Ingram, 1971; Ericsson, 1993) and may also reduce Ca^{2+} concentrations in apple (Goode and Ingram, 1971). Deficit irrigation may therefore have a negative effect on the quality of apple fruit via lowering concentrations of Ca^{2+} although lowering of N could be considered as an advantage for fruit quality. Pear fruit N levels are also reduced under DI, although Ca^{2+} concentration appears to increase (Brun et al., 1985; Raese, 1985). Conflicting information on the influence of deficit irrigation on fruit Ca^{2+} concentration is probably due to differences in the timing of water deficit, and on the mode of transport of Ca^{2+} in the tree. Calcium is transported in the transpiration stream (Mengel and Kirkby, 1987, p. 464) and, therefore, a reduction in transpiration will result in a reduction of Ca^{2+} transport within the plant. However, with reduced plant water status vegetative growth is suppressed, and fruit may therefore be preferentially supplied with Ca^{2+} . A reduction in the shoot growth of pears encourages increased Ca^{2+} levels in the fruit (Raese, 1985). As most Ca^{2+} is transported and accumulated by apple fruit during the early part of the season, water deficit at this time is more likely to influence fruit Ca^{2+} concentration (Ferguson and Watkins, 1989).

In the development of fruit disorders the actual amounts of various minerals within the fruit may not be as important as the ratios between several minerals. For

example, Mg^{2+} as well as K^+ are considered antagonistic to Ca^{2+} , and so play a major role in the development of bitter pit in apple fruit (Faust, 1989, p. 94). Guelfat'Reich et al. (1974) attributed the poor keeping quality of apples from well-watered trees to the mineral imbalances of a high K^+ concentration and a high K^+/Ca^{2+} ratio.

Mineral concentrations in fruit are likely to be affected by irrigation. Nutrients such as N, P, K^+ , and Ca^{2+} , are taken up in the soil solution (Faust, 1989, p. 84). A reduction in soil water may result in an increased concentration of elements in the soil solution to levels where ions may precipitate out and become unavailable to the plant (Mengel and Kirkby, 1987, p. 74). In addition, poor soil aeration or low metabolic activity of roots also limits nutrient uptake. A low metabolic rate of roots may develop indirectly through a decrease in the photosynthetic activity of leaves and consequently a drop in carbohydrate supply to the root (Kramer and Boyer, 1995, p. 117 and 136). Fruit mineral nutrition is a complex area of study but the limited and conflicting information indicates this research area needs to be more fully explored. Fruit mineral concentration under conditions of water deficit are investigated in this thesis.

While there are conflicting reports on the effect of DI on mineral concentration, TA, and firmness, other quality attributes such as colour, storability, and concentrations of TSS and soluble sugars may be enhanced under DI. Depending on the timing, DI may be used as an effective tool in enhancing the overall quality of deciduous fruit. Investigation of changes in fruit quality under DI is the central theme of this research.

2.3 Seasonal timing of deficit irrigation.

The discussion so far indicates that the impact of DI is strongly dependent on the timing of the water deficit, since most events in plant development are seasonal and/or periodic. Deciduous fruit crops are active for approximately nine months out of twelve.

The tree enters dormancy over the winter months so that plant water use is minimal, although root growth can continue in winter (Kramer and Boyer, 1995, p. 125). It is during the active growth phase that DI has the most influence on the performance of the crop. Implementation of DI during different phenological stages constitutes the primary focus of this thesis.

2.3.1 Early-season deficit irrigation.

Water deficit during flowering is likely to inhibit fertilization (Hsiao 1993). Powell (1974) reported reduced fruit set and increased fruit abscission when water deficit was induced during flowering in apple. However, early-season DI following the completion of flowering and fruit set, could result in the same yield as full irrigation with considerable savings in water (eg. Li et al., 1989; Mitchell et al., 1989; Ebel et al., 1995). Early-season DI may decrease some fruit disorders such as alfalfa greening and cork spot in pear (Brun et al., 1985) and watercore in apple (Lötter et al., 1985). But in some cases it can increase the incidence of disorders such as flesh spot decay in 'Nijisseiki' Asian pear (Behboudian and Lawes, 1994). Early-season water stress occurring during fruit cell division may reduce cell number (Hsiao, 1973) and thus the final fruit size. Nevertheless, early-season DI can be used as an effective management tool.

2.4.2 Late-season deficit irrigation.

This refers to a deficit that is imposed during the later stages of fruit growth prior to harvest. In 'Hosui' Asian pears, a late-season deficit did not reduce shoot growth, or total leaf area (Caspari, 1994). Exposing apple trees to a late-season water deficit may reduce fruit yield (Lötter et al., 1985), although not always (Irving and Drost 1987). A reduction in fruit size, which is a concern with late-season DI, may constitute

an advantage in some instances. Examples are for grape (Freeman, 1983; Mathews and Anderson, 1988), peach (Li et al., 1989), and pear (Kappel et al., 1995). But a reduction in fruit size is generally undesirable. Fruit composition and some quality attributes are modified under late-season DI in peach (Li et al., 1989), and apple (Irving and Drost, 1987). Desirable fruit quality changes may make late-season DI advantageous in certain situations. However, more information is required regarding particular species and varieties before it can be widely recommended. A late-season water deficit on apple is studied here.

2.3.3 Deficit irrigation throughout the fruit growing season.

Information on this topic is scarce in the literature. However, indications are that an entire-season water deficit would reduce economic crop yield and total biomass production as assimilate accumulation is reduced under water stress conditions (Hsiao, 1993). As an example, Kilili et al. (1996) showed reduced fruit weight from apple trees exposed to an entire-season DI. An entire-season DI may also advance fruit maturity in apple by encouraging an earlier climacteric rise in ethylene, yellower background colour and increased TSS (Kilili et al., 1996). Deficit irrigation throughout the season is evaluated in this study.

2.3.4 Postharvest deficit irrigation.

In most deciduous fruit crops, especially early maturing varieties, a significant amount of tree growth occurs during autumn. Water deficit at this time has been shown to reduce the pruning requirements of peach, while increasing flower density the following season. Unfortunately it also increased the occurrence of double fruits (Johnson et al., 1992). Postharvest water deficit reduces radial trunk growth more than shoot growth, as shoot growth is predominant during spring. Wilson and Jones (1980)

induced a postharvest water deficit on blackcurrent bushes and observed a reduction in flower buds and fruit set in the following season. A postharvest water deficit may be of benefit to some species and varieties, and it may even help control tree vigour. It may also make the tree more winter hardy by reducing late season growth. However, limited information on this technique makes any conclusion difficult. Because 'Braeburn' apples are harvested late in the season with leaf fall occurring shortly after final harvest, it is not expected that a postharvest water deficit will have a significant influence on vegetative growth and, therefore, this was not studied.

2.4 Conclusion

Global water consumption has tripled in the last 40 years (Postel, 1993b) and will continue to increase as population grows. This accelerating increase in the demand for water has meant that water-limited areas, such as countries in the Middle East, now mine fossil ground water that cannot be renewed (Postel, 1993b). These global problems of water shortage need to be identified and provisions made to ensure the efficient and thoughtful use of this most precious commodity. Since irrigation uses more than 85% of total global water consumption, effective DI management has the potential to conserve water and to limit the environmental impact of irrigation by reducing leaching of nutrients and pesticides into ground water.

Numerous physiological attributes of fruit trees are modified under DI, and the periodic timing of water stress can have benefits for fruit production. Early-season DI, applied during rapid shoot growth and slow fruit growth is now an established method of irrigation management. Significant research in this area has occurred in the last 15 years. Deficit irrigation at other times of the season, however, may have some important implications for fruit quality but it is less studied at present, and thus warrants

further investigation. This thesis primarily investigates the effects of water deficit at various times of the season on 'Braeburn' apple fruit growth and quality. This allows evaluation of the possibilities for DI management in New Zealand. This research is justified in New Zealand as, although we have a humid environment, drought occurs periodically throughout the growing season in most fruit growing regions. Effective water management at these times is critical.

3 GENERAL MATERIALS AND METHODS

All experimental work reported in this thesis was conducted at either the Fruit Crops Unit or the Plant Growth Unit, Massey University, Palmerston North (latitude 40.2° S, longitude 175.4° E), New Zealand. Experimental work spanned three seasons. The apple cultivar 'Braeburn', grown on MM106 rootstock, was used in all experiments. Experiment 1, conducted during the 1992-93 summer, used five-year-old, field grown trees. Experiment 2, conducted during the 1993-94 season, was on three-year-old trees grown in polythene bags in a glasshouse. Experiment 3, also conducted during the 1993-94 season, used six-year-old trees grown in the field. Experiment 4, carried out during the 1994-95 season, employed the lysimeter facility located in the Massey University orchard which was planted with four-year-old trees. All laboratory analysis of fruit attributes was carried out using the laboratory facilities of the Plant Science Department, Massey University.

3.1 Experimental setup

3.1.1 Orchard soil

The predominant soil type within the experimental site is a Manawatu fine sandy loam (sandy, mixed, mesic-Dystric Fluventic Eutrochrept). The fine sandy loam element of this soil overlies gravelly, coarse sand of the C horizon. The depth of this distinct horizon is variable ranging from about 0.6 m to 1.0 m from the surface. This layering acts to impede drainage during times when the profile is unsaturated. However, upon saturation water drains freely through this layer interface as the soil water potential at the interface approaches zero (Clothier et al., 1977).

3.1.2 Experiment 1 (1992-93)

Five-year-old, field grown trees, trained as central leader, were used in this study.

Trees were spaced 2.5 m within rows and 5 m between. A total of 24 trees were assigned in pairs to treatments in a completely randomized design. A pair of trees was designated as a plot with 12 plots being used in total. There were two treatments: irrigated trees (C1) (six plots) receiving adequate irrigation to maintain the soil at field capacity and non-irrigated (D1) (six plots) that received no irrigation throughout the season. The abbreviation D1 has been used for the non-irrigated trees of Experiment 1 for consistency of abbreviation between experiments. Black polythene covers were installed under all trees at 14 days after full bloom (DAFB) to exclude rainfall. Three trees were removed from the analysis of Experiment 1 for the following reasons. One tree was infected with phytophthora root rot and performed poorly. The scion of another was overgrown by the rootstock and therefore the tree was not 'Braeburn'. The third was a non-irrigated tree positioned at the junction of two plastic covers. Rainfall leaking under the covers at this point prevented water deficit from developing in this tree. All other cultural practices in the experimental block were the same as for commercial orchards.

3.1.3 Experiment 2 (1993-94)

Three-year-old trees growing in 60-litre black polythene bags were placed in a naturally-lit glasshouse on 10 November 1993 (24 DAFB). A glasshouse was used for this experiment to minimise the adverse effects that frequently changing weather might have on plant water relations. Following placement in the glasshouse a rigorous spray program was established to control mites, powdery mildew, and aphids. Trees were approximately 2 m tall with some trees requiring additional support which was provided by attaching a piece of twine to support wires running the length of the glasshouse 3 m above the floor to the top of the tree. Once final fruit set was determined (30 DAFB),

fruit number per tree was reduced to 20. The mean glasshouse temperature during the experiment was 22.2°C. Potential evaporation, calculated from meteorological data using the Penman equation (Jones, 1983, p. 92), averaged 2.5 mm day⁻¹. The root medium was a 1:1:1 mix of sand, fine bark (particle size < 0.5 mm) and peat with a bag capacity of approximately 24 litres of water in 60 litres of media. Bag capacity, as referred to for Experiment 2 is defined as the water content maintained within the bag once drainage had ceased. The concentrations (g m⁻³) of nutrients added to the potting mix were : Mg, 110; Ca, 244; P, 42.4; S, 36.55; N, 110; Fe, 4.3; Mn, 0.625; Zn, 0.25; Cu, 0.125; Mo, 0.0125; and K, 46.4. A total of 52 experimental trees were assigned to treatments in a completely randomised design with 21, 18 and 13 trees assigned to control (C2), entire-season deficit (D2), and late-season deficit (LD2) treatments respectively. The treatments were as follows: C2 receiving daily irrigation to initiate drainage from the bag; D2 which was deficit irrigated every second day from 55 to 183 DAFB (final harvest), and LD2 which was irrigated as C2 until 105 DAFB. Then irrigation was reduced to levels of D2 through until 183 DAFB. Deficit irrigation was not induced until 55 DAFB to avoid plant water stress during the cell division phase of fruit growth (Pavel and DeJong, 1995). More trees were assigned to C2 and D2 treatments than to LD2, as the experimental period of the C2 and D2 trees was longer than the duration of LD2 and more samples were to be taken from the C2 and D2 treatments. The C2 plants received 4 litres of water per plant per day, the D2 and LD2 plants received between 1.5 and 4 litres per plant every second day throughout their treatment period. Preliminary soil water determinations gave the estimated daily plant water use. Regular measurements of volumetric water content (θ) and Ψ_1 allowed modification of irrigation levels for deficit irrigated trees. The total irrigation (litres per

tree) given to each treatment was approximately 512 for C2, between 96 and 256 for D2 and between 258 and 356 for LD2.

3.1.4 Experiment 3 (1993-94)

This field experiment was conducted in conjunction with the glasshouse experiment to evaluate whether the changes in fruit attributes observed under deficit irrigation are maintained throughout storage, as well as to compare changes in fruit composition during storage between treatments. Six-year-old trees were used, spaced at 2.2 m within rows and 4.5 m between rows and trained as central leader. Nine trees were randomly assigned to one of three treatments. The first treatment received no irrigation (D3), or rainfall, from 105 DAFB until final harvest at 192 DAFB. The non-irrigated trees were given the abbreviation D3 for consistency of abbreviations between experiments. Rainfall was excluded from the rootzone of these trees by installing 5 m \times 4 m plastic covers around the base of these trees. The second treatment was sprinkler-irrigated (C3) whenever commercial trees within the same block were irrigated. However, rainfall was also excluded from the rootzone of these trees by plastic covers. The third treatment was not covered (NC3) and received both rainfall and irrigation. Total irrigation supplied to C3 and NC3 from 105 DAFB until harvest was approximately 198 mm per tree. Total rainfall during this time was 133 mm. Similarity in the Ψ_1 between C3 and NC3 (Fig. 2) justified the combining of these two treatments. This is referred to as C3 in all subsequent discussions.

3.1.5 Experiment 4 (1994-95)

Twelve four-year-old trees, designated as controls during Experiment 2, were planted in the twelve-cylinder outdoor lysimeter facility during July 1994. The individual steel lysimeter cylinders were 1.2 m deep and 1 m in diameter. Each cylinder

was surrounded by a concrete sleeve giving a 1.2 m tree spacing within the row. The bottom 0.15 m of each cylinder was filled with sand, the bottom of the cylinder being conical in shape to provide easy drainage to a central discharge point. Eight of the cylinders were packed with Manawatu fine sandy loam excavated from the B horizon of the surrounding orchard. The remaining four cylinders were packed with 0.4 m of gravelly coarse sand excavated from the C horizon of the surrounding orchard soil. The B horizon was then placed on top. Trees were trained as central leaders with central support wires installed to give additional support. Trees were pruned at the time of planting according to commercial winter pruning practices for apples. A commercial pesticide spray program was used from planting. As for Experiment 2, treatments were not initiated until 55 DAFB to ensure that the cell division phase of fruit growth was complete. Full bloom occurred on 20 October 1994. Once final fruit set was determined, fruit number per tree was reduced to 40. Although 40 fruit per tree is a high crop load for these small trees (approximately 2 m tall), this fruit number was required as fruit quality and fruit water relations assessments is an important aspect of this thesis. Three treatments were assigned randomly, with four trees designated to each treatment: they were control (C4) which received irrigation that maintained soil moisture within the lysimeter cylinder at or close to pot capacity; ED4 trees which were deficit irrigated from 55 DAFB until 100 DAFB when irrigation was increased to levels equivalent to C4; and LD4 trees which were deficit irrigated from 105 DAFB until final harvest at 177 DAFB. Pot capacity, as referred to here, indicates irrigation to drainage each day. Irrigation amounts applied to each C4 tree approximated 4 litres per day. For ED4 and LD4, θ was reduced by as much as 50% compared to C4 trees. Fertigation, using a modified Hoagland's solution, was supplied to each tree via a closed nutrient-

irrigation system fed from two 9100-litre tanks. The nutrient concentration of the solution was (mg litre⁻¹): N, 105; P, 31; K, 68.4; Ca, 125; Mg, 48.6; S, 98; Fe, 3.0; Cl, 26.6; B, 0.5; Mn, 0.5; Zn, 0.05; Cu, 0.02; and Mo, 0.05. The pH of the solution was adjusted to 6.5 by adding sulphuric acid. The solution was pumped, filtered and divided into three lines. Each line was controlled by a solenoid (model M886N24D, Bermad, Israel) which was independently operated and supplied nutrient solution to four individual lysimeters each containing one tree. The nutrient solution was applied to the surface of the soil in each lysimeter via four pressure-compensating trickle emitters (Netafim, Israel). Each emitter was rated at 2 litres /h. However, calibration of individual emitters indicated some variability. The emitters were placed in a circle approximately 0.3 m from the trunk of the tree in an attempt to provide a uniform water distribution across the rootzone. Each individual lysimeter was covered with white reflective plastic covers to exclude rainfall from the rootzone.

3.2 Determination of soil water content

Soil volumetric water content was determined in experiments 1, 2, and 4 using Time Domain Reflectometry (TDR) equipment (model 1502C, Tektronix, Redmond, Ore., USA). The TDR system, and its application in irrigation scheduling, is relatively new. These techniques have been developed over the last 10 to 15 years (Zegelin et al., 1992). The TDR system involves the measurement of the propagation velocity of electromagnetic waves with the dielectric constant of the soil depending on various soil properties, but predominantly soil water content (Werkhoven, 1993). A detailed discussion on the theory of TDR technique and its use in soil moisture determinations is outlined in White and Zegelin (1995). The TDR probes differed in length between experiments. Two-pronged, 1 m and 0.5 m probes were used in Experiment 1. Three-

pronged, 0.4 m, probes used in Experiment 2 and two-pronged, 1 m, probes used in Experiment 4. No TDR measurements were made in Experiment 3. The more accurate three-pronged system was developed during 1993, and was therefore only available for use in the 1993-94 season. However, a shortage of the three-pronged 1 m probes made this system unavailable for the 1994-95 season. In Experiment 1, TDR probes were installed in each plot with 5 sets of 1 m probes and five sets of 0.5 m probes installed within each plot. The sets of TDR probes were placed on either side of both trees at 1m from the base of the trunk towards the grassed access way. This gave 4 sets of 1 m rods and 4 sets of 0.5 m rods. Another two sets, one set of 1 m and one set of 0.5 m, were installed between the two trees of the plot, i.e. within the row. In Experiment 2, one three-pronged TDR probe was installed in each bag with the probe being inserted from the top of the bag approximately 0.2 m from the base of the trunk. It was on such an angle as to penetrate the root mass of these trees. The TDR probes used in Experiment 4 were installed at about 0.2 m from the base of the trees with two sets of probes installed in water deficit trees during the stress period and one set of probes installed in the C4 trees.

3.3 Meteorological data

Meteorological data for experiments 1, 3 and 4 were obtained from a weather station located approximately 1 km from the experimental sites. Meteorological data for Experiment 2 that was conducted in the glasshouse were collected using a Campbell CR10 datalogger (Campbell Scientific Inc., Logan, UT, USA). Radiation (380 - 1500 nm) (Li-Cor short wave radiation sensor, Lincoln, Neb., USA), air temperature, humidity (model CR207 temperature and humidity sensor, Campbell Scientific Inc., Logan, UT, USA) and root medium temperature (model LM35, National Semiconductor Corporation,

Santa Clara, CA., USA) were recorded.

3.4 Evaluation of plant parameters

3.4.1 Plant water status

The Ψ_1 was measured frequently throughout all experiments using a Scholander pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA, USA). Leaves were picked from the tree and immediately placed into a small plastic bag while they were transported to the pressure chamber. The time from leaf removal until placement in the pressure chamber was approximately 30 s. The pressure chamber was lined with a moist paper towel to reduce water loss from the sample during measurement. Measurements were generally made at solar noon (midday Ψ_1) on the youngest fully expanded leaves, growing on current season's wood and in full sun at the time of measurement. The diurnal sequence of Ψ_1 was also evaluated at fortnightly intervals in experiments 2 and 4.

3.4.2 Photosynthesis and stomatal conductance

These parameters were evaluated using a portable photosynthesis system (model 6200, Li-Cor, Lincoln, Neb., USA). The selection criteria for leaves used for these measurements was as above for Ψ_1 determination. These were generally measured at midday. However, for Experiment 2 a diurnal sequence of these measurements was also made at fortnightly intervals during the season. Dark respiration rate was measured at three times during the LD2 and D2 stress period of Experiment 2. Leaves used for respiration measurements were the youngest mature leaves on the current season's wood. Respiration measurements were made between 10 pm and 11 pm. Sunset occurred at approximately 8 pm on the days when respiration measurements were made.

3.4.3 Determination of tree size and growth

Trunk circumference measurements were taken at the beginning and end of experiments 1 and 2. Weekly measurements of trunk diameter were made during Experiment 4. The measurement was always made above the graft union at a clearly marked position on the trunk. Increases in trunk circumference or diameter were then calculated for the season.

Leaf area was determined for experiments 1, 2 and 4. In Experiment 1 all leaves were removed from each experimental tree following final fruit harvest. Total leaf area per tree was then measured using an area meter (model LI 3100; Li-Cor, Lincoln, Neb., USA). In Experiments 2 and 4 leaf area was estimated by removing every tenth leaf from each tree. The leaf area of this fraction was then measured with the area meter, and the total leaf area per tree subsequently inferred.

Shoot growth was measured weekly on two labelled shoots per tree in Experiments 1, 2 and 4. Non-destructive fruit diameter measurements were also made weekly using digital callipers (Mitutoyo, Japan) on two fruit per tree in Experiments 1 and 2, four fruit per tree were measured in Experiment 4.

Total root length of 18 trees harvested from Experiment 2 at 184 DAFB were estimated using a Comair root length scanner (Commonwealth Aircraft Corp. Ltd., Melbourne, Australia). All roots were removed from the pot and potting mix washed away with a high pressure hose. Once washed, the roots were cut into small sections and floated in water covering a grid of equally sized squares. The water was used to suspend the roots and allow an even distribution of the roots over the grid. It was then drained. The squares of the grid were then used to collect a 10% subsample of the total roots per tree. The subsampled roots were then measured and total root length

subsequently estimated

3.4.4 Evaluation of return bloom

Return bloom was evaluated in Experiments 1 and 4. In Experiment 1 two branches per tree of similar size were selected during full bloom and all flowers counted. The circumference of the base of each branch was also measured and return bloom calculated using branch circumference as the covariate. In Experiment 4 all flowers per tree were counted at full bloom and return bloom evaluated using trunk circumference as the covariate.

3.4.5 Evaluation of $^{13}\text{CO}_2$ discrimination

Determination of $^{13}\text{CO}_2$ discrimination in leaves was carried out at the end of the ED4 and LD4 stress periods of Experiment 4. Leaves were harvested prior to rewatering of the LD4 and ED4 trees. Leaves were dried at 70°C for three days, then ground to a fine powder. Carbon isotope analyses were performed at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah, Salt Lake City. The dried, ground tissue was combusted in a CHN analyser. The purified CO_2 from combustion was introduced into an isotope ratioing gas mass spectrometer (delta S, Finnigan MAT, San Jose, California) for determination of isotopic composition. Overall precision of the analysis was 0.11 per mil (‰).

3.5 Fruit harvest and quality assessment

3.5.1 Harvest protocol

For all experiments fruit was sampled throughout the season as well as at commercial maturity.

3.5.1.1 Experiment 1 Fruit samples were collected at 30-day intervals starting at 63 DAFB. Each sample included four fruit per tree, picked from all experimental

trees and selected from the middle portion of the canopy. At final harvest, 18 fruit per tree were selected, six from each of the top, middle and bottom portions of the tree. At final harvest trees were strip-picked in two stages. At stage 1 (S1), one tree per plot (12 trees total) were harvested within three days to assess the impact of water deficit on fruit maturity, based on colour and other fruit quality attributes reported in section 3.5.2. Stage 2 (S2) harvest was spread over two weeks and started ten days after S1 was complete. Trees in S2 were strip picked only when overall fruit colour on each tree indicated adequate maturity. The S2 harvest evaluation of quality attributes was on fruit of similar maturity levels assessed on the basis of colour. Despite the harvest dates for S2 trees being spread over two weeks, data for this harvest are shown as occurring on the same date for clarity of representation of figures in the subsequent discussions. Nine trees were picked at S2 due to the removal of three trees for reasons outlined in section 3.1.2.

3.5.1.2. Experiment 2 Fruit samples were taken eight times at fortnightly intervals. For the first seven sampling dates, two trees per treatment, previously assigned to specific sampling times, were strip picked and all fruit analysed. At final harvest seven trees for C2 and LD2, and four trees for D2 were sampled. The "strip-pick" sampling protocol was considered necessary to avoid any influence that declining crop load over the season might have had on the measured fruit parameters. Once trees had been strip picked they were removed from the experiment.

3.5.1.3 Experiment 3 Fruit samples were taken at five times during the season at two- to three-week intervals commencing at 130 DAFB. Five fruit per tree were sampled from the middle portion of the canopy for the first four sampling dates. At final harvest (192 DAFB) ten fruit per tree were sampled. Some fruit harvested at 192

DAFB were placed in storage at $0 \pm 0.5^{\circ}\text{C}$, and relative humidity of 93% - 95%. At four times during the 12 week storage period, ten fruit per tree were removed from storage and assessed for various fruit quality attributes as described later.

3.5.1.4 Experiment 4 Fruit samples were taken eight times during the 1994-95 season from the middle portion of the canopy starting 65 DAFB. Final harvest was at 177 DAFB. Three fruit per tree were harvested at each date. One fruit per tree was picked pre-dawn, one at midday, and one at dusk. This timing schedule for fruit picking within the sampling day was used so as to evaluate diurnal changes in fruit water potential (Ψ_{fw}) and its components. Fruit harvested at 177 DAFB, but not used in fruit quality assessment at the time of harvest, were placed in cool storage at $0 \pm 0.5^{\circ}\text{C}$ and relative humidity of 93% - 95% for 5 months. Fruit was then removed from storage and inspected for the incidence of storage disorders.

3.5.2 Fruit quality analysis

The fruit quality attributes assessed during the season, and at final harvest, included fresh weight (Mettler AE160, Greifensee, Switzerland) and total soluble solids (TSS) as measured using an automatic temperature compensating refractometer (ATC-1; Atago, Tokyo, Japan). Fruit firmness was determined in Experiment 1 using a penetrometer (Model FT327, R. Bryce, Alfonsine, Italy) mounted on a drill stand with a lever to allow application of a constant and even pressure to the fruit. Fruit colour was measured using a chroma meter (CR-200, Minolta, Osaka, Japan). Measurements of colour were made on the blush and the green sides of the fruit. Fruit dry matter content was determined for individual fruit throughout the sampling period in Experiment 4 by weighing a 5 g fruit sample from each fruit, drying the fruit sample at 70°C for two weeks, and measuring fruit sample dry weight.

Measurement of fruit water relations were taken using the Wescor hygrometer (C-52 sample chamber with HR-33T microvoltmeter, Wescor Inc., Logan, UT, USA) in Experiments 2 and 4. In Experiment 2 fruit water relations were determined at seven times throughout the season on two fruit per treatment sampled between 7 am and 8 am. Disks of fruit were taken from the outer equatorial portion of the fruit, excluding the skin, and placed within the sample chamber and left to equilibrate for one hour. The fruit water potential (Ψ_{fw}) was then determined. Fruit disks were then wrapped in clear plastic and aluminium foil and dipped into liquid air. After thawing fruit osmotic potential (Ψ_{fs}) was measured with the hygrometer following one hour equilibration time. The fruit turgor potential (Ψ_{fp}) was calculated as the difference between Ψ_{fw} and Ψ_{fs} . The fruit water relations for Experiment 4 were evaluated on eight days throughout the season with at least two fruit per treatment being measured at pre-dawn, midday or dusk. The procedure was as outlined above.

Titrateable acidity was determined on composite fruit samples for Experiments 1, 2 and 3. For Experiment 4, titrateable acidity was measured on individual fruit. Titrateable acidity was measured using an automatic titrator (model DL21, Mettler, Greifensee, Switzerland). The composite fruit samples for Experiment 1 during the season comprised 5 fruit from each experimental tree. At final harvest composite samples comprised six fruit from each of the top, middle, and bottom positions of the tree. For Experiment 2, 20 fruit were harvested per tree and four composite samples each consisting of five fruit were prepared for measurement of titrateable acidity. For Experiment 3 composite fruit samples comprised five fruit. One composite sample per tree was prepared at the sampling dates prior to final harvest. Two composite samples per tree were prepared at final harvest. Fruit was prepared for titrateable acidity

determinations by first homogenizing the sample. Once homogenized, 1 g of fruit pulp was mixed with 39 ml of distilled water and then titrated with 0.1 M NaOH to an end point of 7.1. Values for titratable acidity are expressed as percent malic acid (Smith, 1985, p. 18).

Sugar concentration of fruit samples was determined by high performance liquid chromatography (HPLC) system (Waters, Milford, MA, USA) using a carbohydrate analysis column (Aminex HPX87C, Life Science Group, Hercules, CA., USA) maintained at 85°C with a de-ashing guard column. The detector (Optilab 5922 RI Chromotography Module, Tekator AB, Högnäs, Sweden) was maintained at 40°C. The flow rate was 0.6 ml min⁻¹. Composite fruit samples as described above were also prepared for sugar analysis in Experiments 1, 2 and 3. Fruit samples of 0.5 g were taken from the outer equatorial portion of each fruit, excluding the skin. Sample preparation was done according to Pesis et al. (1991). Once samples, immersed in 95% ethanol, had been stored below 0°C for more than one month and the cell components had precipitated, 1 ml aliquotes were taken and completely dried using a concentrator (model AS290 automatic speedvac, Savant Instruments Inc., Farmingdale, NY, USA). Samples were then filtered using 0.3 µm nylon membrane filters with 3 ml of Barnstead nano-pure water. Experiment 4 used individual fruits with 3 g samples taken from each fruit. Sugar concentrations were determined for the four main sugar groups in apples: fructose, sucrose, glucose, and sorbitol (Chan et al., 1972).

Fruit mineral concentrations were also determined on composite samples as above for Experiments 1, 2 and 3. Individual fruits were evaluated in Experiment 4. A 1-g flesh sample was taken from each fruit (giving 5 or 6 g fresh weight for composite samples) for Experiments 1, 2, and 3. A 5 g sample was taken from

individual fruit for Experiment 4. Samples were then dried at 70°C for 14 days. Once dried, samples were ground and a 0.1 g dry weight sample was taken and digested with concentrated nitric acid for Ca^{2+} , Mg^{2+} , and K^{+} determination. An atomic absorption spectrometer (model GBC 904AA, GBC Scientific Equipment, Dandenong, Victoria, Australia) was used for these determinations. Determinations of N and P were by Kjeldahl digestion of 0.1 g dry weight of fruit tissue.

Fruit ethylene production was determined during Experiments 1 and 2. For Experiment 1 internal ethylene was measured by extracting a gas sample from the core cavity of harvested fruit using a gas-tight syringe (model 1710N, Hamilton Ltd., Nevada, USA) inserted through the calyx of the fruit. The gas sample was extracted while the fruit was submerged in water to prevent contamination of the sample from the air. A 100- μl gas sample was injected into a Photovac portable photoionization gas chromatograph (model 10S50, Photovac, Canada). The time lapse between fruit harvest and ethylene determination was a maximum of 4 hours. Ethylene measurements were taken at four fruit harvest dates during Experiment 1.

An alternative method of gas sample collection was tried in Experiment 2 in an attempt to take ethylene samples in a non-destructive way. Modified 2.5 ml glass vials were attached over a fruit skin lenticel three days prior to ethylene measurements being taken to allow gases within the vial to equilibrate. Appendix 1 illustrates the vial attached to the fruit. Gas samples were taken from the vial using a gas-tight syringe inserted through the rubber septum into the vial cavity above the fruit lenticel. This was immediately injected into the Photovac. The vial was always positioned on the top shoulder of the fruit (Appendix 1). Gas samples were always collected between 7 am and 9 am.

3.6 Statistical analysis

All statistical analysis was performed using SAS software (SAS Institute, Cary, NC, USA).

3.6.1 Experiment 1 The statistical procedure used was analysis of variance (ANOVA) using the GLM procedure of SAS. Plant data collected during the season were analysed as a randomized design, with pairs of trees (plots) denoted as individual experimental units. Data on fruit characteristics were analysed as a split-plot design, with stage of harvest accounting for plot splits. Leaf area and trunk circumference increase were analysed using initial trunk circumference as a covariate.

3.6.2 Experiment 2 Treatment differences were determined by ANOVA using the GLM procedure of SAS as for Experiment 1. All data were analysed by sample date and pooled standard errors calculated. Leaf area was assessed periodically throughout the season on trees as they were harvested. Therefore time of leaf area measurement was used as a covariate in the leaf area analysis. Total length of first-year wood and trunk circumference increase were analysed using initial trunk circumference as a covariate. Multiple regression analysis was performed on the photosynthetic data that is presented in section 4.2. These data were standardised prior to analysis using unit length scaling (Montgomery and Peak, 1982, p. 167-173).

3.6.3 Experiment 3 Analysis was performed by ANOVA using the GLM procedure of SAS. The nine trees were arranged in a completely randomized design, individual trees being denoted as individual experimental units. Pooled standard errors were calculated.

3.6.4 Experiment 4 Analysis was performed by ANOVA using the GLM

procedure of SAS. The twelve trees were arranged in a completely randomized design, individual trees being denoted as individual experimental units. For measurements of fruit water potential and its components, variance due to time of measurement was also included in the model statement of the GLM procedure. Photosynthesis data were analysed as described for Experiment 2.

4 RESULTS AND DISCUSSION

In this chapter results from all experiments outlined in chapter 3 will be grouped according to subject and discussed in conjunction with relevant literature. This format has been chosen to avoid any repetition that may have arisen had the results been discussed individually for each experiment.

4.1 Development and maintenance of plant water deficit

Although soil water has an influence on plant water status, plants may experience a water deficit under atmospheric conditions favouring high transpiration rates even though the soil moisture in the root zone remains close to field capacity (Lakso, 1985; Hsiao, 1990). Plants may also show limited response to soil water status and maintain their water potential under varying levels of soil water due to stomatal closure (Jones et al., 1983; Zhang et al., 1987). These observations highlight the interactive nature of the plant response to soil water, and they indicate that both environmental and physiological factors are important for plant water status. Increasing evidence in recent years suggests that a reduction in soil water induces root signalling to the above ground portion of the plant, and this affects physiological responses such as stomatal closure (Schulze, 1986; Gollen et al., 1986; Jones, 1990a) which can alter plant water status through the reduction of transpiration, and may also reduce Pn rate (eg. Bunce, 1982; Flore et al., 1985; Quick et al., 1992).

In this section, data on the volumetric water content (θ) of the soil is discussed in conjunction with the plant water status which indicates the level of plant water deficit induced during this series of experiments.

4.1.1 Soil water content

As water was withheld from the rootzone θ was reduced (Fig. 1A, 1B, and 1C)

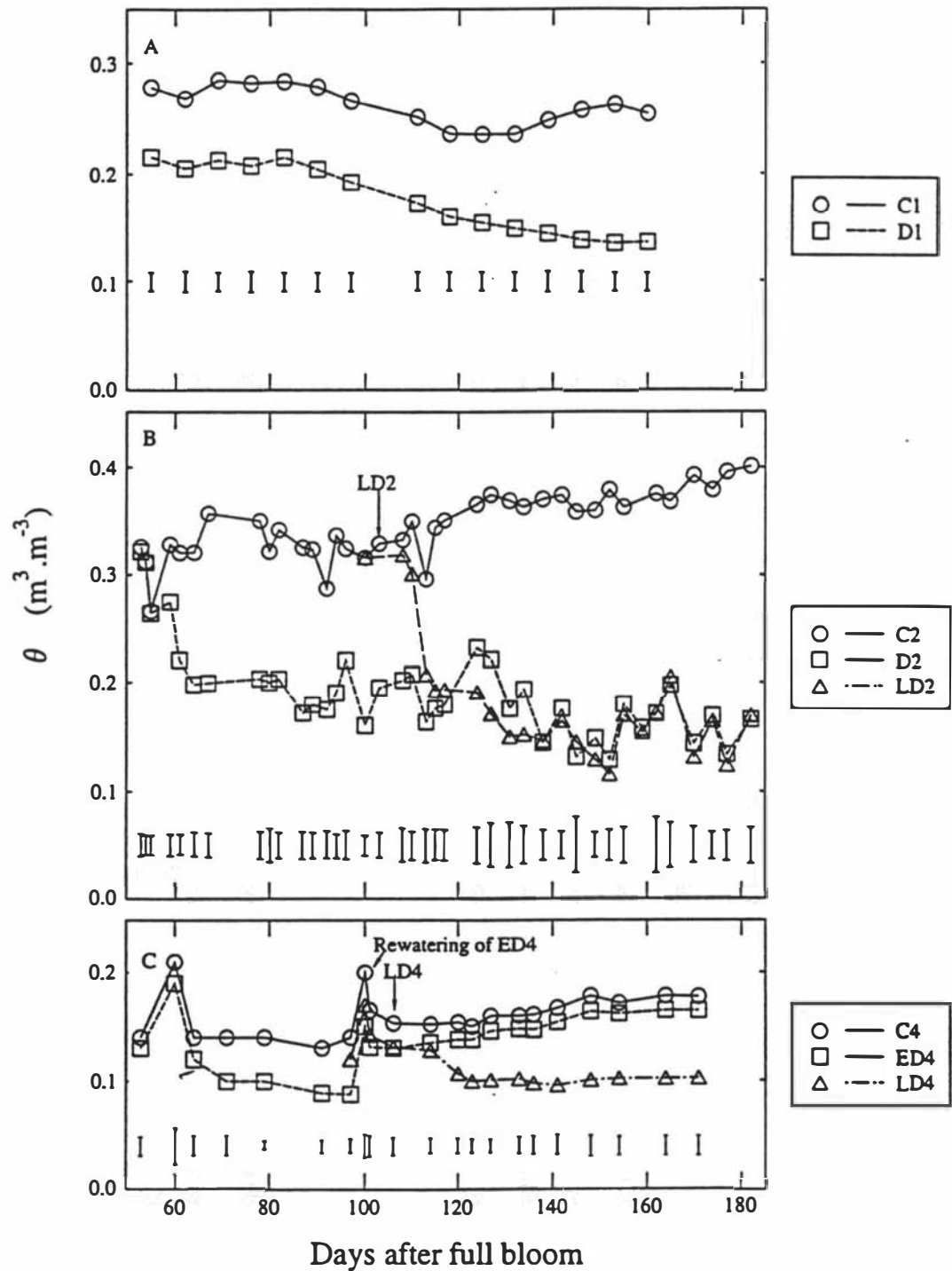


Fig. 1 Water content of root medium (θ) for Expts. 1 (A), 2 (B), and 4 (C). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21, 18 and 12 experimental units (trees) for A, B, and C respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n \geq 7); D2=deficit, Expt. 2 (n \geq 4); LD2=late deficit, Expt. 2 (n \geq 7); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

compared to controls. The θ values reported for Experiment 1 are those measured using the 1 m probes in preference to the 0.5 m probes. The longer probes integrate a larger portion of the rootzone and are, therefore, more relevant. Soil type has an important influence on water holding capacity, with sandy soils retaining less water than soils with a high clay content (Kramer and Boyer, 1995, p. 90). Thus, a sandy soil will give consistently lower values of θ when compared to a clay soil at the same water potential. Soil type also influences the amount of water available to the plant, for example, clay soils hold more water very tightly, and which is less available to the plant than a sandy soil at an equivalent θ (Kramer and Boyer, 1995, p. 89). These differences in soil type are important when interpreting TDR information, as soil type influences both the θ observed and the influence that any specific θ will have on the water supply to the plant. These differences in soil properties are illustrated in Fig. 1 by comparing the θ of the control trees between experiments. The θ surrounding the rootzone of potted, greenhouse trees is markedly higher than the θ recorded on the sandy loam predominant in the field which is, in turn higher than the θ for the lysimeter grown controls. The increased θ in the field when compared to the lysimeter on the same soil (section 3.1.5) may be due to the presence of a coarse gravel layer impeding the unsaturated drainage from the upper profile of the orchard soil (Clothier et al., 1977). Soils underlain by a coarse textured stratum, such as coarse sand or gravel store more water at field capacity. This can be explained on the basis of the relative shape of the hydraulic conductivity-pressure potential curves. A full account of this phenomenon is in Clothier et al. (1977).

A gravel layer was packed in 4 of the 12 lysimeters when this facility was set up and planted with Asian pear (Chalmers et al., 1992). Upon removal of the Asian pear trees and replacement with 3-year-old apple trees, this gravel layer, initially present in 4

lysimeter cylinders, may have been considerably disturbed resulting in the effective removal of this coarse layer which acts to impede drainage in the field. Additionally, Caspari (1993) observed that despite the presence of a well-defined gravel layer in these 4 lysimeter cylinders, the increase in their water content, compared to those without the gravel layer, was minimal and not significant at pot capacity.

The influence of θ on Ψ_1 is variable because of the influence that other environmental factors such as air humidity (Schulze, 1986; Jones 1990b), radiation and windspeed (Jones, 1990b) have on Ψ_1 . The relationship between θ and Ψ_1 is also species dependent. Xiloyannis et al. (1988) found no relationship between midday Ψ_1 and available soil water for kiwifruit, or peach, but a good correlation for olive. Regression analysis of midday Ψ_1 and θ for Experiment 2 in the greenhouse gave a significant linear relationship as follows: $\theta = 0.462 + 0.012 \times \Psi_1$ ($R^2 = 0.44$, $n = 465$, $P < 0.0001$) where θ is $\text{m}^3 \text{m}^{-3}$ and Ψ_1 is MPa. The low R^2 value indicates large variation within the data. Figure 2 illustrates a reduction in Ψ_1 in DI trees. Figure 3 indicates that although Ψ_1 is reduced in Experiments 2 and 4, and that this causes a reduction in transpiration (T), T still continues even at low Ψ_1 (Fig. 2). A reduction in Ψ_1 therefore does accompany a reduction in θ . Although soil water determinations alone may not provide accurate information on plant water status, the significant relationship between θ and Ψ_1 in apples suggests in this case that the former is indicative of the latter.

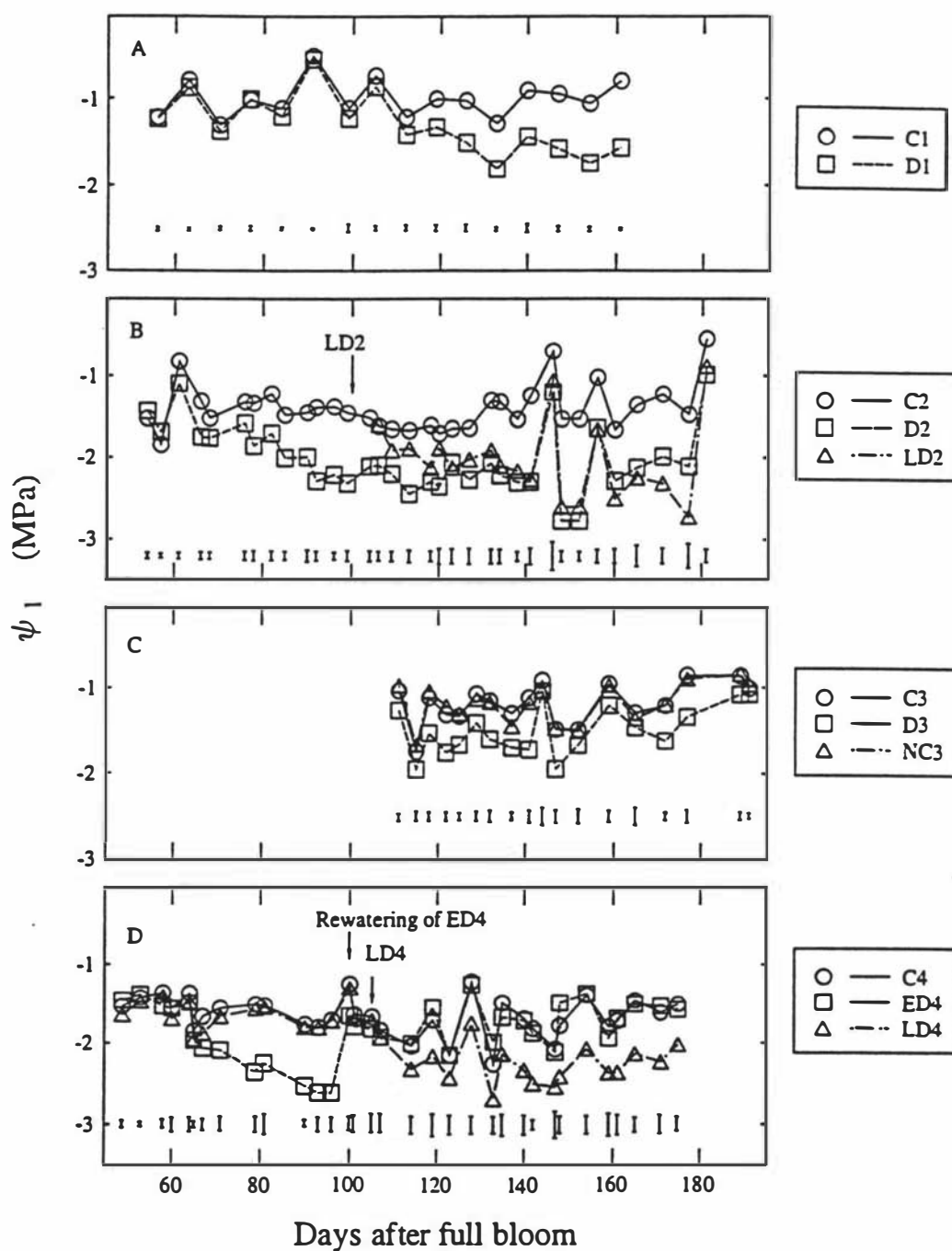


Fig. 2 Midday leaf water potential (Ψ_1) for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21, 18 and 12 experimental units (trees) for A, B, and C respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 ($n=10$); D1=deficit, Expt. 1 ($n=11$); C2=control, Expt. 2 ($n \geq 7$); D2=deficit, Expt. 2 ($n \geq 4$); LD2=late deficit, Expt. 2 ($n \geq 7$); C3=control, Expt. 3 ($n=6$); D3=deficit, Expt. 3 ($n=3$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$); and LD4=late deficit, Expt. 4 ($n=4$). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

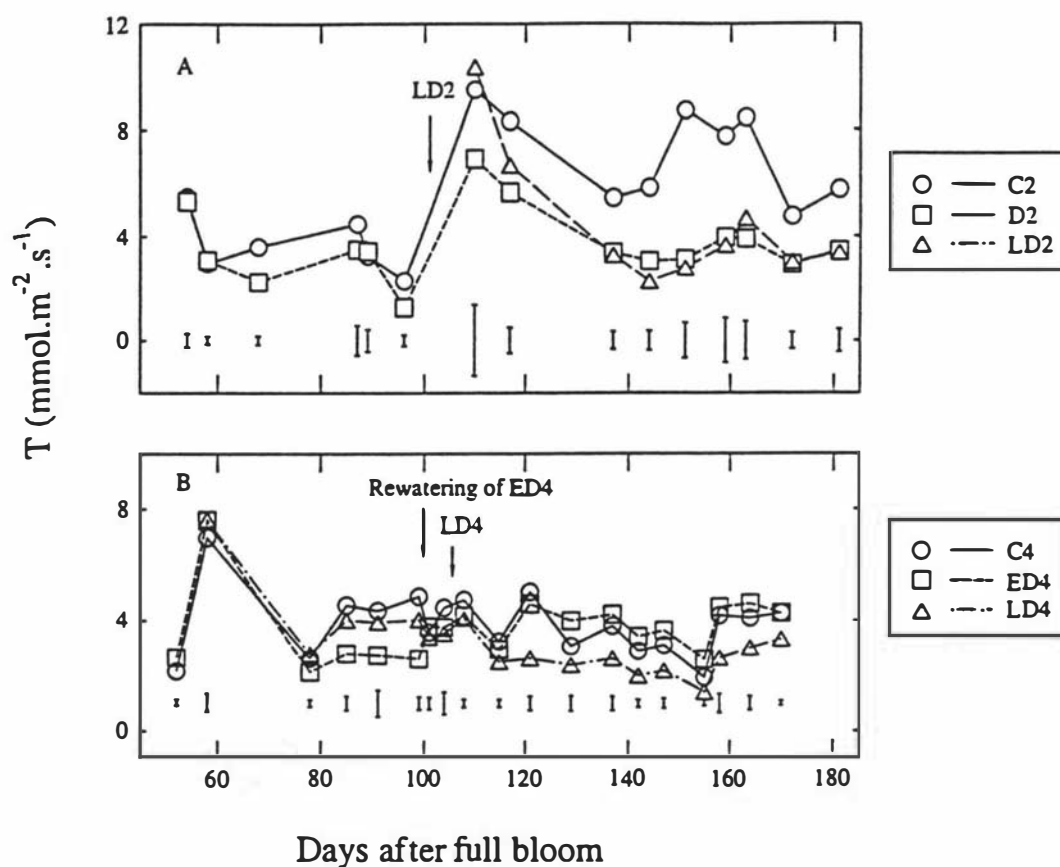


Fig. 3 Mean midday transpiration rate (T) for Expts. 2 (A), and 4 (B). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 18 and 12 experimental units (trees) for A, and B respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C2=control, Expt. 2 ($n \geq 7$); D2=deficit, Expt. 2 ($n \geq 4$); LD2=late deficit, Expt. 2 ($n \geq 7$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$); and LD4=late deficit, Expt. 4 ($n=4$). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

4.1.2 Plant water potential

Figure 2 shows midday Ψ_1 values measured using the pressure chamber throughout the season in each of the four experiments. Differences in Ψ_1 between treatments developed rapidly in Experiments 2 and 4 (Fig. 2B and 2D). However, both field experiments (Fig. 2A, and 2C) showed a more gradual decline of Ψ_1 of the stressed

treatments, and less of a difference between deficit and control treatments was established. Jones et al. (1983) observed that in droughted apple trees, reduced stomatal conductance can be effective in maintaining midday Ψ_1 at levels comparable to well-watered controls and that pre-dawn measurements may be more clearly indicative of treatment differences in plant water status. Additionally, environmental conditions are often more stable pre-dawn than those prevailing during the middle of the day (Jones, 1990a). Pre-dawn measurement of Ψ_1 is therefore often favoured. These were recorded in Experiments 2 and 4 (Fig. 4).

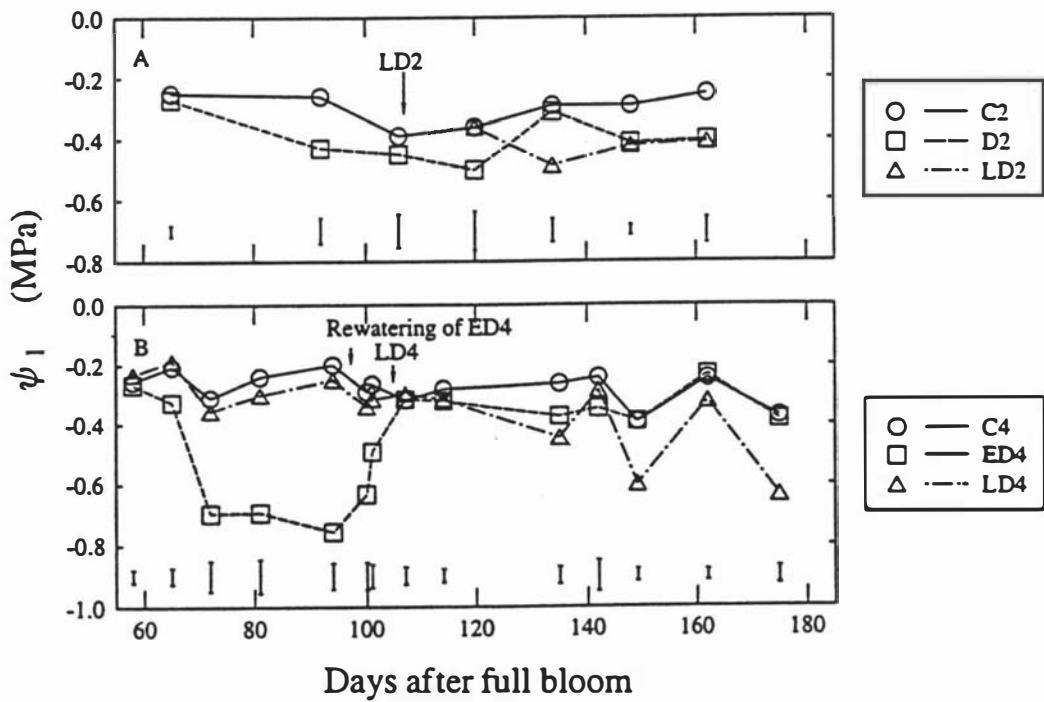


Fig. 4 Pre-dawn leaf water potential (Ψ_1) for Expts. 2 (A) and 4 (B). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 from 120 DAFB) and 12 experimental units (trees) for A and B respectively. C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=late deficit (n=2), Expt. 2; C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Differences in pre-dawn Ψ_1 between treatments were generally significant in both experiments, although these differences were smaller than those recorded at midday. Unlike for Jones et al. (1983), reduced stomatal conductance in deficit irrigated trees (Fig. 8) reduced their T (Fig. 3), but did not eliminate it. The Ψ_1 of the DI trees was therefore lower than the controls. Pre-dawn Ψ_1 are reported to provide an effective indication of soil water status (Jones et al., 1985; Xiloyannis et al., 1988). As soil moisture was not evaluated predawn, a correlation between soil water potential and predawn Ψ_1 was not attempted.

Day-to-day fluctuations in Ψ_1 reflect changes in prevailing environmental conditions (Grimes and Williams, 1990) (Fig. 2). Diurnal changes in Ψ_1 also occur with a maximum Ψ_1 being recorded pre-dawn and a minimum occurring during the middle of the day (Fig. 5). Diurnal measurements of Ψ_1 made during three days of Experiment 2 are presented in Figure 5. Minimum Ψ_1 for the stressed plants for the three days generally follows VPD. Interesting to note is that minimum Ψ_1 for C2 trees do not show any difference in time or value recorded on these three days, whereas the stressed plants show differences in both time and minimum value of Ψ_1 between days of measurement. Predawn values of Ψ_1 in the D2 and LD2 trees are only marginally reduced compared to C2 trees and the recovery of Ψ_1 during the evening was slower in these treatments compared to C2. Measurements of pre-dawn, midday and dusk Ψ_1 were also made for Experiment 4 (Fig. 6). Analysis of variance (ANOVA) of these data indicate a significant reduction in ED4 and LD4 Ψ_1 compared to controls during their respective stress periods. A slower recovery of Ψ_1 in the ED4 and LD4 trees during the evening is also illustrated.

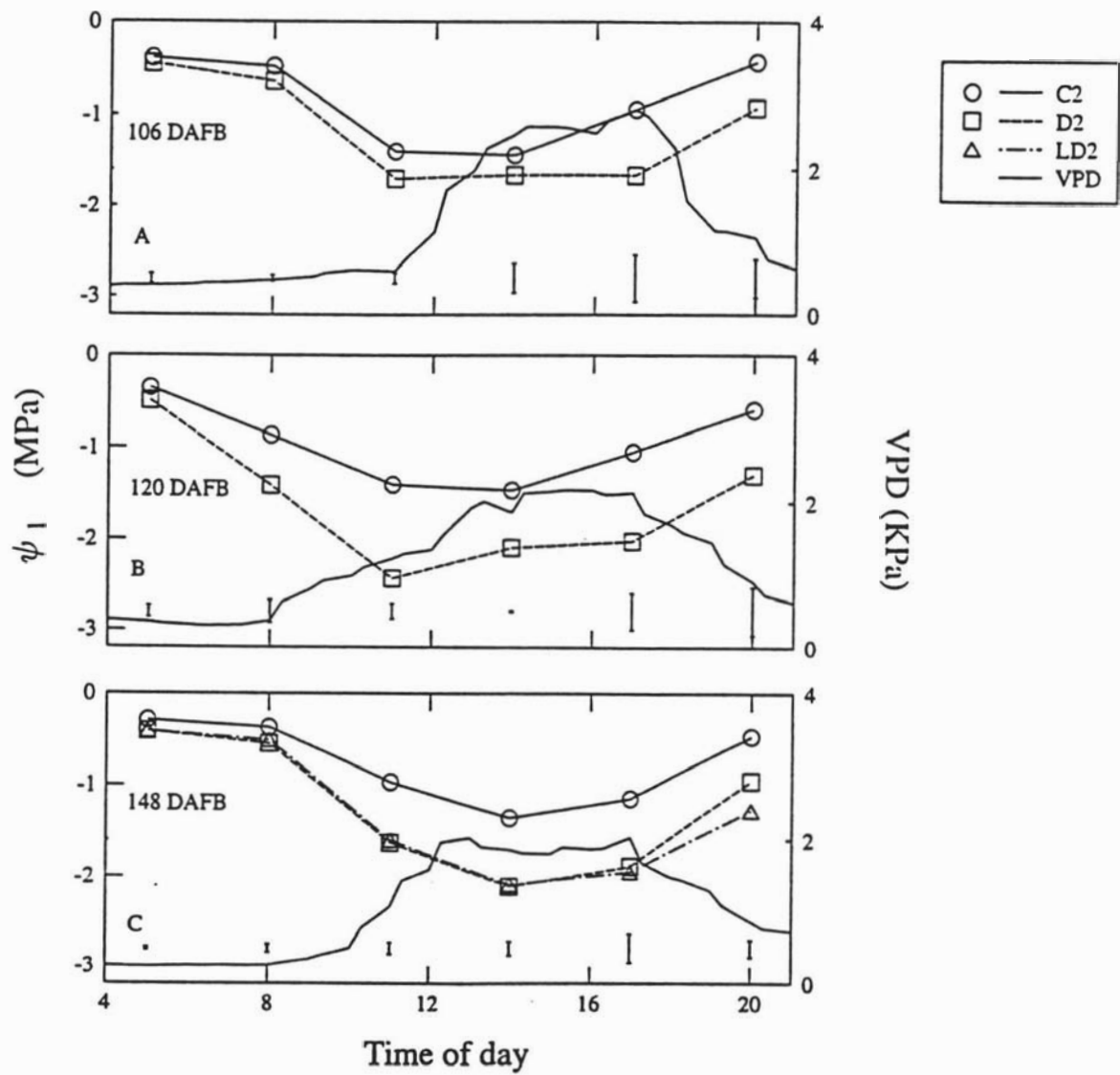


Fig. 5 Diurnal leaf water potential (Ψ_l) and vapour pressure deficit (VPD) within the glasshouse at 106, 120 and 148 days after full bloom during Expt. 2. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 at 148 DAFB) experimental units (trees). Abbreviations are C2=control (n=2); D2=deficit (n=2); LD2=late deficit (n=2).

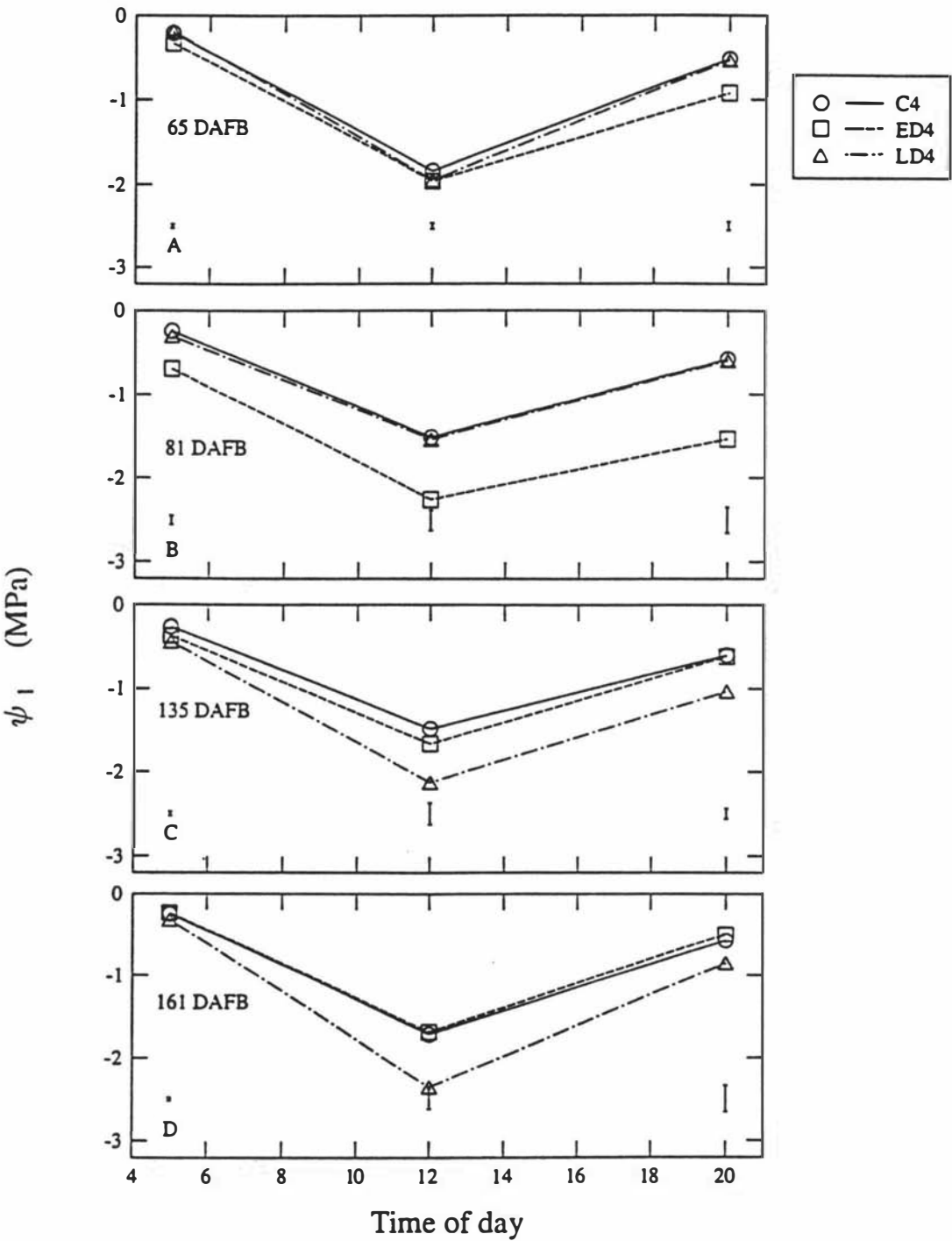


Fig. 6 Diurnal leaf water potential (Ψ_l) at 61, 81, 135 and 161 days after full bloom during Expt. 4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 12 experimental units (trees). Abbreviations are C4=control (n=4); ED4=early deficit (n=4); and LD4=late deficit (n=4).

The data presented in Figures 1 to 6 are indicative of water deficit in plants under reduced irrigation, and they reinforce the suitability of the pressure chamber technique for measuring Ψ_1 . The establishment of a reduced Ψ_1 in all experiments, as θ was reduced, indicates that a water deficit was established in the stressed plants. At no time during any of the experiments were any visual indicators of water stress observed.

4.2 Carbon Assimilation under reduced plant water status

A reduction in Pn in plants under water stress has been reported by many researchers (eg. Flore and Lakso, 1989; Hsiao, 1993). In this section data on Pn and g_s differences between irrigation treatments are discussed in conjunction with the environmental data. Discrimination against $^{13}\text{CO}_2$ is evaluated and differences between treatments discussed. Diurnal changes in Pn and g_s are also reported.

4.2.1 Photosynthetic rate

Reduced plant water status caused no reduction in Pn rate of the D1 trees throughout the season in Experiment 1 (Fig. 7A). However, a reduction in Pn was observed in the water stressed treatments of Experiments 2 and 4 (Fig. 7B and 7C). The lack of reduction of Pn in the D1 field-grown trees of Experiment 1 may be due to the relatively mild water deficit that was established in these trees. As an example, Warrit and Thorpe (1977) observed that apple trees grown in the field showed no measurable reduction in Pn at a Ψ_1 of ~ 1.8 to ~ 2.0 MPa. This is an equivalent range to that observed for the D1 trees of Experiment 1 (Fig. 2A). However, g_s was reduced in Experiment 1 (Fig. 8A). A reduction in g_s without an accompanying reduction in Pn is because g_s only partly contributes to the diffusion of CO_2 into leaves for Pn. Other resistances such as mesophyll and boundary layer resistance will also contribute. A reduction in g_s does not always result in a reduction of Pn.

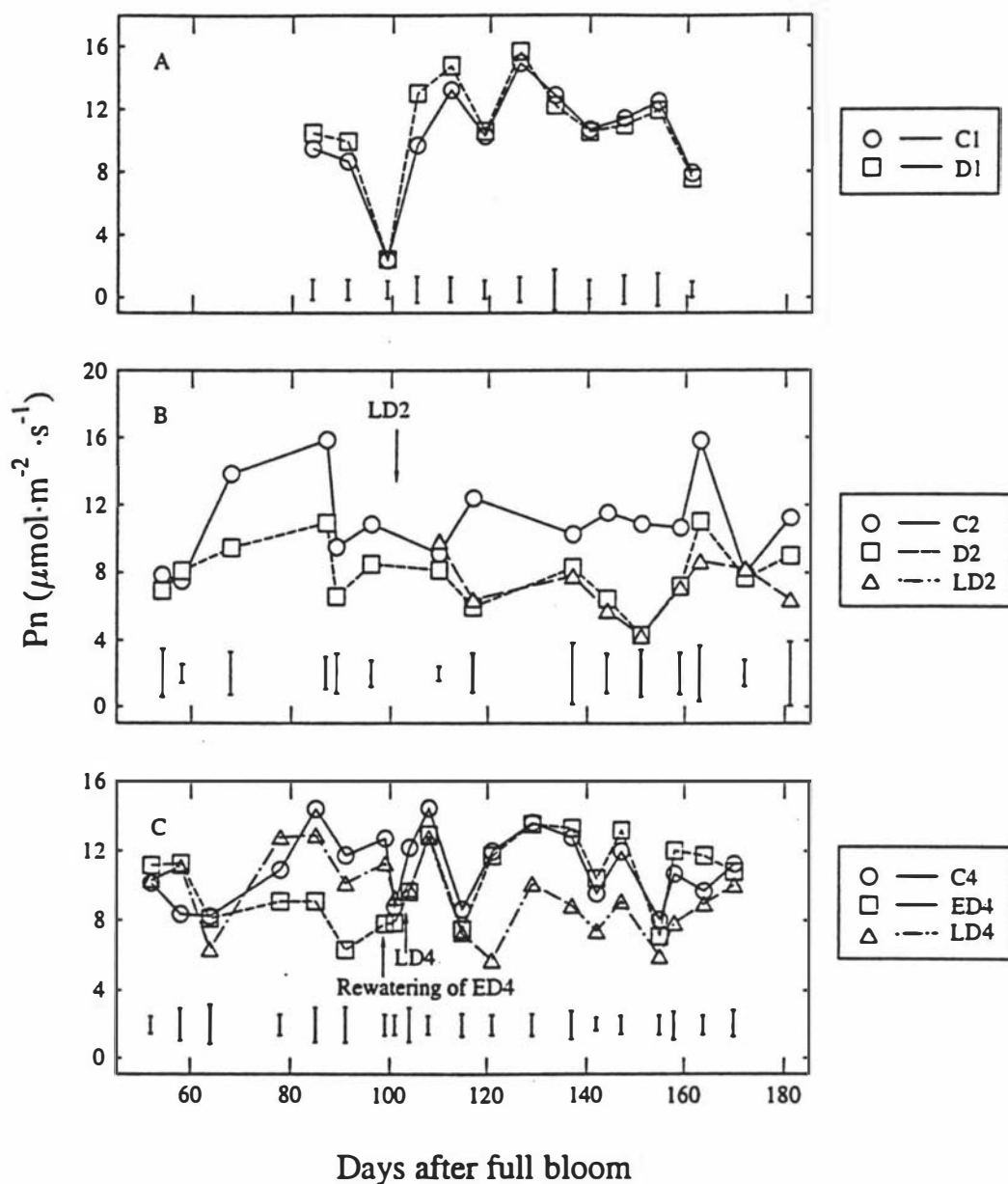


Fig. 7 Photosynthetic rate (Pn) for Expts. 1 (A), 2 (B), and 4 (C). Measurements were taken at midday. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21, 18 and 12 experimental units (trees) for A, B and C respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n≥7); D2=deficit, Expt. 2 (n≥4); LD2=late deficit, Expt. 2 (n≥7); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

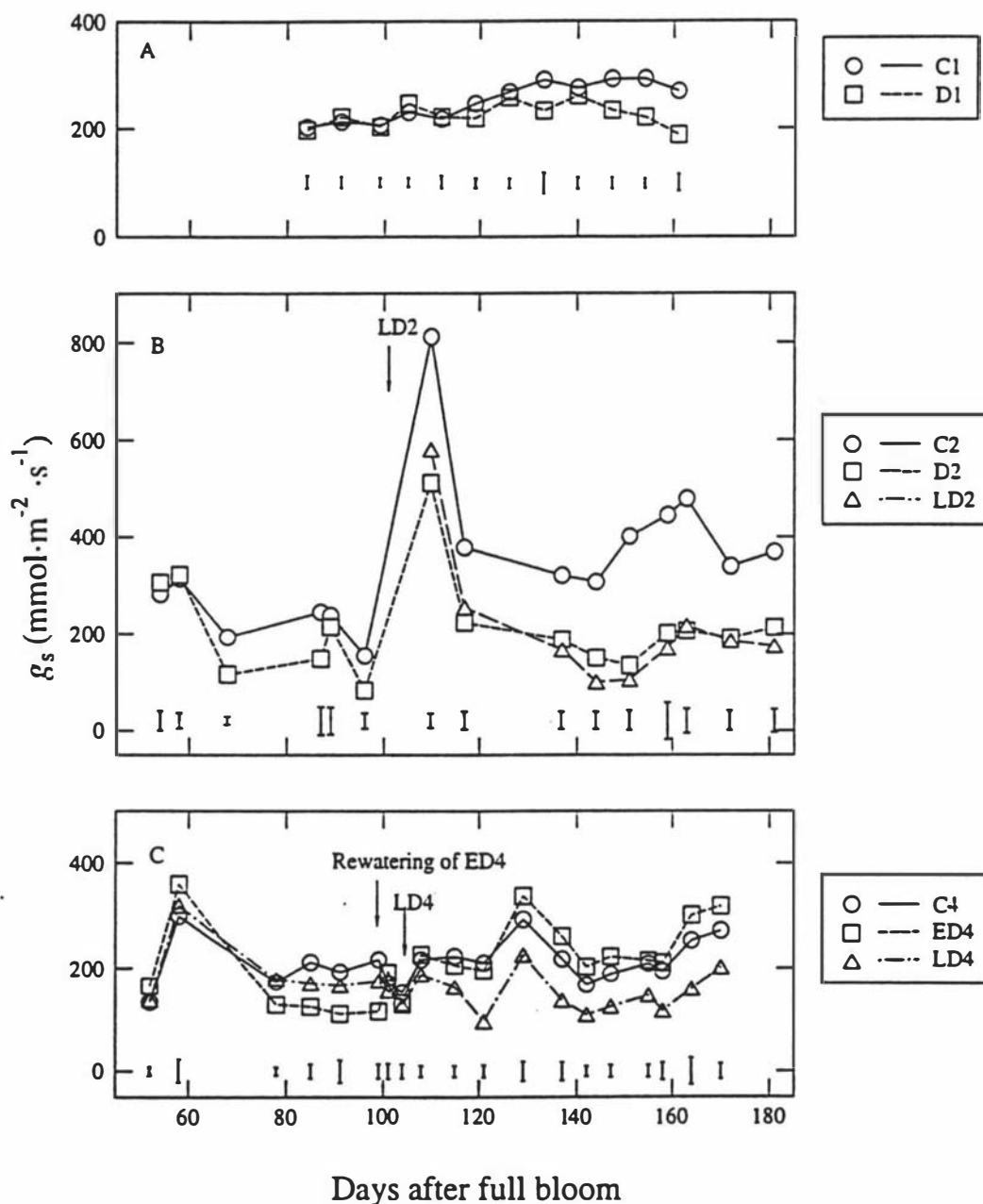


Fig. 8 Stomatal conductance (g_s) for Expts. 1 (A), 2 (B), and 4 (C). Measurements were taken at midday. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21, 18 and 12 experimental units (trees) for A, B, and C respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 ($n=10$); D1=deficit, Expt. 1 ($n=11$); C2=control, Expt. 2 ($n \geq 7$); D2=deficit, Expt. 2 ($n \geq 4$); LD2=late deficit, Expt. 2 ($n \geq 7$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$); and LD4=late deficit, Expt. 4 ($n=4$). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

A reduction in Pn did not appear sensitive to the seasonal timing of plant water deficit. In Experiment 2 the LD2 trees showed a reduction in Pn equivalent to the reduction observed in the D2 trees as plant water status was reduced. This indicates that a late season deficit reduced Pn to a level similar to that recorded in trees which had been exposed to a water deficit throughout the season (Fig. 7B). Important to note is that the reduction in Ψ_1 of both D2 and LD2 trees was similar (Fig. 2B). Additionally, the LD4 trees of Experiment 4 had reduced Pn rates which were similar to the reduction observed in the ED4 trees. The reduction in Ψ_1 was also similar between treatments. The ED4 trees also showed a recovery of Pn upon rewatering. Respiration rate tended to be lower in the D2 and LD2 trees of Experiment 2 compared to the controls. The mean value ($\mu\text{mol m}^{-2} \text{s}^{-1} \pm \text{SE}$) of the three measurement times during the LD2 stress period were 2.54 ± 0.32 , 1.70 ± 0.46 , and 1.61 ± 0.33 for C2, D2 and LD2. Reduced respiration rate in apple trees subjected to water deficit has been previously reported (Bergamini and Jones, 1988). Jones and Fanjul (1983) suggest that a reduction in apple leaf respiration during water stress is related to a similar reduction in Pn. This may be the result of the close linkage between the photosynthetic carbon reduction cycle and the photorespiratory carbon oxidation cycle and indicates that a common component such as the amount of ribulose-bis phosphate carboxylase/oxygenase enzyme is affected by water stress. Elaboration on this, however, is beyond the scope of my data.

Although differences in Pn between treatments is apparent, the correlation between Ψ_1 and Pn was weak, as has also been reported in the literature (Lakso and Seeley, 1978; Downton et al., 1987). A poor relationship is predominantly due to the numerous environmental and physiological factors which influence Pn (Jones, 1983, p. 150-157; Flore and Lakso, 1989). Multiple regression analysis was performed on

standardised data of Experiments 2 and 4. Data were standardised as the variables used for this analysis varied in magnitude, for example, P_n had values between 0 and 20 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and I_r ranged between 0 and 1500 $\mu\text{mol s}^{-1}\text{m}^{-2}$. Data standardisation and its applications are outlined in Montgomery and Peak (1982, p. 167-173). Multiple regression analysis of P_n data, including I_r , g_s , CO_2 concentration of the air, and Ψ_1 for experiments 2 and 4 indicates that under normal irrigation, I_r level generally contributes most to the standardised regression coefficient (Tables 1 and 2). However, under water deficit conditions g_s is generally the most important factor governing P_n (Table 1, and 2). In Table 1, when data collected throughout the experimental period is analysed, g_s does not significantly contribute to the P_n of ED4 trees. However, if data only collected during the ED4 stress period (55 - 100 DAFB) is analysed (Table 2) then g_s shows a significant contribution to P_n of ED4. The g_s makes no significant contribution to the R^2 of the unstressed C4 or LD4 trees during this time whereas I_r contributes significantly (Table 2). In all treatments the contribution of Ψ_1 to the model is not significant (Table 1). The level of CO_2 in the air within the Li-Cor chamber also contributes to the total R^2 in some instances. Although atmospheric CO_2 concentration should be relatively constant the CO_2 within the Li-Cor chamber varied between 350 - 390 $\mu\text{mol mol}^{-1}$ in the glasshouse and between 340 - 380 $\mu\text{mol mol}^{-1}$ in the field. These ranges of CO_2 of the air within the Li-Cor Chamber appear to have influenced the P_n of the experimental trees. Stomatal conductance appears to play a role in the P_n rate of water deficit trees. However, internal CO_2 concentration (C_i) within the leaves shows no consistent difference between treatments (Fig. 9). If stomatal closure was the main reason for reduced P_n in deficit irrigated trees, we would expect to see a reduction in C_i in these trees (Hsiao, 1993). Lack of consistent differences in C_i

treatments indicates that non-stomatal factors appear to influence Pn under water deficit. The Ψ_1 is generally the most important variable influencing g_s using multiple regression analysis which includes Ψ_1 , Ir, CO₂, and VPD (Table 3).

Table 1. The partial R² contribution and total standardised R² for multiple variable regression analysis of Pn data during Experiments 2, and 4. All data collected during experiments 2 (55 - 183 DAFB) and 4 (55 - 177 DAFB) are analysed. Abbreviations are C2=control, Expt. 2; D2=deficit, Expt. 2; LD2=late deficit, Expt. 2; C4=control, Expt. 4; ED4=early deficit, Expt. 4; LD4=late deficit, Expt. 4.

1994	C2	D2	LD2
Irradiance (Ir)	0.35 **	0.11 **	0.16 **
Conductance (g_s)	0.087 **	0.33 **	0.18 **
CO ₂ of air ^Z	0.013 ns	0.14 **	0.18 **
Water Potential	0.010 ns	0.02 ns	0 ns
Total R ²	0.46	0.61	0.52
1995	C4	ED4	LD4
Irradiance (Ir)	0.17 ns	0.38 **	0.008 ns
Conductance (g_s)	0.025 ns	0.005 ns	0.42 **
CO ₂ of air ^Z	0.26 *	0.12 *	0.02 ns
Water Potential	0.0013 ns	0.0002 ns	0.0003 ns
Total R ²	0.46	0.52	0.45

ns, *, and **, indicate no significant contribution to the model, or significance at $P < 0.1$, or $P < 0.05$.

^Z CO₂ of air within the Licor chamber

Table 2. The partial R^2 contribution and total standardised R^2 for multiple variable regression analysis of Pn data during the stress period of ED4 and prior to stress in LD4 (55 - 100 DAFB). Abbreviations C4=control, Expt. 4; ED4=early deficit, Expt. 4; LD4=late deficit, Expt. 4.

Variable	C4	ED4	LD4
Irradiance (Ir)	0.16 **	0.005 ns	0.18 **
Conductance (g_s)	0.006 ns	0.11 **	0.02 ns
CO ₂ of air ^z	0.07 **	0.0009 ns	0.025 ns
Total R^2	0.24	0.12	0.23

ns, *, and **, indicate no significant contribution to the model, or significance at $P < 0.1$, or $P < 0.05$.

^z CO₂ of air within the Licor chamber

Table 3. The partial R^2 contribution and total standardised R^2 for multiple variable regression analysis of stomatal conductance (g_s) data during Experiments 2, and 4. All data collected during Experiment 2 (55 - 183 DAFB) and Experiment 4 (55 - 177 DAFB) are analysed. Abbreviations are C2=control, Expt. 2; D2=deficit, Expt. 2; LD2=late deficit, Expt. 2; C4=control, Expt. 4; ED4=early deficit, Expt. 4; LD4=late deficit, Expt. 4.

1994	C2	D2	LD2
Water Potential (Ψ_1)	0.11 **	0.40 **	0.16 **
VPD	0.08 *	0.006 ns	0.03 ns
CO ₂ of air ^z	0.03 ns	0.01 ns	0.07 *
Irradiance (Ir)	0.02 ns	0.10 **	0.01 ns
Total R^2	0.25	0.52	0.28
1995	C4	ED4	LD4
Water Potential (Ψ_1)	0.52 **	0.03 ns	0.03 ns
VPD	0.08 ns	0.07 ns	0.74 **
CO ₂ of air ^z	0.07 ns	0.03 ns	0.024 ns
Irradiance (Ir)	0.0002 ns	0.34 **	0.07 ns
Total R^2	0.67	0.45	0.84

ns, *, and **, indicate no significant contribution to the model, or significance at $P < 0.1$, or $P < 0.05$

^z CO₂ of air within the Licor chamber

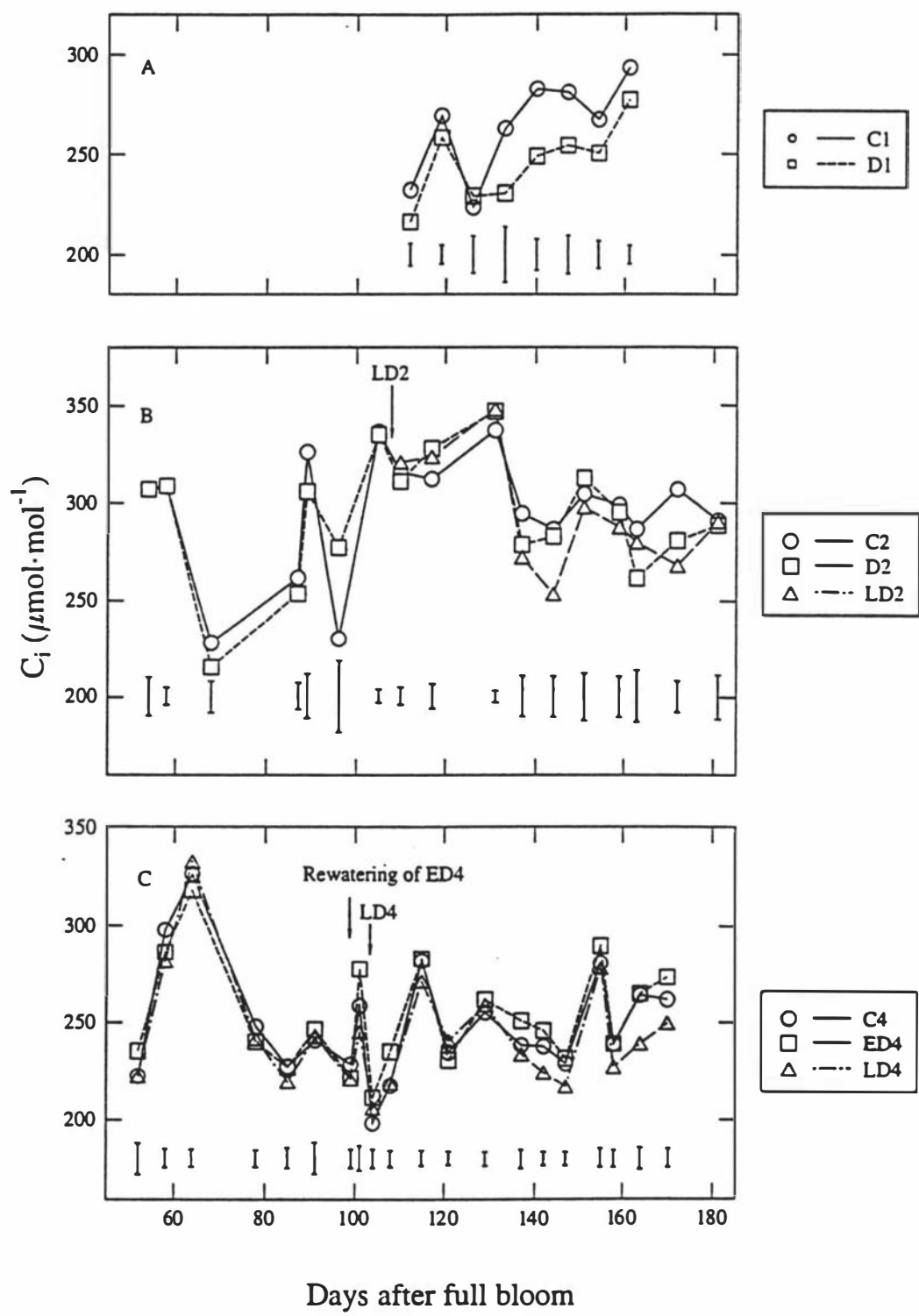


Fig. 9 Internal CO₂ (C_i) for Expts. 1 (A), 2 (B), and 4 (C). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21, 18 and 12 experimental units (trees) for A, B, and C respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n≥7); D2=deficit, Expt. 2 (n≥4); LD2=late deficit, Expt. 2 (n≥7); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

4.2.2 Stomatal conductance.

It has long been observed that Pn rate is reduced under water deficit due to reduced g_s and therefore reduced CO_2 uptake (Hsiao, 1973). However, during the last 15 years researchers have found that a reduction in g_s does not always fully account for changes in Pn under water deficit conditions (Flore and Lakso, 1989). As with Pn, differences in the response of g_s to water deficit varies between and within species depending on pre-conditioning treatments (Jones, 1983, p. 119). Quick et al. (1992) investigated four species of pot-grown plants (Lupin, eucalyptus, sunflower, and grape) in the field to determine the relative dependence of photosynthesis on g_s . They concluded that in three of the four species evaluated, g_s made a significant contribution to Pn. The exception was grape where they speculated that non-stomatal mechanisms significantly contribute to the Pn rate. The environmental factors reported to influence g_s are VPD, Ir, CO_2 concentration of the air, and air temperature (Jones, 1983, p. 117-120; Syvertsen, 1985). Figure 8 illustrates differences in g_s between treatments throughout the season for experiments 1, 2 and 4. A reduction in g_s for deficit irrigated trees was observed in all experiments. In ED4 trees the recovery of g_s was observed on the day following rewatering (Fig. 8C). This is in contrast to reports on other crops, such as peach, where full recovery of g_s did not occur until several days after rewatering (Tan and Buttery, 1982). Flore et al. (1985) also reported that three days were required for full recovery of g_s in previously water stressed apple and cherry leaves. Rodrigues et al. (1993) reported only partial recovery of g_s in grape leaves on the day following rewatering. Throughout the remaining experimental period the g_s of the ED4 trees tended to be higher than the controls.

The linear relationship between Ψ_1 and g_s , although significant, was weak.

Multiple regression analysis of data from Experiments 2 and 4 including Ψ_1 , Ir, VPD, and CO_2 regressed on g_s , showed that in 4 of the 6 treatments reported in Table 3, Ψ_1 contributed more to explanation of the regression model than any other variable. Although Ψ_1 makes a significant contribution to g_s , other factors such as VPD, Ir, and CO_2 also contribute significantly in some cases. The relative importance of the latter three environmental variables shows variation between treatments and seasons. A weak linear relationship between Ψ_1 and g_s is not surprising, due to the contributions of environmental factors outlined above. Some other authors have also found poor agreement between Ψ_1 and g_s (Warrit et al., 1980; Lakso, 1985; Rodrigues et al., 1993). Warrit et al. (1980) indicated that under normal field conditions the effect of Ψ_1 on apple stomata could often be ignored, as there was no effect until a threshold value of about -2.0 MPa was reached. Additionally, Turner (1974, p. 427) suggested that stomata have a clear threshold Ψ_1 above which they are unaffected. Below this they close rapidly. From another perspective, Gollan et al. (1986) showed that the stomatal response of sunflower and wheat leaves is more closely related to extractable soil water content than to leaf water potential. They concluded that roots, which sense that the soil is drying, send a hormonal message, probably cytokinin, to the leaves which induces stomatal closure despite the leaves being maintained near full turgor. Gollan et al. (1986) also suggest that the message may also be related to changes in nutrient uptake by the roots that occur as the soil dries out. Additionally, Düring and Dry (1995) speculated that chemical signals such as ABA are synthesised in the roots and transported to the leaves which act to induce stomatal closure. If roots osmotically adjust, this signal is suppressed and stomatal closure is reduced. Naor et al. (1995) showed good correlation of g_s with Ψ_{stem} and Ψ_{soil} but poor correlation between g_s and Ψ_{leaf} . A good

correlation with Ψ_{soil} further indicates that root signals play an important role in the control of g_s . As an example, linear regression of θ with g_s for Experiment 2 is presented. Observation of the scatter plot of θ with g_s indicated a greater variation within the data at high values of θ and g_s . To ensure homogeneity of variance a log transformation was performed on the data prior to the regression analysis. The regression equation following log transformation is as follows: $g_s = -1.92 + 2.37 \times \theta$ ($R^2 = 0.40$, $n=155$, $P < 0.0001$).

Midday values of both P_n and g_s remained relatively constant throughout the season (Figs. 7 and 8). This is in agreement with Poni et al. (1994) who stated that no reduction in the P_n of well exposed leaves of apple spurs throughout the season occurs. Daily fluctuations in both P_n and g_s are apparent and are presumably due to variation in the ambient environmental conditions at the time of measurement.

Air temperature has been reported to have an influence on both g_s and P_n (Barden, 1971; Bar-Tsur et al., 1985) with a rise in temperature increasing the rate of both P_n and g_s up to an optimum temperature. At temperatures above 35°C, P_n is reduced in apple (Barden, 1971). Although air temperature within the glasshouse was periodically above 35°C it was always below this temperature at the time of P_n measurement. The increased temperature does not seem to have consistently influenced the P_n or g_s of the glasshouse trees when compared to field grown plants (Figs. 7 and 8). However, the g_s of the C2 trees tends to be higher than the g_s of the C4 trees.

Overall a reduction in Ψ_1 is coupled with a decline in both P_n and g_s in the water stressed apple trees studied in these experiments. Multiple regression analysis highlights the numerous contributing factors influencing both P_n and g_s and illustrates the integrated nature of these data. Tardieu and Davies (1993) emphasise the fact that it is

inadequate to discuss the concept of stomatal control either based only on chemical signals (ie. via the roots) or solely on plant water relations. These influences are integrated within the plant under water deficit conditions. These data here allow discussion of water relations only as the role of other factors such as chemical signals are outside the scope of this study.

4.2.3 Diurnal patterns of P_n and g_s under water deficit

Plant P_n and g_s increased to a maximum value during the middle of the day followed by a decline towards dusk (Figs. 10 and 11).

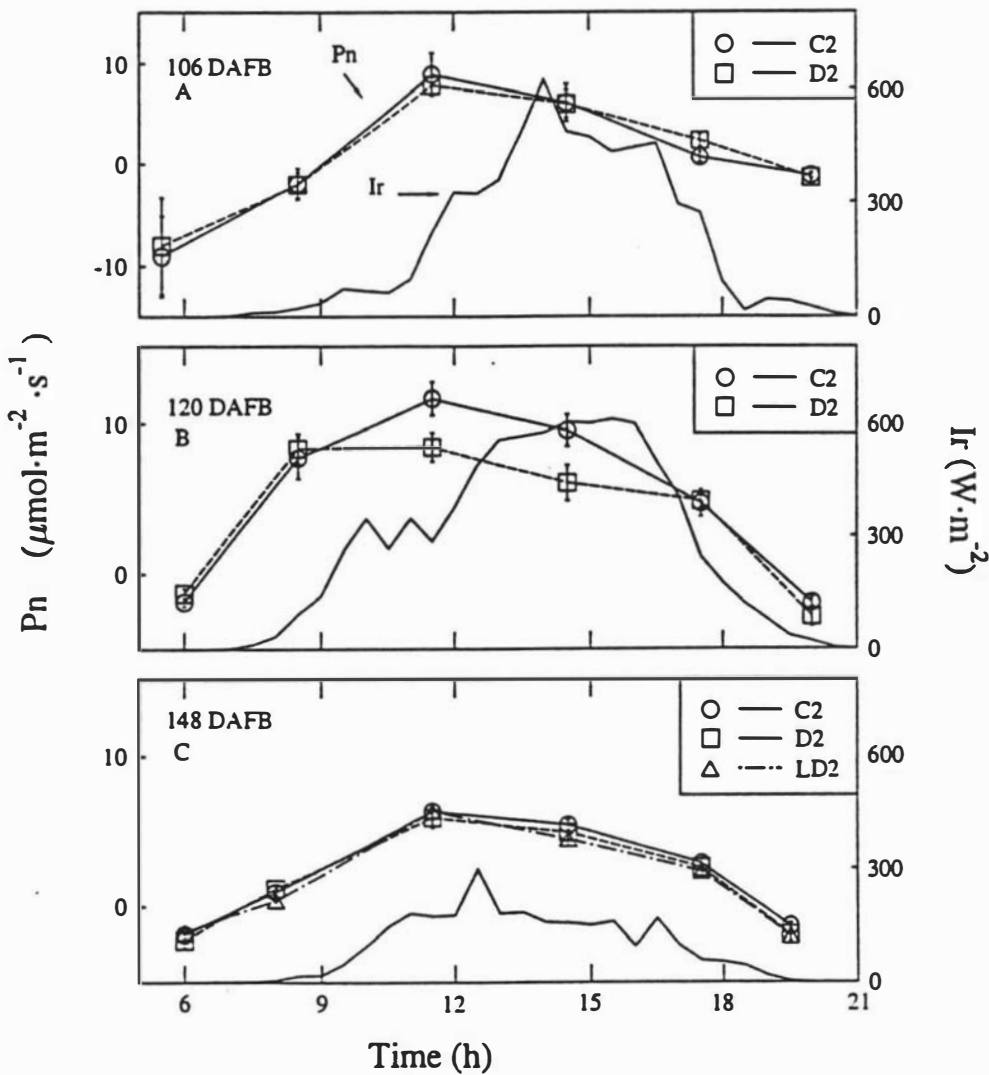


Fig. 10 Diurnal Photosynthetic rate (P_n) and irradiance (I_r) at 106, 120 and 148 day: after full bloom (DAFB) during Expt. 2. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 at 148 DAFB experimental units (trees). Abbreviations are C2=control (n=2); D2=deficit (n=2); LD2=late deficit (n=2).

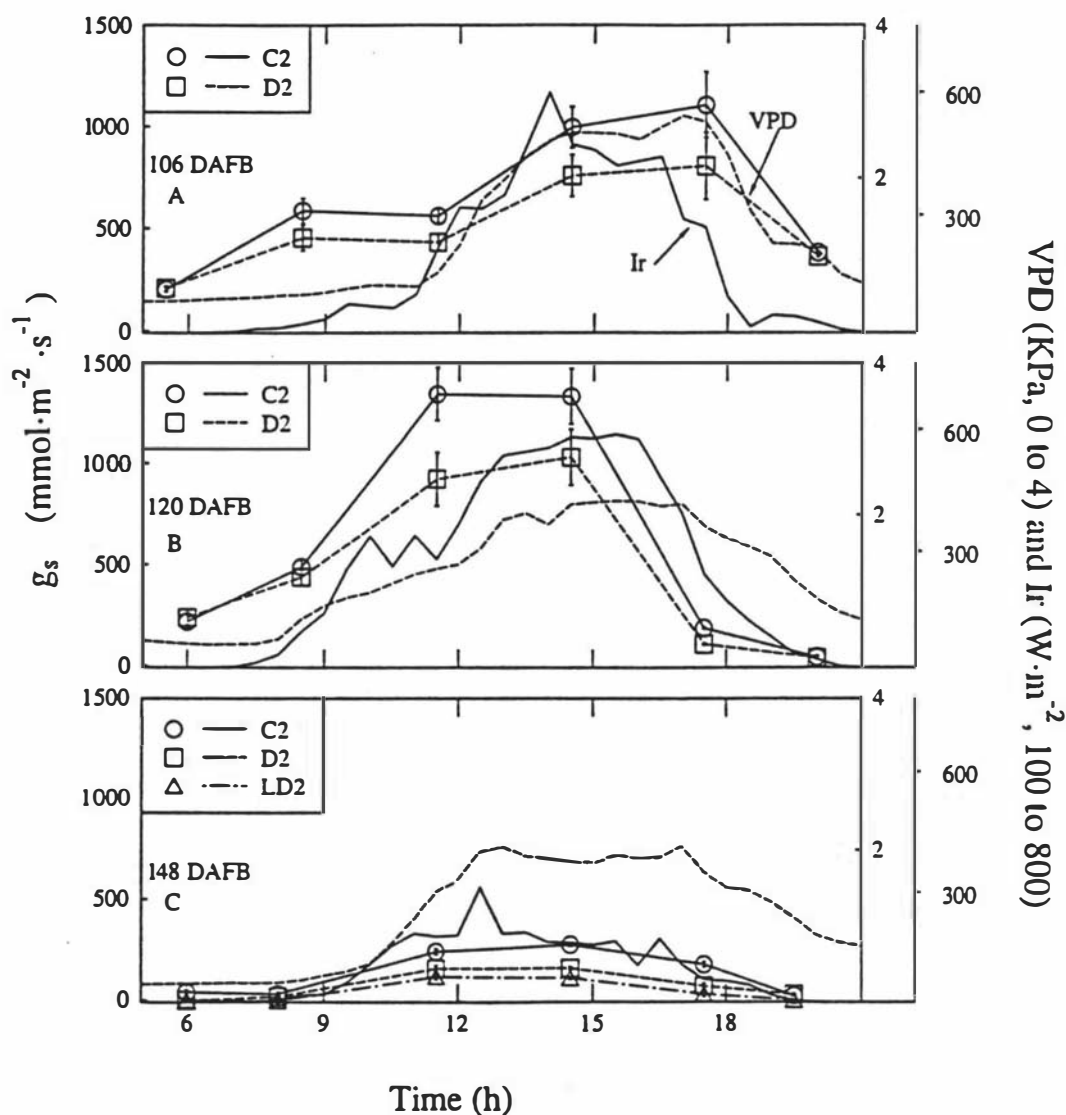


Fig. 11 Diurnal stomatal conductance (g_s) and vapour pressure deficit (VPD) at 106, 120 and 148 days after full bloom (DAFB) during Expt. 2. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 at 148 DAFB) experimental units (trees). Abbreviations are C2=control (n=2); D2=deficit (n=2); LD2=late deficit (n=2).

The similar diurnal pattern of P_n and g_s does not necessarily indicate a cause and effect relationship but rather that both of these parameters are influenced by the diurnal rhythm of environmental factors such as I_r . The fact that Ψ_1 (Figs. 5 and 6) follows an inverse trend compared to P_n and g_s throughout the day indicates that other

factors such as I_r and VPD have an overriding influence on the level of P_n and g_s . Other authors have reported similar diurnal rhythm for a diverse range of plants. For example, Caspari et al. (1993) studying well-watered Asian pears observed an increase in g_s during the day to a maximum during the middle of the day, after which time g_s either dropped or showed an initial drop followed by some recovery prior to stomatal closure during darkness. Additionally, Jones (1983, p. 121) and Lakso (1985) observed an increase in g_s in well watered apples up to midday, after which time a steady decline in g_s occurred as the afternoon progressed. Turner (1974, p. 424) also observed a steady increase in g_s during the morning and a decline during the afternoon in tobacco, maize and sorghum. In contrast, Jarvis (1976) illustrated that in well watered spruce trees g_s showed a steady decline as the day progressed. Quick et al. (1992) illustrated a steady decline in the g_s of grape leaves during the day. Downton et al. (1987) also show a steady decline in both g_s and P_n in the leaves of grape through the day with recovery commencing at 1400 hours. These differing patterns highlight the differences in diurnal stomatal response between species.

At 106 DAFB, g_s reached a maximum value late in the day and more unusually during the time of maximum VPD (Fig. 11A). The relationship between g_s and VPD is outlined by Thorpe et al. (1980) and by Jones (1983, p. 120). Both references indicate that g_s is reduced as VPD is increased. Data observed at 120 DAFB (Fig. 11B) shows a more typical response where maximum g_s occurs prior to the development of peak daily VPD. Explanation for the unusual response at 106 DAFB may be that I_r remained low during the morning (Fig. 10A). As maximum stomatal aperture of apple occurs at about 200 W m^{-2} (Jones, 1983, p. 117) a lag in stomatal opening at 106 DAFB may have been associated with low I_r values during the morning. At 148 DAFB,

Ψ_1 values were similar to those recorded at 106 and 120 DAFB (Fig. 5). However, both P_n and g_s were lower at 148 DAFB. The lower I_r values at 148 DAFB when compared to 106 and 120 DAFB may contribute to reduced P_n and g_s on this day when compared to values recorded at 106 and 120 DAFB.

Maximum g_s values recorded at 106 DAFB were lower than the maxima measured at 120 DAFB. This may be related to the higher VPD at 106 DAFB when compared to 120 DAFB. Differences between the control and deficit treatments at 106 and 120 DAFB are similar.

Caspari et al. (1994) showed that stomata close earlier in the day in Asian pear trees subjected to water deficit relative to well-watered control. This does not appear to be the case in my experiments where P_n and g_s declined in deficit irrigated and control trees at similar times of the day.

Measurements of P_n at 106 and 148 DAFB show that despite a significant reduction in g_s (Fig. 11) P_n remains unchanged between treatments throughout the day (Fig. 10). This indicates that g_s does not account for the total reduction in P_n rate under water deficit conditions, as indicated in section 4.2.1. Transpiration data were not included in the discussions above as g_s values presented are calculated from these data.

4.2.4 Discrimination against $^{13}\text{CO}_2$

A significant reduction in discrimination against $^{13}\text{CO}_2$ occurred in trees during DI in Experiment 4 as indicated by less negative values of $\delta^{13}\text{C}$ (Table 4). Values were measured prior to rewatering of the ED4 trees and also at final harvest (170 DAFB). Less negative values of $\delta^{13}\text{C}$ indicates less discrimination against $^{13}\text{CO}_2$ which in turn indicates a lower ratio of intercellular to atmospheric partial pressure of CO_2 in the leaves of water stressed trees. This may be attributed to lower g_s recorded

in the ED4 and LD4 trees during the water deficit period.

Table 4. Carbon isotope discrimination differences between deficit irrigation treatments of Experiment 4. Abbreviations are for C4=control, ED4=early deficit, upto 100 DAFB, and LD4=late deficit, from 105 upto 177 DAFB. Column values followed by different letters are significantly different at $P < 0.05$.

Treatment	$\delta^{13}\text{C}$ at 100 DAFB	$\delta^{13}\text{C}$ at 170 DAFB
C4	$-25.15 \pm 0.09^{\text{Z}}\text{a}$	$-25.96 \pm 0.09\text{a}$
ED4	$-24.50 \pm 0.09\text{b}$	$-25.96 \pm 0.09\text{a}$
LD4	Not applicable	$-25.55 \pm 0.09\text{b}$

^z Mean \pm SE of four replicates per treatment.

Water deficit therefore resulted in a reduction of both Pn and g_s and less discrimination against $^{13}\text{CO}_2$. The reduction in Pn was not solely due to g_s and other mechanisms appear to be involved. Identification of these factors is however beyond the scope of my investigation.

4.3 Vegetative growth

Deficit irrigation was initially developed as a management tool to control unwanted vegetative vigour of perennial fruit crops (Chalmers et al., 1981). If DI is to control tree growth, it must be applied during the stages of active vegetative growth. It has been successfully used to reduce shoot and trunk growth in peach (Chalmers et al., 1981), pear (Mitchell et al., 1984), Asian pear (Caspari et al., 1994) and apple (Lötter et al., 1985; Durand, 1990).

Vegetative growth, as referred to in this section, includes shoot growth, trunk growth, leaf area, and root growth. Return bloom is also included as being an aspect of growth.

4.3.1 Shoot growth

A reduction in shoot growth of trees under water deficit is generally due to the early termination of extension growth with the formation of dormant buds (Jones, 1983, p. 213; Mitchell et al., 1986; Irving and Drost, 1987). Predominantly, shoot growth in 'Gala' apples occurs between 40 - 90 DAFB (Durand, 1990), and between 0 - 105 growing season days for 'Granny Smith' (Lötter et al., 1985). Figure 12 indicates that shoot growth of 'Braeburn' apples predominantly occur between 0 - 100 DAFB. Lötter et al. (1985), Durand (1990) and Ebel et al. (1995) observed a reduction in shoot growth of apples when DI was imposed during times of active shoot growth.

Final fruit size of apple is influenced by fruit cell number (Denne, 1961; Westwood et al., 1967). Fruit cell number is determined by cell division which may be reduced under water deficit (Hsiao et al., 1976; Jones, 1983, p. 213). Therefore, water deficit during the cell division phase of fruit growth may reduce cell number and result in smaller fruit. The cell division phase of apple fruit occurs during the first 2 to 6

weeks of fruit growth depending on apple cultivar (Pavel and DeJong, 1995). For this reason water deficit was not imposed in this study until the cell division phase of fruit growth was completed. Reduced plant water status was therefore induced on both D2 (Expt. 2) and ED4 (Expt. 4) trees after 50 DAFB.

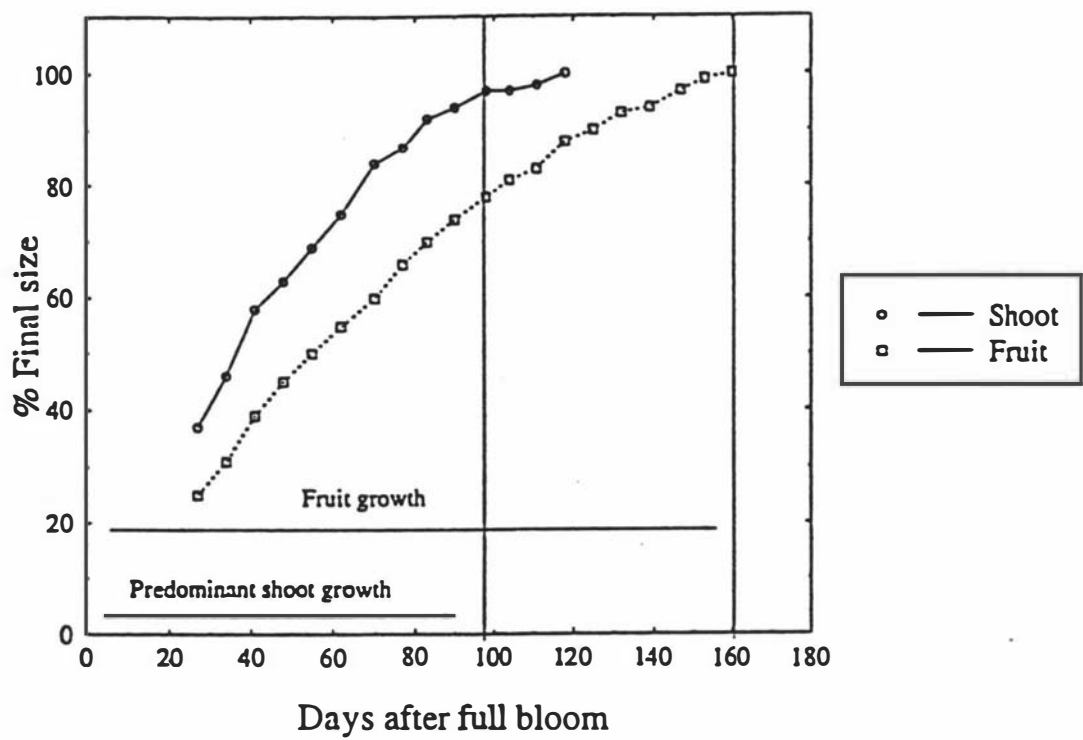


Fig. 12 Percent final fruit diameter and shoot length with days after full bloom for control trees of Expt. 1

The greenhouse experiment shown in Fig. 13B illustrates a reduction in shoot length of trees from the D2 treatment when compared to the C2 and LD2 trees. Because plant water deficit was not induced until 61 DAFB when approximately 65 % of total shoot growth had already been completed, the impact of deficit irrigation on shoot extension growth was minimal. Similarly, in Experiment 4 (Fig. 13C), approximately 75% of shoot growth had occurred prior to the development of water

deficit in these trees meaning the influence of water deficit on vegetative growth was not significant between treatments.

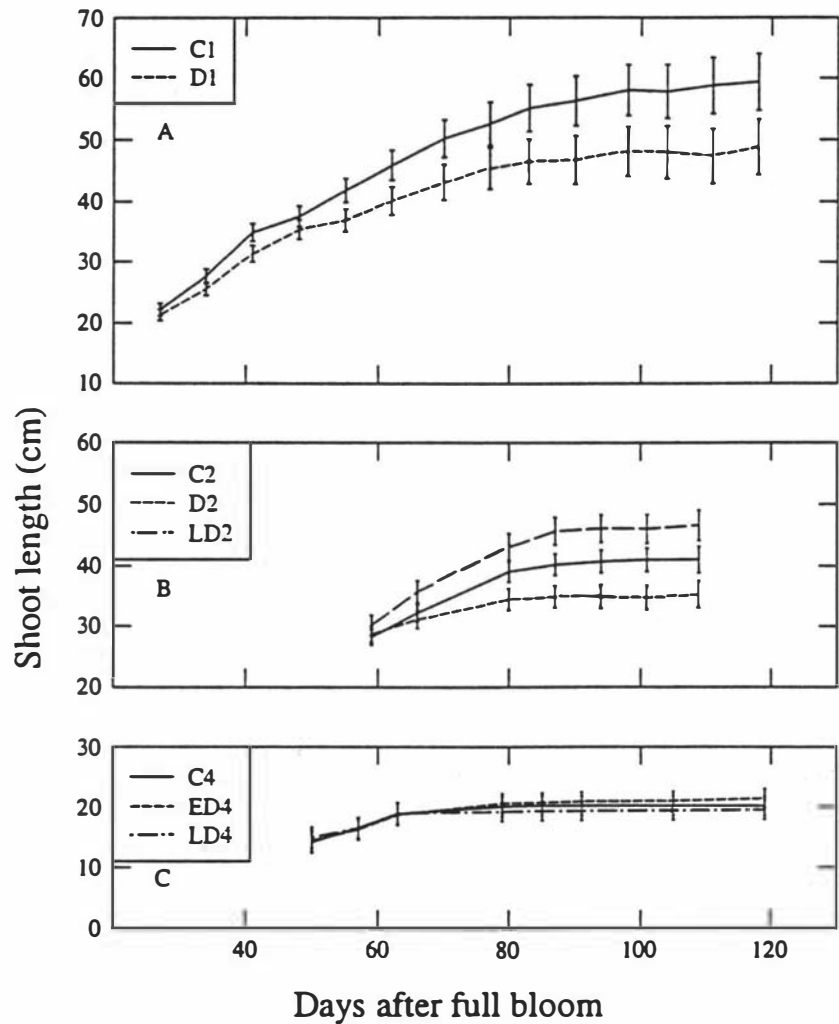


Fig. 13 Shoot length for Expts. 1 (A), 2 (B), and 4 (C). Separate bars are standard errors of the means. Abbreviations are for C1=control, Expt. 1(n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n≥13); D2=deficit, Expt. 2 (n≥10); LD2=late deficit, Expt. 2 (n=13); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4).

Interesting to note from Fig. 13B is that despite similarity of Ψ_1 in the C2 and LD2 trees during the early part of the season (Fig. 2B), LD2 trees appear to show increased shoot growth compared to C2. Factors other than plant water status can

influence shoot growth such as crop load (Forshey and Elfving, 1989; Blanco et al., 1995) and total tree size (Ebel et al., 1995). Fruit number per tree was the same between treatments. However, trees from the LD2 treatment tended to have a larger initial trunk circumference. Because crop load is often expressed in terms of number of fruit per unit tree size as indicated by trunk circumference (Blanco et al., 1995), crop load levels of the LD2 trees would be lower. Initial trunk circumference values ($\text{mm} \pm \text{SE}$) were: 74.2 ± 1.48 , 76.9 ± 1.96 and 77.9 ± 1.48 for C2, D2 and LD2. The value of LD2 trees was significantly higher ($P = 0.11$) than C2 trees when analysed using the ANOVA procedure in SAS. The larger LD2 trees when compared to C2 trees may have caused the shoot growth of the former to be enhanced. In support of the above speculation, if shoot growth is analysed using initial trunk circumference as a covariate no significant difference in shoot growth between LD2 and C2 exists. However, a significant reduction in the shoot growth of the D2 trees compared to LD2 and C2 is observed due to the treatment effect.

Shoot growth recorded during Experiment 4 (Fig. 13C) was low for all treatments despite the maintenance of θ of the C4 trees at pot capacity. As noted, cropload affects shoot growth (Forshey and Elfving, 1989; Blanco et al., 1995). Reduced shoot growth may be related to the crop load of the lysimeter trees which was higher than the greenhouse trees which were of a similar size. A high cropload was retained on the lysimeter trees as fruit quality assessment was an important part of that study. Cropload may also affect fruit quality (Volz et al., 1993) via its influences on Ψ_l (Erf and Proctor, 1987). A general reduction in average Ψ_l of the lysimeter trees compared to trees from other experiments may also be related to cropload. Shoot growth stopped earlier in Experiment 4 than in either Experiment 1 or 2 which is in

agreement with Jones (1983, p. 213) who stated that water deficit results in earlier cessation of shoot growth. The lower average Ψ_1 in the lysimeter trees caused earlier termination of shoot growth when compared to the less water stressed trees of the other experiments.

Indications that factors aside from plant water status play an important role in shoot growth are illustrated in Fig. 13A. Here differences in shoot growth between treatments are developed despite no significant reduction in Ψ_1 or P_n being recorded during the early stages of the season (Fig. 2A). Soil water content of D1 trees was significantly reduced from the commencement of the experiment (Fig. 1A). Proebsting et al. (1989) assumed that roots in dry soil are physiologically inactive. The drier soil surrounding the rootzone of the D1 trees may have restricted the rooting volume of these trees. This in turn could have restricted the vegetative growth of the above ground portion of the tree (Richards and Rowe, 1977a, 1977b; Mandre et al., 1995). Growth hormones, produced in the roots, have been implicated as the mechanism by which vegetative growth is restricted under reduced root growth. Thus shoot growth may be subjected to internal regulation by the roots due to the production and supply of growth substances. Data to substantiate this are not available in this study.

Although there is some evidence that a reduction in plant water status during the early part of the season will reduce shoot growth in 'Braeburn' apples (Fig. 13B) the results here do not seem as convincing as those already reported for peach (Chalmers et al., 1985), pear (Chalmers et al., 1986), Asian pear (Caspari et al., 1994) and 'Granny Smith' apple (Lötter et al., 1985). It is likely that because plant water status was not reduced until more than 50% of total shoot extension growth had occurred, the influence of DI on shoot growth in this study was minimal.

4.3.2 Leaf area

Leaf area is reported to be highly sensitive to reduced plant water status (Hsiao, 1993). Leaf area in apple develops mostly during the first two months of the season (Palmer, 1988). Leaf area is sensitive to water deficit during the early part of the season because most shoot growth and leaf development occurs at this time (Lötter et al., 1985; Palmer, 1988). Once the canopy is developed, water stress will have a minimal influence on leaf area, unless the water deficit is severe enough to cause leaf abscission (Castel and Fereres, 1982; Behboudian et al., 1994a). Table 5 shows that no reduction in leaf area occurred when water deficit was induced early or late in the season. The only significant reduction in leaf area was recorded in the D2 trees which were stressed throughout the season. The minimal influence of a late-season deficit on leaf area is expected as the leaf area was already established at the time of stress development. A minimal impact of the ED4 treatment on leaf area may also be related to predominant leaf area development occurring prior to the imposition of water stress at 55 DAFB.

Table 5. Leaf area for experiments 1, 2, and 4. Abbreviations are for C1=control, Expt. 1; D1=deficit, Expt. 1; C2=control, Expt. 2; D2=deficit, Expt. 2; LD2=late deficit, Expt. 2; C4=control, Expt. 4; ED4=early deficit, Expt. 4; and LD4=late deficit, Expt. 4. Column values followed by the same letter are not significantly different at $P < 0.05$.

TRT 1993 (Expt.1)	Leaf area 1993 ^z (m ²)	TRT 1994 (Expt.2)	Leaf area 1994 ^y (m ²)	TRT 1995 (Expt.4)	Leaf area 1995 ^x (m ²)
C1	9.14 ± 0.25a ^w	C2	1.84 ± 0.84b	C4	1.55 ± 0.25a
D1	8.66 ± 0.23a	D2	1.37 ± 0.92a	ED4	1.29 ± 0.25a
		LD2	1.76 ± 1.04b	LD4	1.52 ± 0.25a

^z Mean values of 10 trees for C1 and 11 trees for D1
^y Mean values of 19 trees for C2, 16 trees for D2 and 13 trees for LD2
^x Mean values of 4 trees per treatment
^w Mean ± SE

4.3.3 Trunk growth

Deficit irrigation tends to reduce trunk growth in apple (Iancu, 1985; Irving and Drost, 1987). Trunk size is a good indicator of total tree size (Westwood and Roberts, 1970), and is also closely correlated to total leaf area. For example, leaf area regressed significantly on trunk circumference in Experiment 1 ($\text{Leaf area (m}^2\text{)} = -9.42 + 0.0802 \times \text{Circumference (mm)}$, $R^2 = 0.88$, $n = 21$, $P < 0.0001$) for the range of values measured. Table 6 gives the trunk circumference increase recorded throughout the three years of this study and shows that a significant reduction under deficit irrigation in the D2 trees of Experiment 2 only. This is also the only treatment showing a significant reduction in leaf area (Table 5). As leaf area is generally maintained in trees exposed to an early or a late deficit (Table 5), a reduction in total biomass accumulation by trees

subjected to a water deficit is also minimal. This, in turn, may have minimised the impact of deficit irrigation on trunk growth.

Table 6. Trunk circumference increase for experiments 1, 2, and 4. Abbreviations are for C1=control, Expt. 1; D1=deficit, Expt. 1; C2=control, Expt. 2; D2=deficit, Expt. 2; LD2=late deficit, Expt. 2; C4=control, Expt. 4; ED4=early deficit, Expt. 4; and LD4=late deficit, Expt. 4. Column values followed by the same letter are not significantly different at $P < 0.05$.

1993	Trunk	1994	Trunk	1995	Trunk
(Expt.1)	circumference	(Expt.2)	circumference	(Expt.4)	circumference
	increase		increase		increase
	1993 ^z		1994 ^y		1995 ^x
C1	33.8 ± 2.0a ^w	C2	13.5 ± 1.3a	C4	14.9 ± 1.5a
D1	28.8 ± 1.9a	D2	4.07 ± 1.6b	ED4	14.1 ± 1.5a
		LD2	9.87 ± 1.3a	LD4	16.0 ± 1.5a

^z Mean value of 10 trees for C1 and 11 trees for D1
^y Mean value of 7 trees for C2 and LD2, 4 trees for D2)
^x Mean value of 4 trees for C4,ED4, and LD4 respectively
^w Mean ± SE

4.3.4 Root growth

Total root length was evaluated on 18 trees at the end of Experiment 2. Root growth is reportedly less sensitive to reduced plant water status than is shoot growth (Chalmers, 1989). No difference in root length was found between treatments. Shoot growth was therefore more sensitive to plant water deficit than root growth in this study. Values of root length (m ± SE) at final harvest were 1209 ± 103, 1318 ± 137, and 1143

± 103 for C2, D2 and LD2, respectively. No difference in the mean temperature of the rooting medium existed between treatments.

4.3.5 Return Bloom

Return bloom was evaluated in Experiments 1 and 4. In Experiment 1 no difference in return bloom was observed between treatments (Table 7). In Experiment 4, however, a significant reduction in return bloom was observed in the ED4 trees (Table 7). Final trunk circumference was used as a covariate in the analyses of Experiment 4 data. We may expect a reduction in return bloom of the ED4 trees as water deficit was imposed during flower bud formation in early summer (Westwood, 1988, p. 171). Faust (1989, p. 159) states that flower bud formation is a photosynthate-requiring process, and water deficit at this time may therefore reduce the crop in the following year. The Pn of the ED4 trees was reduced during the stress period (Fig. 7C). The influence of the D1 treatment on return bloom would not be expected to be significant as the water deficit imposed on these trees was not established until late summer after flower bud formation was complete (Westwood, 1988, p. 171). Other researchers have presented conflicting results regarding the influence of DI on return bloom as reported in the literature review (section 2.4). Factors such as the rate and timing of stress development are cited. The timing of stress imposition appears to have influenced the effect of DI on return bloom of 'Braeburn' in this study with DI induced during flower bud formation (ED4 treatment) being detrimental to return bloom.

Table 7. Return bloom (number of flowers) recorded for Experiments 1 and 4. Abbreviations are for C1=control, Expt. 1; D1=deficit, Expt. 1; C4=control, Expt. 4; ED4=early deficit, Expt. 4; and LD4=late deficit, Expt. 4. Column values followed by the same letter are not significantly different at $P < 0.05$.

TRT 1993	Return Bloom ^z (number of flowers per branch)	TRT 1995	Return Bloom ^y (number of flowers per tree)
C1	13.8 ± 1.015a ^x	C4	296 ± 22.13a ^w
D1	13.3 ± 0.967a	ED4	209 ± 22.13b
		LD4	248 ± 22.15a

^z Calculated using branch circumference as a covariate.

^y Calculated using trunk circumference as a covariate.

^x Mean bloom number per branch (mean ± SE).

^w Mean bloom number per tree (mean ± SE).

It is therefore concluded that the minimal impact of deficit irrigation on vegetative growth observed in this study was because the water deficit was not imposed until a large portion of both shoot growth and leaf area development had taken place.

4.4 Fruit Quality

Deficit irrigation studies have focused predominantly on the control of vegetative growth. But modification of some fruit quality attributes have also been reported (eg. Guelfat'Reich et al., 1974; Irving and Drost, 1987; Crisosto et al., 1994) This section discusses the influence of DI on fruit quality attributes and illustrates that despite a minimal impact of DI on the vegetative growth, some important fruit quality attributes are modified.

4.4.1 Fruit size

Fruit size is both a yield and a quality attribute. Although fruit size is discussed as a yield parameter in the literature review the results will be discussed as a quality attribute. Adequate fruit size is fundamental to successful apple production as economic returns generally favour larger fruit. Oversized fruit are also undesirable, however, and may be discriminated against by consumers. Large fruit may also show poor keeping quality as exemplified for apple (Guelfat'Reich et al., 1974). For these reasons there is an optimum size range for all fruit. If deficit irrigation is to be used as a management tool, the fruit produced must lie within this optimum size range.

The characteristic growth pattern for apples is sigmoidal (Westwood, 1988, p. 200; Pavel and DeJong, 1995) although this is not clearly shown in Fig. 12. Fruit growth may be divided into one short post-anthesis stage and two major subsequent stages. The post-anthesis stage shows a slow increase in fruitlet weight that is predominantly due to cell division. The second stage is characterised by rapid fruitlet growth and the third stage shows a slowing of the rate of fruit growth up to harvest. Some researchers do not recognise this third stage of growth (Schechter et al., 1993), but rather consider a distinct stage I (post-anthesis) where slow growth predominates and

cell division occurs, and then stage II, commencing as cell enlargement takes over (Schechter et al., 1993). Weekly increase in fruit diameter from 27, 58 and 50 DAFB is illustrated in Figure 14. Because fruit diameter measurements were not started until after the post-anthesis stage, this stage is not illustrated in Figure 14. Water deficit was not induced until after the completion of cell division. The third stage of fruit growth is illustrated to a limited extent in these data.

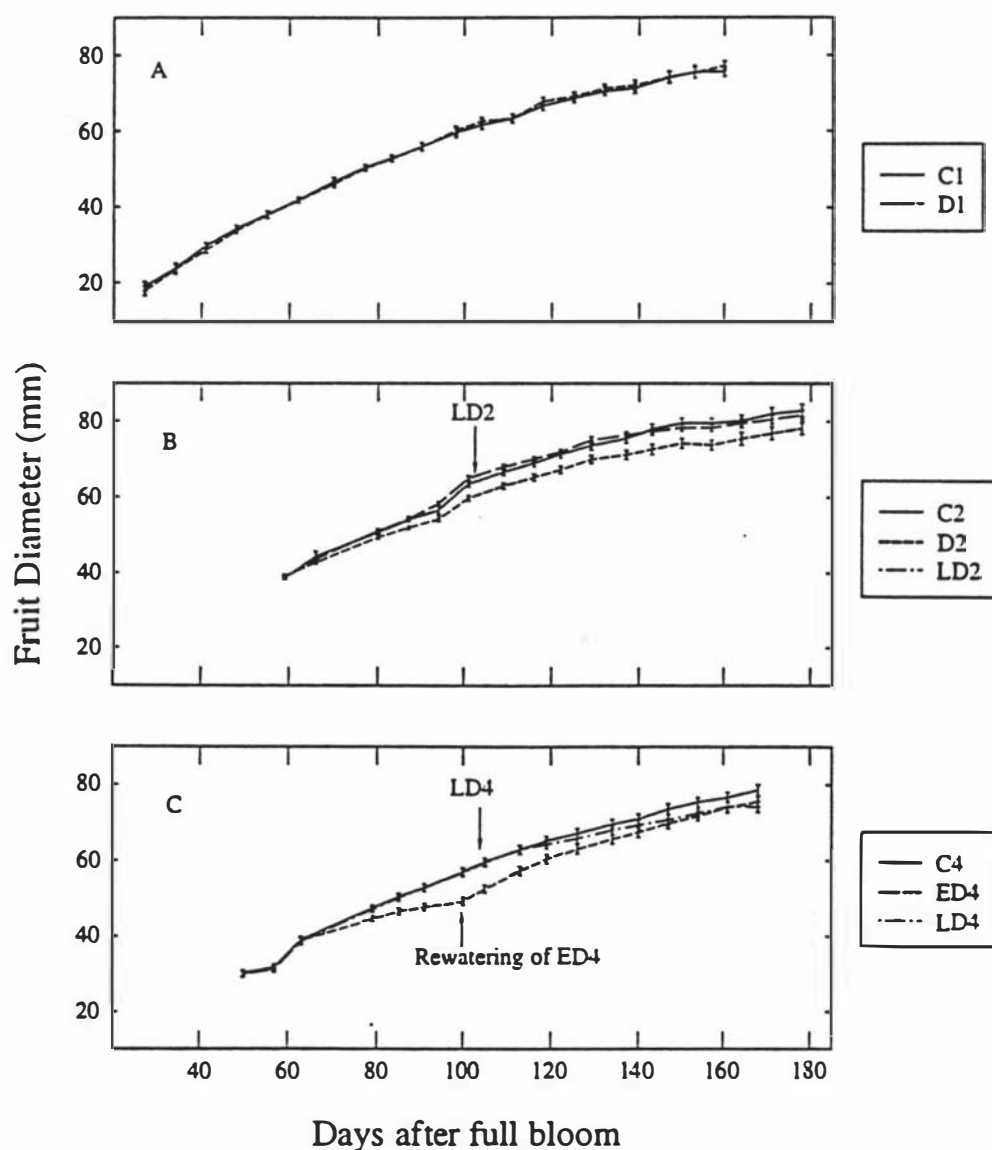


Fig. 14 Mean fruit diameter for Expts. 1 (A), 2 (B) and 4 (C). Bars indicate standard errors of the means. Abbreviations are for C1=control, Expt. 1 (n=10); D1=deficit, Expt. 1 (n=11); C2=control, Expt. 2 (n=7); D2=deficit, Expt. 2 (n=4); LD2=late deficit, Expt. 2 (n=7); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Fruit growth is reported to be sensitive to plant water status and has been used as an indication of irrigation requirements (Assaf et al., 1982). My data indicate that fruit diameter may be reduced under reduced plant water status. But the impact of water deficit on fruit diameter is strongly dependent on the duration and degree of water deficit. The field study in 1993 (Fig. 14A) indicates that despite a significant reduction in Ψ_1 later in the season in the D1 trees, there was no significant reduction in fruit diameter. Similar results were found in Experiment 2 (Fig 14B) when water deficit was induced on LD2 trees late in the season. However, a late-season water deficit during Experiment 4 resulted in a reduction ($P < 0.1$) in fruit diameter at harvest. This may be due to the lower average Ψ_1 for those trees during the stress period when compared to the LD2 trees. Average Ψ_1 (MPa \pm SE) for LD2 and LD4 trees during the stress period was -2.02 ± 0.085 and -2.25 ± 0.092 , respectively.

In contrast, water deficit induced earlier in the season resulted in a significant decline in the weekly fruit growth rate (Fig. 14B and 14C). When water deficit was maintained throughout the season fruit diameter was significantly reduced at harvest (Fig. 14B). However, if trees were subjected to an early water deficit followed by rewatering (Fig. 14C, ED4) fruit growth recovered and was not different from controls at final harvest. This recovery has been reported in other fruit crops such as peach (Chalmers et al., 1981) and pear (Chalmers et al., 1986; Mitchell et al., 1986). In pears, an increase in yield following an early-season deficit was attributed to fruit osmotic adjustment which maintains, or increases fruit growth at the expense of inhibited vegetative growth (Chalmers et al., 1986).

The weekly evaluation of fruit diameter was carried out non-destructively and the same tagged fruit were repeatedly measured. Fruit were also harvested and weighed

at fortnightly intervals during the season for all experiments (Fig. 15) (see page 92).

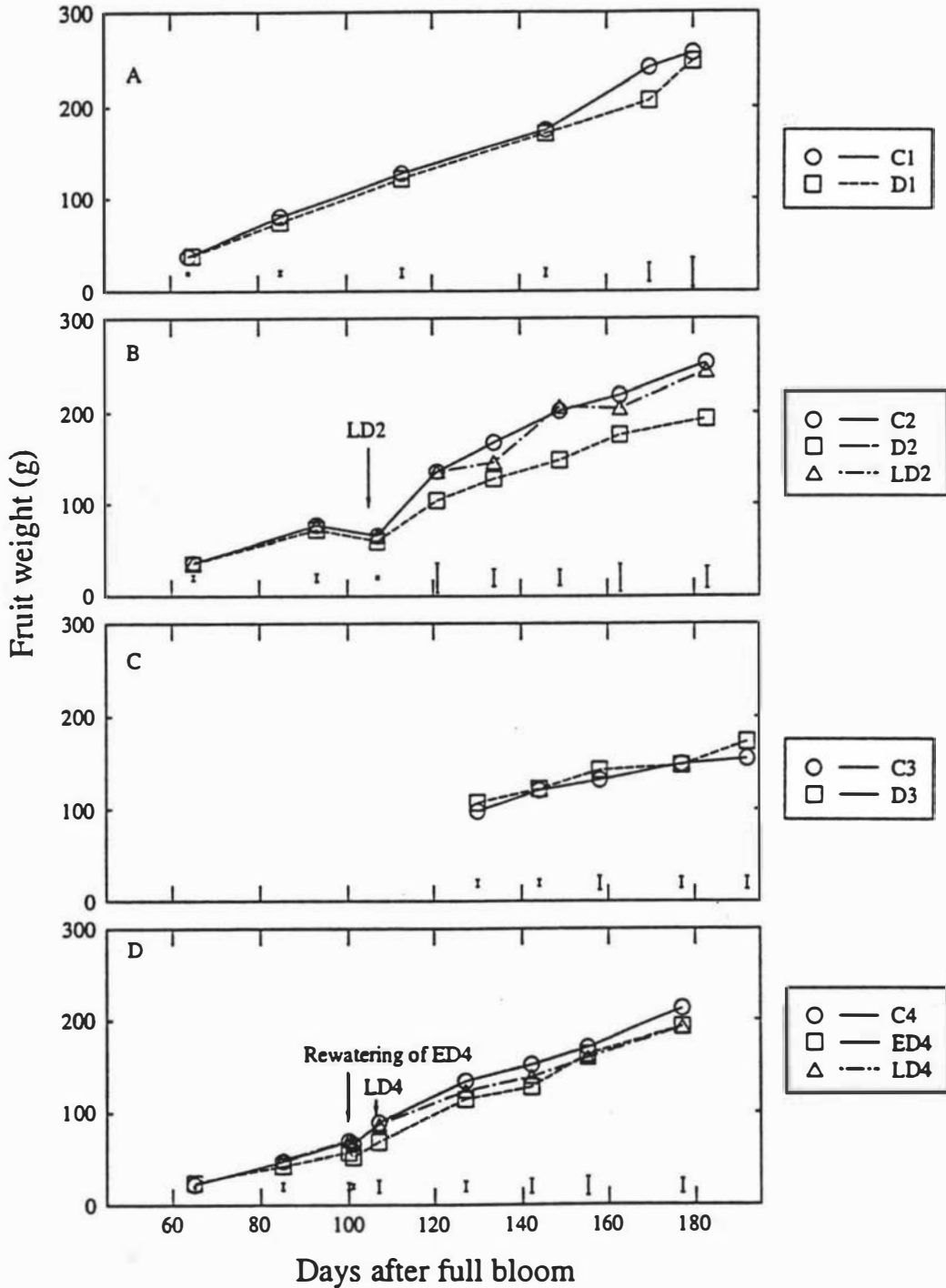


Fig. 15 Mean fruit weight for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 18, 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control ($n=10$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) when $n=4$), D1=deficit ($n=11$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) where $n=5$); C2=control, Expt. 2 ($n \geq 7$); D2=deficit, Expt. 2 ($n \geq 4$); LD2=late deficit, Expt. 2 ($n \geq 7$); C3=control, Expt. 3 ($n=6$); D3=deficit, Expt. 3 ($n=3$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$); and LD4=late deficit, Expt. 4 ($n=4$). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

The relationship between fruit weight and fruit diameter is well established. For example, data from 1995 where the weight ranged between 22 and 205 g, and the diameter ranged between 45 and 78 mm, showed a highly significant regression between these parameters (weight = $-181.92 + 4.85 \times \text{Diameter}$, $n = 359$, $R^2 = 0.94$, $P < 0.0001$). Therefore the similarity between Figures 14 and 15 is expected. No significant difference in fruit weight at final harvest was observed for any experiments if water deficit was imposed during the later stages of the season. Similarly fruit weight recovered to values equivalent to C4 in the ED4 trees following rewatering. Only fruit from the D2 treatment showed a significant reduction in fruit weight when compared to the controls. Diameter recorded for these harvested fruit also showed results similar to those illustrated in Figure 15 (data not shown). I conclude that a late-season water deficit has a minimal impact on fruit size of 'Braeburn' apple. This may be partly due to the timing of a late season water deficit coinciding with the reduction in fruit growth during the later stages of apple fruit development. 'Braeburn' appears to demonstrate the ability to increase growth rates following an early-season stress period which results in these fruit matching the final harvest weight of the controls. These results agree with those of Behboudian et al. (1994a) who found that a late-season water deficit or an early-season water deficit followed by rewatering did not reduce the final fruit size of Asian pears. For other apple cultivars reduced irrigation has resulted in a reduction in final fruit size. For example, Assaf et al. (1975) studying 'Calville de St. Sauveur' showed reduced fruit size and Naor et al. (1995) studying 'Golden Delicious' also showed a reduction in total yield. Both of these studies imposed a water deficit throughout the season. These results are therefore in agreement with our data on a full

season water deficit such as experienced by the D2 trees.

These results indicate that apple fruit growth is resilient to periodic reductions in plant water status which have a minimal influence on the fruit size. Only if a water deficit is maintained throughout the season is fruit size significantly reduced.

4.4.2 Fruit firmness

The effects of water deficit on fruit firmness are not clear, as indicated by the conflicting results reported in section 2.2.3.2.1 A decline in fruit firmness as the apple fruit mature is illustrated in Figure 16. However, there are no differences in fruit firmness between treatments. It is likely that fruit size plays an important role in fruit firmness (Ebel et al., 1993) with small fruit generally being firmer than large ones. These data are insufficient to conclude the effects of water deficit on fruit firmness. However they do indicate that DI has no effect on fruit firmness.

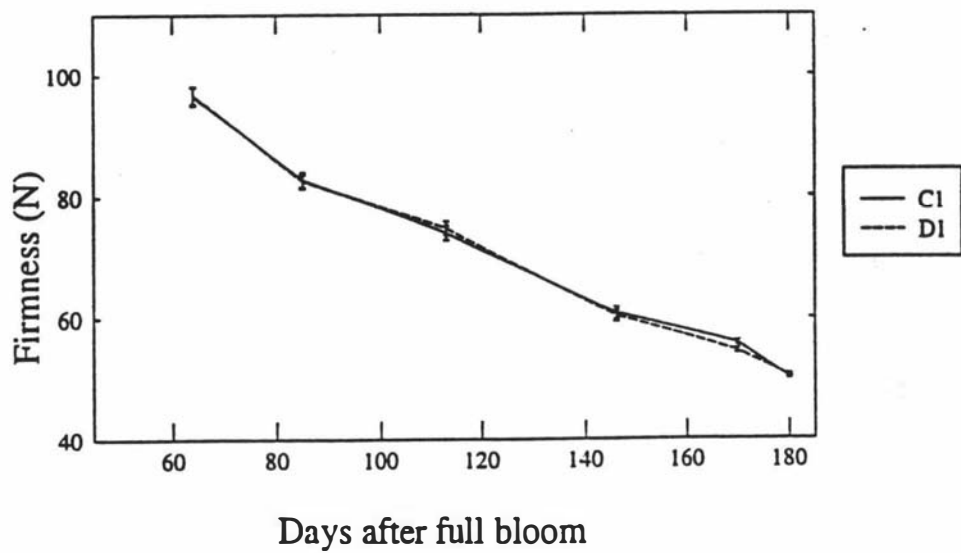


Fig. 16 Fruit firmness for Expt. 1. Bars indicate standard errors of the means. Abbreviations are for C1= control (n=10 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4), D1=deficit (n=11 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) where n=5).

4.4.3 Total soluble solids

An increase in TSS of apple fruit has been reported under water deficit (Irving and Drost, 1987; Rumayor-Rodriguez and Bravo-Lozano, 1991; Ebel et al., 1993). Similar results are apparent in this research (Fig. 17). An increase in TSS occurred following the imposition of water deficit, irrespective of its timing. If water deficit was imposed early and was followed by rewatering, as in ED4 (Fig. 17D), the level of TSS showed a rapid initial decline upon rewatering from its elevated level during the stress period. The TSS then stabilised at a level lower than that recorded for the C4 fruit by final harvest ($P = 0.05$ at 177 DAFB). This finding is in agreement with that on European pear found by Chalmers et al. (1985) who suggested that because full irrigation was supplied to trees after early deficit treatments, the increased fruit water content of the previously-stressed fruit may dilute soluble solids, thereby giving a lower TSS value.

Increased TSS during an early-season deficit may be associated with a reduction in fruit water concentration. Figure 18 illustrates a significant increase in fruit dry matter concentration in the ED4 treatment during the stress period which corresponded with an increase in TSS at this time (Fig. 17D).

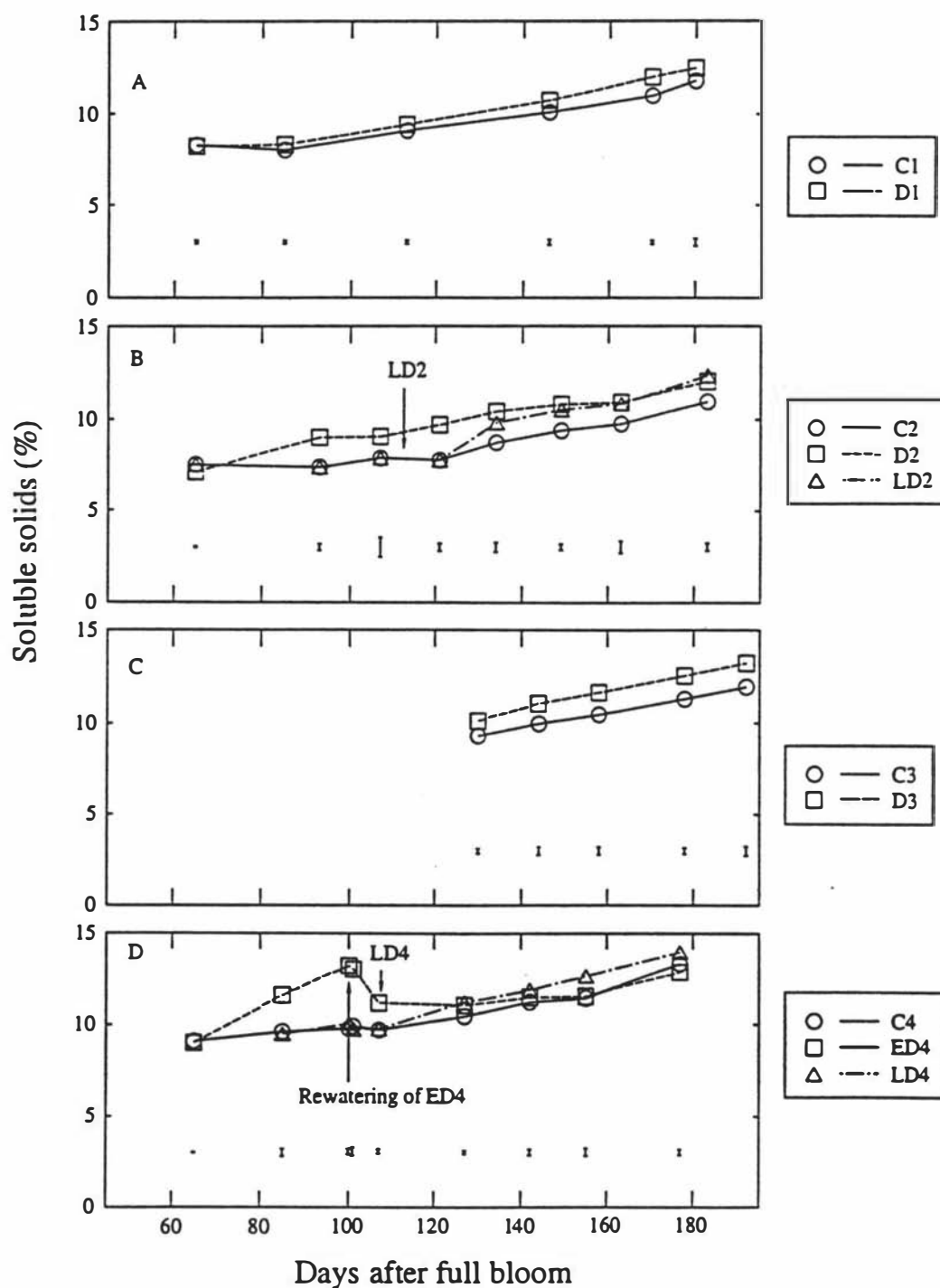


Fig. 17 Mean total soluble solids for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 ($n=10$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) when $n=4$); D1=deficit, Expt. 1 ($n=11$ upto 170 DAFB (stage 1 harvest) where $n=6$ and 180 DAFB (stage 2 harvest) where $n=5$); C2=control, Expt. 2 ($n=2$); D2=deficit, Expt. 2 ($n=2$); LD2=late deficit, Expt. 2 ($n=2$); C3=control, Expt. 3 ($n=6$); D3=deficit, Expt. 3 ($n=3$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$); and LD4=late deficit, Expt. 4 ($n=4$). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

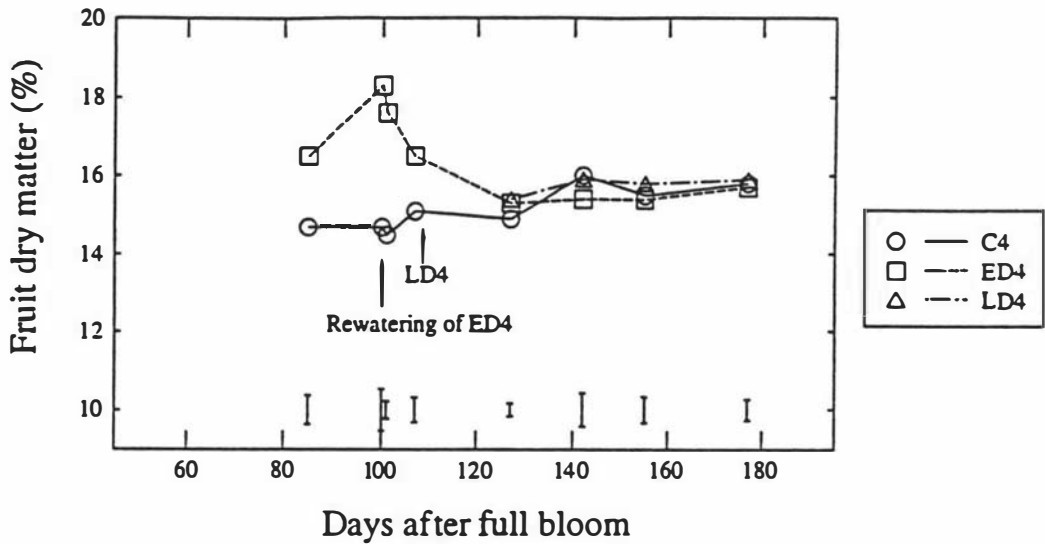


Fig. 18 Fruit dry matter for Expt. 4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 12 experimental units (trees). Abbreviations are for C4= control (n=4), ED4=early deficit (n=4), and LD4=late deficit (n=4). Arrows indicate rewatering of ED4 treatment, and the beginning of LD4 treatment.

After rewatering, fruit TSS dropped, as did fruit dry matter concentration, until both TSS and dry matter concentration were similar to controls at 127 DAFB. At final harvest, a slightly lower dry matter concentration of the ED4 fruit corresponded to a significant reduction of TSS at this time. Additionally, fruit weight is significantly lower in the ED4 than C4 trees during this early stress period (Fig. 15) indicating that the increased level of TSS recorded in these fruit may be due to increased concentration in the smaller fruit.

An increase in TSS during a late-season water deficit is not coupled with a reduction in fruit water concentration as indicated by the dry matter concentration (Fig. 18) and weight is equivalent between LD2 and C2 and LD4 and C4 fruit (Fig. 15). It may be that an increase in TSS for a late-season water deficit is due to the preferential partitioning of solutes to the fruit under water stress (Chalmers et al., 1986; Chalmers, 1989), rather than fruit dehydration resulting in increased TSS. Conversion of starch to

sugar may also be increased under DI resulting in higher TSS in DI fruit (Landsberg and Jones, 1981).

4.4.4 Titratable acidity

Titrateable acidity decreases as fruit mature (Fig. 19). The TA was generally higher in fruit grown under early-season water deficit. Titratable acidity was higher in D2 than in LD2 and C2 fruit and that of ED4 was higher than LD4 and C4. Late deficit treatments in Experiments 2 and 4 did not affect TA. Field experiments (Fig. 19A and 19C) indicate that a late-season deficit may increase TA levels in apple fruit, but differences were not always significant. Increased levels of acid in fruit from early season deficit treatments may contribute to osmotic adjustment, as acids have been implicated as solutes which may contribute to fruit solute potential (Ho et al., 1987). This hypothesis is explored more fully in a following section (4.6.2). As for TSS, this increase in TA in early-season deficit fruit may be due to a reduction in fruit water content resulting in an increased concentration of malic acid.

Information in the literature regarding changes in TA under water deficit is conflicting as are my results between seasons. Generally TA either increased under deficit irrigation or showed no difference between treatments. An increase in TA coupled with an increase in TSS at final harvest has important implications for fruit sensory quality (Ackermann et al., 1992). Although sugar to acid ratios in relation to apple fruit palatability has not been assessed, this ratio is commonly used to evaluate citrus fruit. It gives a better assessment of palatability of the fruit than either sugar or acid levels alone (Wills et al., 1982, p. 94).

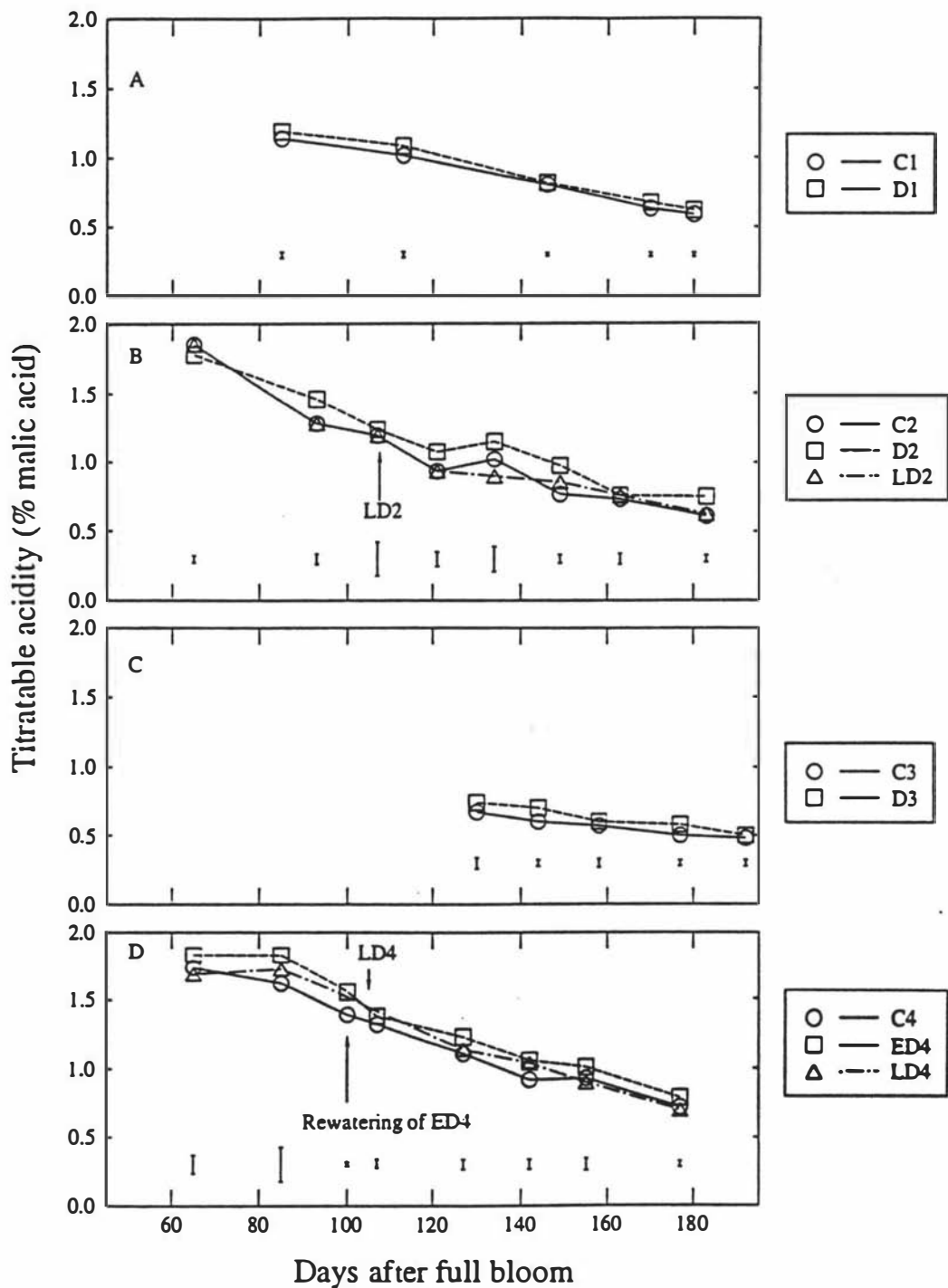


Fig. 19 Fruit titratable acidity for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4); D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=5); C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=late deficit, Expt. 2 (n=2); C3=control, Expt. 3 (n=6); D3=deficit, Expt. 3 (n=3); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Sensory evaluation of apple fruit grown under DI would have to be carried out to establish whether or not changes in TA and TSS as observed in this study significantly change the taste of the fruit.

4.4.5 Colour

In many apple varieties the red colouration which is due to anthocyanins and flavonols (Lancaster, 1992), is a desirable attribute (Lancaster et al., 1994). Red apple varieties are required to have a minimum level of red pigmentation if they are to be suitable for export. For example, 'Braeburn' must have at least 40% red blush for export from New Zealand (Kupferman, 1994). Cultural practices that enhance the development of red pigmentation in apple fruit are, therefore, beneficial. Proebsting et al. (1984) and Ebel et al. (1993) observed no change in red colouration under either an entire- or an early-season water deficit, respectively, in 'Delicious' apples. However, work on grapes indicate that anthocyanin development is enhanced under water deficit conditions (Freeman, 1983; Freeman and Kliwer, 1983; Matthews and Anderson, 1988; Matthews et al., 1990). The data presented in Table 8 show that during the 1993 field experiment red pigmentation was not significantly increased in the D1 fruit compared with controls, but green colouration was significantly reduced. On the contrary, field experiments conducted during 1994 showed that red colouration was increased in D3 fruit, but green colour was not significantly reduced. In Experiment 4 no difference in red colour was observed between C4 and LD4 fruit. However, the ED4 fruit had significantly lower red colour than C4. Green colour showed similar trends to red colouration data for Experiment 4. Colour was not evaluated in Experiment 2 conducted in the greenhouse.

Table 8. Difference in the red and green colouration of 'Braeburn' apple fruit at final harvest for experiments 1, 3, and 4. Abbreviations are for C1= control, Expt. 1, D1=deficit, Expt. 1, C3=control, Expt. 3, D3=deficit, Expt. 3, C4=control, Expt. 4, ED4=early deficit, Expt. 4, and LD4=late deficit, Expt. 4. For each year column values followed by the same letter are not significantly different at $P < 0.05$.

Treatment / year	Red colour (Hue angle, ^o) ^z	Green colour (Hue angle, ^o) ^y
C1, 1993	39.11 ± 2.33a ^x	87.23 ± 3.27b
D1, 1993	34.55 ± 2.23a	77.44 ± 3.12a
C3, 1994	50.55 ± 2.65b	90.11 ± 2.93a
D3, 1994	38.40 ± 3.75a	84.22 ± 4.14a
C4, 1995	40.35 ± 2.51a	83.14 ± 1.74a
ED4, 1995	50.78 ± 2.71b	91.14 ± 1.74b
LD4, 1995	45.31 ± 2.71ab	86.41 ± 1.75 ab

^z Hue angle measured on the blush side of the fruit. A lower value indicates redder fruit.

^y Hue angle measured on the green side of the fruit. A lower value indicates less green fruit.

^x Mean ± SE.

The development of anthocyanins in apple may be influenced by the level of carbohydrates (Saure, 1990; Lancaster, 1992). Multiple regression of sugar data (sucrose, glucose, fructose and sorbitol) on red colouration from Experiment 4 at final harvest was significant ($R^2 = 0.99$). The greatest contribution to the regression model is due to glucose which accounts for a partial R^2 of 0.84. Sorbitol was also important,

contributing a partial R^2 of 0.14. Important to note here is that sugar concentration at final harvest was significantly lower in the ED4 fruit than in either C4 or LD4 fruit at final harvest (Fig. 34). Total sugar concentration of D1 fruit was not significantly higher than C1 fruit at final harvest (data not shown) and no difference in red colour existed between treatments (Table 8). However, in Experiment 3 total sugar concentration was higher in D3 than in C3 fruit at final harvest (Fig. 28) and red colour was increased in the former (Table 8). Regression analysis of sugar concentration with fruit colour was not possible in experiments 1 and 3 as sugar analysis was not performed on individual fruit but on composite fruit samples as described in section 3.5.2. These data appear to agree with Westwood (1988, p. 238), who stated that factors that increase carbohydrates in the fruit will encourage anthocyanin development. A more comprehensive analysis of fruit sugar composition is discussed in sections 4.5.4 and 4.6.2.

Previous discussion in the literature review (2.2.3.2.4) indicated that N may play a role in green colouration of apple fruit. A trend towards lower N concentration is discernible under reduced irrigation in experiments 1 and 3 (Fig. 20A and 20C). Other experimental work conducted in this study showed no consistent reduction in the N concentration of the fruit from the deficit treatments (Fig. 20B and 20D). No correlation between green colouration and N concentration existed in Experiment 4.

In summary, if water deficit results in an increase in sugar concentration at final harvest then red colouration in these fruit may be enhanced. These data do not give consistent results on the impact of water deficit on fruit N concentration and so a conclusion as to the impact this has on fruit green colour is not possible.

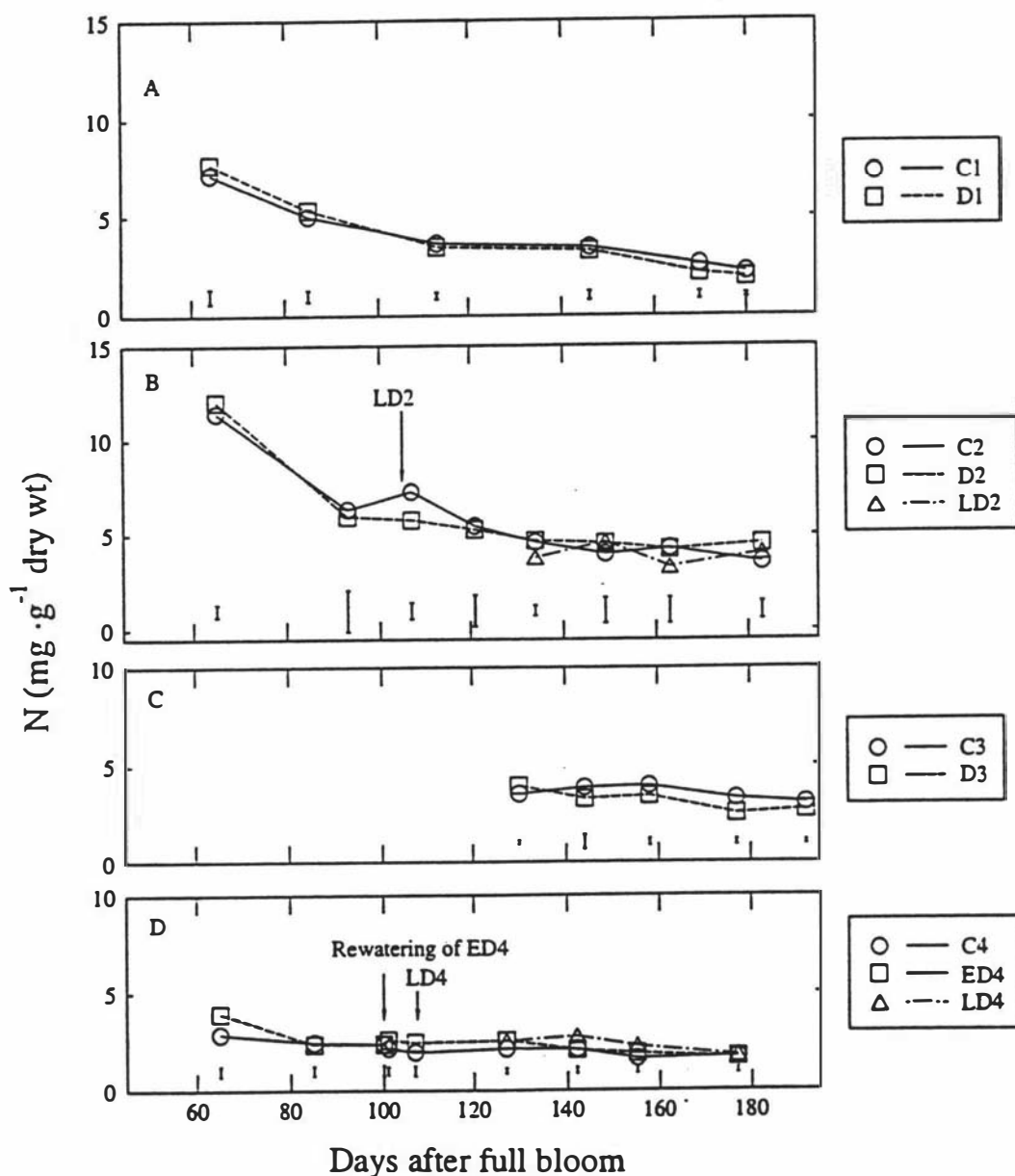


Fig. 20 Fruit N concentration for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different *n* values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (*n*=10 upto 170 DAFB (stage 1 harvest) where *n*=6 and 180 DAFB (stage 2 harvest) where *n*=4); D1=deficit, Expt. 1 (*n*=11 upto 170 DAFB (stage 1 harvest) where *n*=6 and 180 DAFB (stage 2 harvest) where *n*=5); C2=control, Expt. 2 (*n*=2); D2=deficit, Expt. 2 (*n*=2); LD2=late deficit, Expt. 2 (*n*=2); C3=control, Expt. 3 (*n*=6); D3=deficit, Expt. 3 (*n*=3); C4=control, Expt. 4 (*n*=4); ED4=early deficit, Expt. 4 (*n*=4); and LD4=late deficit, Expt. 4 (*n*=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

4.4.6 Fruit ethylene evolution

Ethylene evolution is reported as a good indicator of apple fruit maturity (Watkins et al., 1989). However, it is also considered a poor indicator of apple fruit maturity as it correlates poorly with other methods of fruit maturity assessment such as levels of TSS, TA, and firmness (Testoni and Eccher Zerbini, 1989). Because water deficit appears to modify some fruit maturity parameters, such as TSS, the influence of water deficit on fruit ethylene evolution was investigated. Information on ethylene evolution in 'Braeburn' is scarce. Data presented by Watkins et al. (1989) indicate that ethylene evolution in 'Braeburn' is relatively low, when compared with cultivars such as 'Cox's Orange Pippin', 'Royal Gala', and 'Red Delicious'. Watkins et al. (1989) also show that ethylene evolution increases as the season progresses and that a sudden increase in ethylene evolution indicates the initiation of the climacteric period. Ebel et al. (1993), studying the influence of DI on ethylene evolution of 'Red Delicious', indicated that apple fruit grown under deficit irrigation showed a significant increase in ethylene evolution when compared to control fruit.

Figure 21 illustrates ethylene evolution in fruit from experiments 1 and 2. Ethylene levels increase as the season progresses, but an obvious climacteric rise is not apparent in these data. This may be because ethylene levels were assessed immediately following harvest rather than after 24 hours at 20°C (Watkins et al., 1989), or because fruit was harvested prior to the climacteric. No consistent difference in ethylene evolution was established between treatments. These data give no indication that ethylene evolution is modified under conditions of plant water deficit.

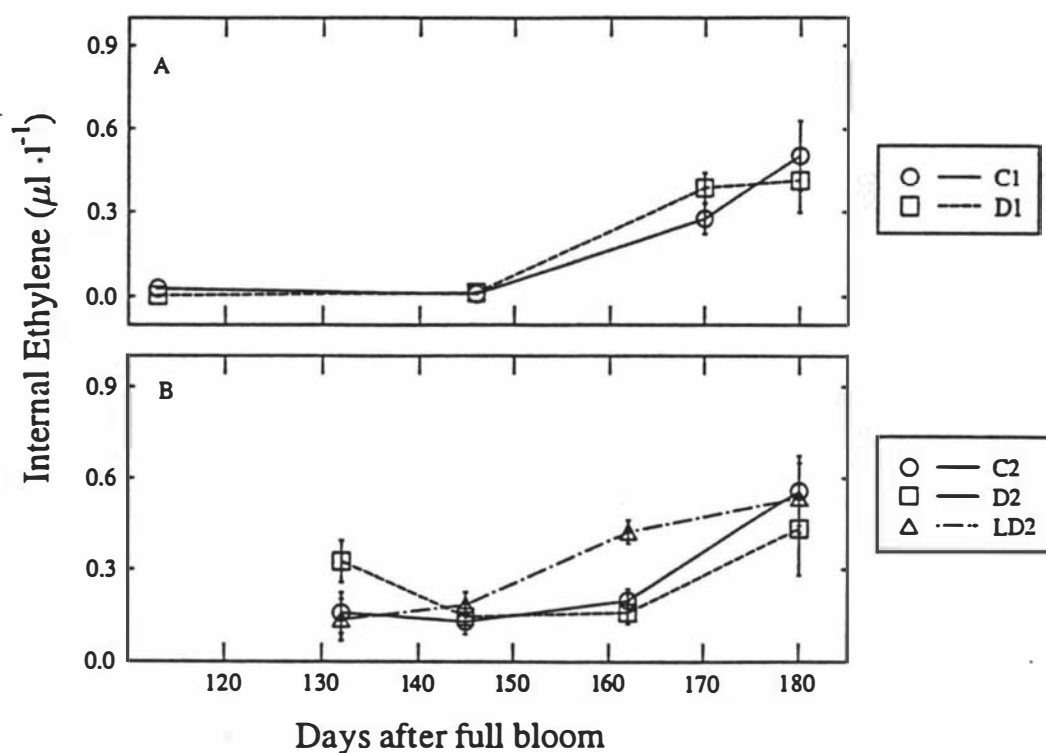


Fig. 21 Ethylene evolution for Expts. 1 (A), and 2 (B). Bars indicate standard errors of the means. Abbreviations are for C1= control, Expt. 1 (n=10 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4); D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) where n=6 and 180 DAFB (stage 2 harvest) where n=5); C2=control, Expt. 2 (n=2 upto 180 DAFB where n=7); D2=deficit, Expt. 2 (n=2 upto 180 DAFB where n=4); and LD2=late deficit, Expt. 2 (n=2 upto 180 DAFB where n=7).

4.4.7 Mineral concentration

Fruit mineral concentration affects the quality and storability of apple fruit as it influences the development of disorders both at harvest and during storage (Faust, 1989, p. 55). Data on changes of N concentration of apple fruit under DI have already been illustrated (Fig. 20) in relation to fruit colour development. Nitrogen is also important as increased levels in apple fruit may lead to more storage rot (Ericsson, 1993). Bramlage (1993) stated that apple fruit high in N tend to be larger, have poorer colour development, and be more predisposed to the development of cork spot, bitter pit,

internal breakdown, scald, and soggy breakdown. Richardson (1986) also observed that an increased N concentration in apple fruit resulted in larger fruit which were softer and had a greener background colour. Bramlage (1993) also pointed out that many of these changes observed in relation to increased fruit N concentration are probably also due to the accompanying reduction in fruit Ca^{2+} concentration associated with increased tree growth under high nitrogen conditions. Additionally, an increase in fruit size under high N conditions effectively dilutes fruit Ca^{2+} concentration.

The importance of adequate Ca^{2+} concentration in the fruit has been widely published (Perring, 1984 and 1989; Johnson et al., 1987; Failla et al., 1990; Ferguson and Watkins, 1993). Low Ca^{2+} concentrations may result in the increased incidence of bitter pit and senescent breakdown (Johnson et al., 1987; Perring, 1989; Tomala and Dilley, 1990). A low level of fruit Ca^{2+} may also increase the rate of fruit softening during storage (Poovaiah et al., 1988).

The expectation that mineral concentration of the fruit will be reduced under water deficit is thought to be due to the difficulty of nutrient uptake by the plant from the soil solution (Mengel and Kirkby, 1987, p. 74). A reduction in irrigation reduces this uptake. We may expect therefore that reduced irrigation will have both beneficial and harmful effects depending on the nutrient. A reduction in the levels of N, P, K^+ , Ca^{2+} and Mg^{2+} were recorded for Asian pear fruit under an early-season water deficit, while no consistent effect on fruit nutrition was observed under a late-season deficit (Behboudian and Lawes, 1994). In contrast, Caspari (1996) reported no significant effects on fruit mineral concentration in early-, or late-season DI in Asian pears.

There were no consistent differences in N concentration (Fig. 20) and in Ca^{2+} concentration (Fig. 22) between control and deficit treatments. Data for Mg^{2+} , P and

K^+ levels for each experiment are illustrated in Figures 23, 24, and 25 (see over).

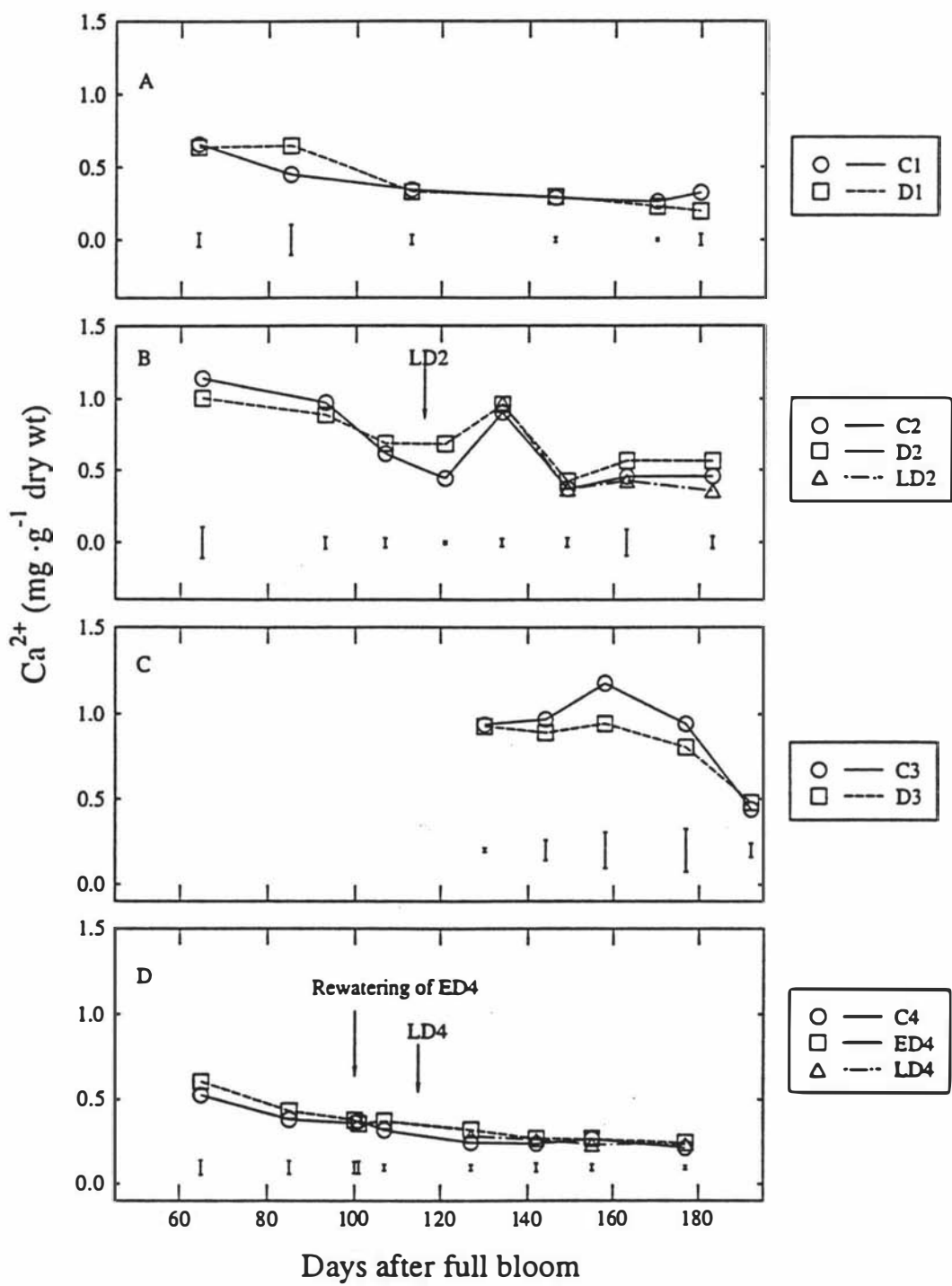


Fig. 22 Fruit Ca^{2+} concentration for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standar error bars of treatment means for each measurement time are based on the poole experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB 9, and 12 experimental units (trees) for A, B, C, and D respectively. When poole experimental error differed between treatments due to different n values per treatment, th maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10 up 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4 D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) where n=6 and 180 DAFB (stag 2 harvest) where n=5); C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=la deficit, Expt. 2 (n=2); C3=control, Expt. 3 (n=6); D3=deficit, Expt. 3 (n=3); C4=control, Exp 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arro indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning LD4 treatment.

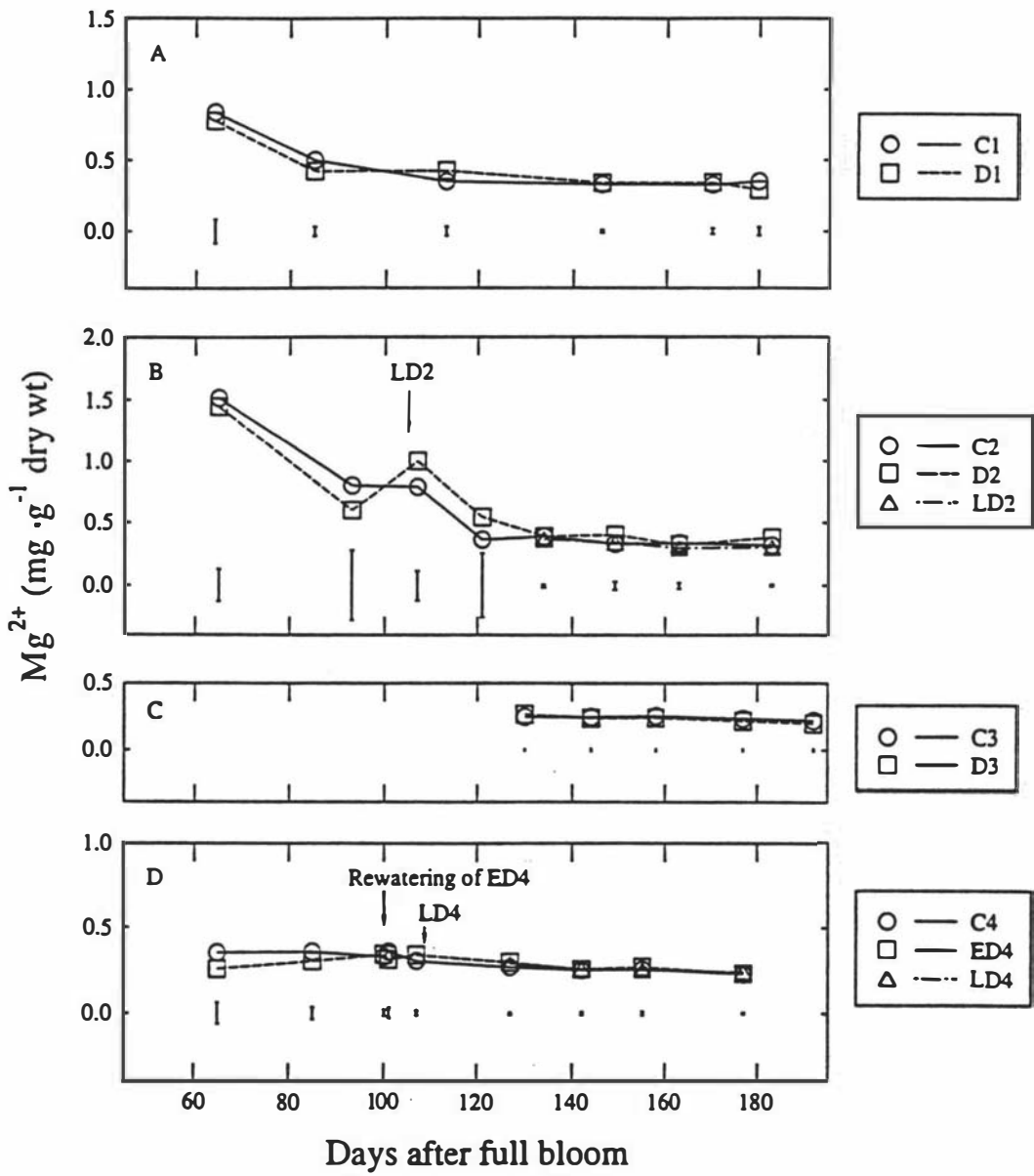


Fig. 23 Fruit Mg^{2+} concentration for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB) 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (n=10 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=4; D1=deficit, Expt. 1 (n=11 upto 170 DAFB (stage 1 harvest) when n=6 and at 180 DAFB (stage 2 harvest) when n=5); C2=control, Expt. 2 (n=2); D2=deficit, Expt. 2 (n=2); LD2=late deficit, Expt. 2 (n=2); C3=control, Expt. 3 (n=6); D3=deficit, Expt. 3 (n=3); C4=control, Expt. 4 (n=4); ED4=early deficit, Expt. 4 (n=4); and LD4=late deficit, Expt. 4 (n=4). Arrow indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

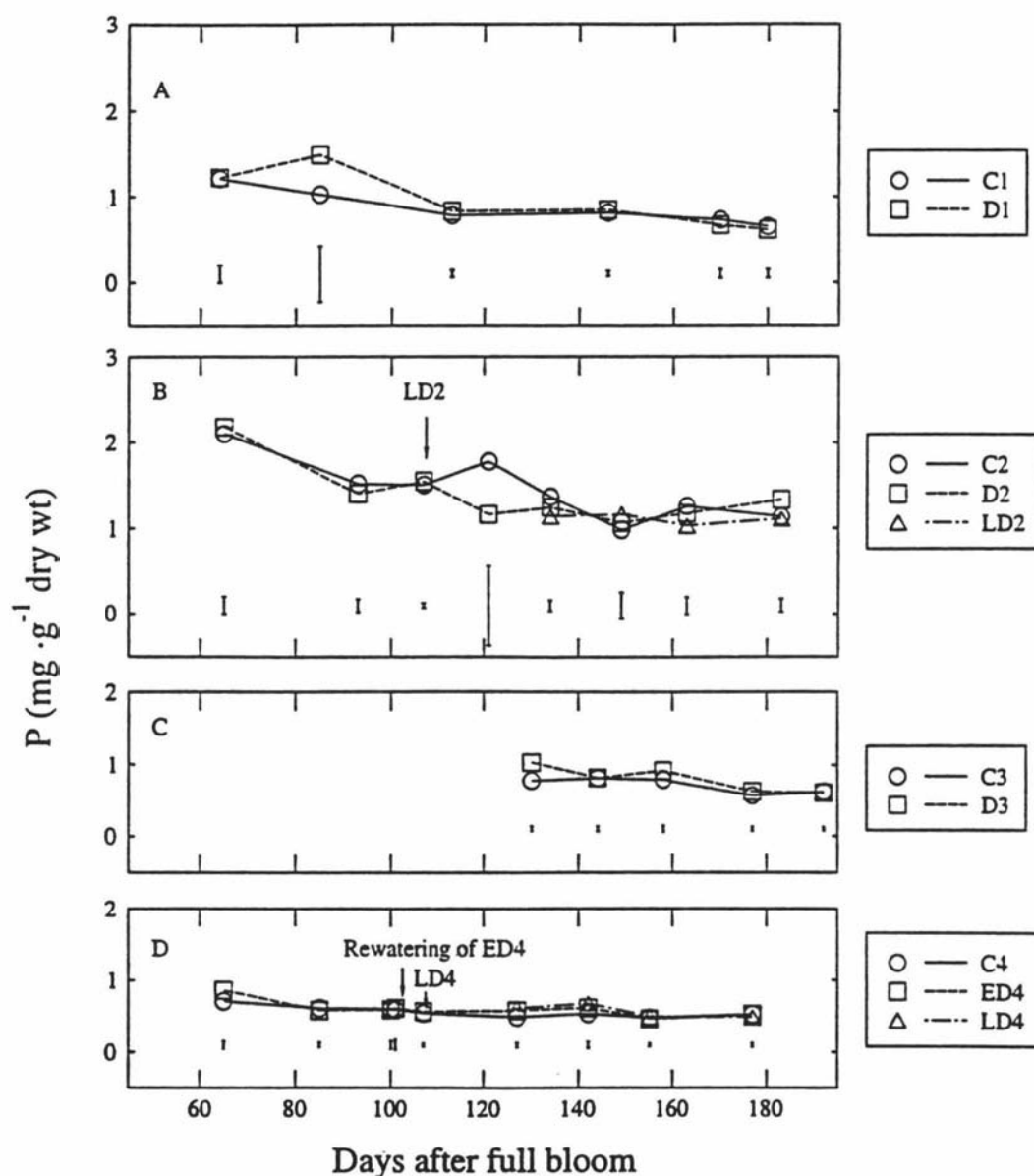


Fig. 24 Fruit P concentration for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different *n* values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 (*n*=10 upto 170 DAFB (stage 1 harvest) when *n*=6 and at 180 DAFB (stage 2 harvest) when *n*=4); D1=deficit, Expt. 1 (*n*=11 upto 170 DAFB (stage 2 harvest) when *n*=6 and at 180 DAFB (stage 2 harvest) when *n*=5); C2=control, Expt. 2 (*n*=2); D2=deficit, Expt. 2 (*n*=2); LD2=late deficit, Expt. 2 (*n*=2); C3=control, Expt. 3 (*n*=6); D3=deficit, Expt. 3 (*n*=3); C4=control, Expt. 4 (*n*=4); ED4=early deficit, Expt. 4 (*n*=4); and LD4=late deficit, Expt. 4 (*n*=4). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

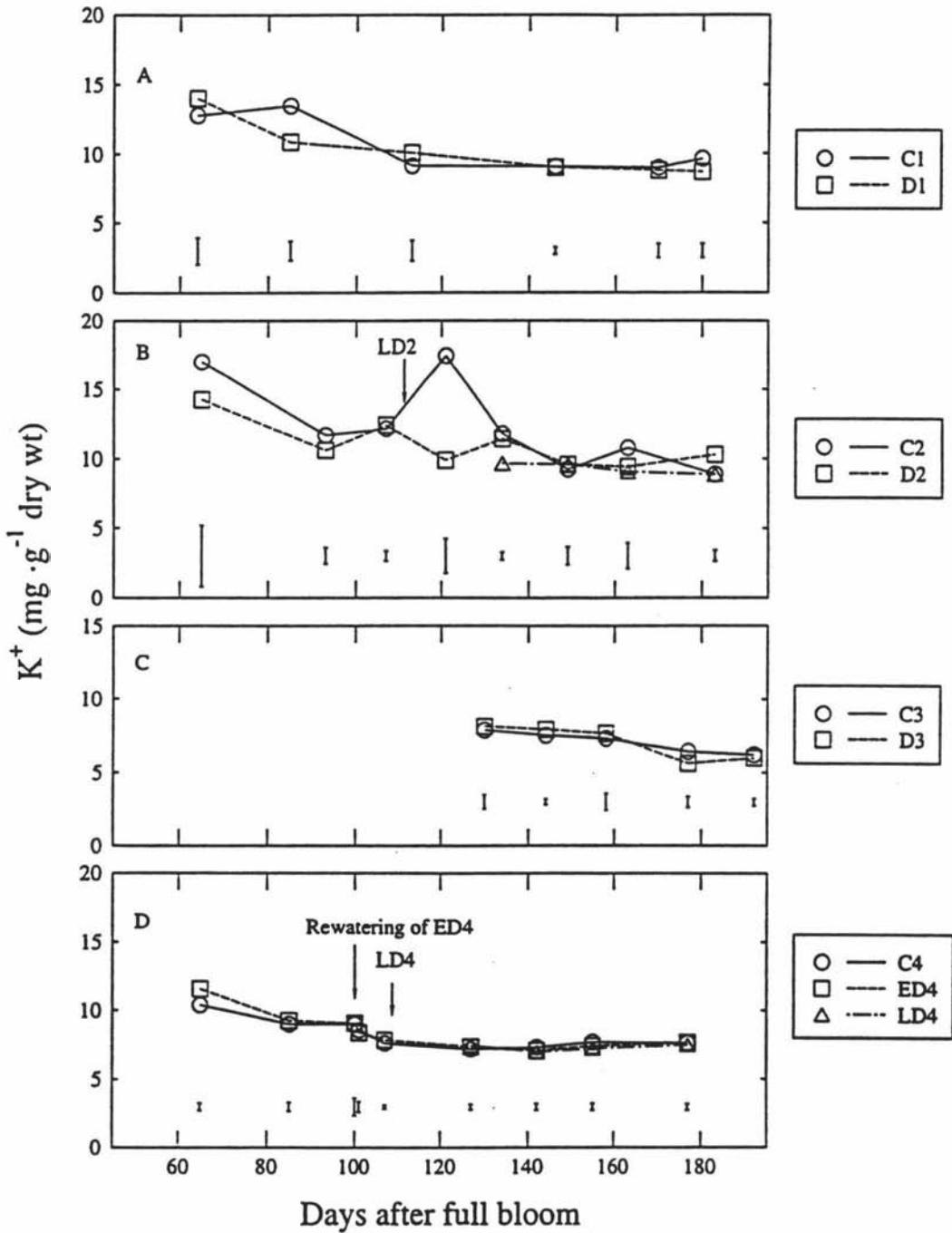


Fig. 25 Fruit K^+ concentration for Expts. 1 (A), 2 (B), 3 (C) and 4 (D). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 21 (or 12 at 170 DAFB and 9 at 180 DAFB), 4 (or 6 from 120 DAFB), 9, and 12 experimental units (trees) for A, B, C, and D respectively. When pooled experimental error differed between treatments due to different n values per treatment, the maximum error has been presented. Abbreviations are for C1=control, Expt. 1 ($n=10$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) when $n=4$); D1=deficit, Expt. 1 ($n=10$ upto 170 DAFB (stage 1 harvest) when $n=6$ and at 180 DAFB (stage 2 harvest) when $n=5$); C2=control, Expt. 2 ($n=2$); D2=deficit, Expt. 2 ($n=2$); LD2=late deficit, Expt. 2 ($n=2$); C3=control, Expt. 3 ($n=6$); D3=deficit, Expt. 3 ($n=3$); C4=control, Expt. 4 ($n=4$); ED4=early deficit, Expt. 4 ($n=4$); and LD4=late deficit, Expt. 4 ($n=4$). Arrows indicate the beginning of LD2 treatment, rewatering of ED4 treatment and the beginning of LD4 treatment.

Again differences between treatments are minimal. We can therefore conclude that water deficit has no consistent influence on fruit mineral concentration in 'Braeburn'. Similarly no significant incidence of storage disorders were observed in experiments 1, 3, and 4 for any treatments. Experiment 2 was not evaluated. Proebsting (pers. comm., 1996) suggested that although the idea may be appealing, the possibility of plant water deficit affecting fruit quality by way of influencing fruit mineral nutrition may be premature. Our results seem to support this.

Deficit irrigation has a minimal influence on fruit size, fruit firmness and fruit mineral concentration. Fruit colour, TSS and TA may be improved. Water deficit appears to have a limited impact on fruit physiological maturity based on ethylene evolution. These results indicate that deficit irrigation may be used to enhance some fruit quality attributes whilst having a minimal influence on others and that benefits obtained from DI management does not compromise yield of the fruit.

4.5 Storage attributes of fruit grown under deficit irrigation

Because fruit storage quality is of such importance in apple production, an investigation of the changes in fruit composition during storage was undertaken in Experiment 3. In this section data illustrating changes, both pre-harvest and during a 12-week storage period, in fruit composition between treatments are presented.

4.5.1 Titratable acidity

For the nine occasions that TA was measured in stored fruit, it was either slightly higher (four occasions), or significantly higher (four occasions) in D3, than in C3 fruit (Fig. 26A). Marangoni and Rossi Pisa (1985) observed an increase in the level of malic acid towards the end of the season in fruit grown under no irrigation. This observation is in agreement with our data. An overall decline in TA during fruit development was observed for all experiments (Fig. 19). This decline is partly due to higher acid synthesis within apple fruit during the early stages of cell expansion (Hansen, 1979). Synthesis of acids is reduced as the season progresses and therefore the existing acids within the fruit are diluted due to fruit growth (Ackermann et al., 1992). Acids synthesised during the early part of the season also break down as the season progresses (Hansen, 1979). A continuing but slower decline in acid content was observed during the storage period. This may be attributed to increased fruit respiration using malic acid as a metabolic substrate (Ackermann et al., 1992). The observed decline in acid content during storage was generally less in D3 than in C3 fruit (Fig. 26A).

4.5.2 Total soluble solids

Total soluble solids were higher in the D3 fruit at all measurement times and increased in both D3 and C3 fruit during storage (Fig. 26B) which is in agreement with Proebsting et al. (1984). Durand (1990) also observed an increase in TSS during storage

of 'Royal Gala' apple which had higher values in DI fruit than in the well-watered controls. She suggested that this may be due to higher starch level in the water deficit fruit at harvest which, when hydrolysed, are converted to sugars. Ebel et al. (1993) showed increased starch levels in fruit from an early-season deficit treatment at final harvest.

An increase in both TSS and TA levels in the D3 fruit both at harvest and after storage may indicate an enhancement in eating quality of these fruit (Ackermann et al., 1992) as indicated in section 4.4.4.

4.5.3 Fruit weight

The fresh weight of fruit sampled for quality assessment was not different between treatments at any collection date (Fig. 26C). The lack of difference in fruit weight between treatments under a late-season deficit is also illustrated in Fig. 15 (A, B and D), and this has been previously reported (Irving and Drost, 1987). The mean weight of all fruit per tree for Experiment 3 was also not different between treatments (data not shown). During the storage period there was a slight reduction in fruit weight which is probably due to water loss in storage. However, there was no difference in fruit weight loss between treatments. In contrast, Kilili et al. (1996) showed that weight loss of 'Braeburn' apples during storage was higher in the well watered control than in DI fruit. Similarly, Crisosto et al. (1994) reported less water loss from 'O'Henry' peach during storage if trees had been exposed to a water deficit throughout the season. There was no significant difference in crop load between treatments. Values for crop load (fruit number per tree \pm SE) were 394 ± 50.2 and 342 ± 71.0 for C3 and D3.

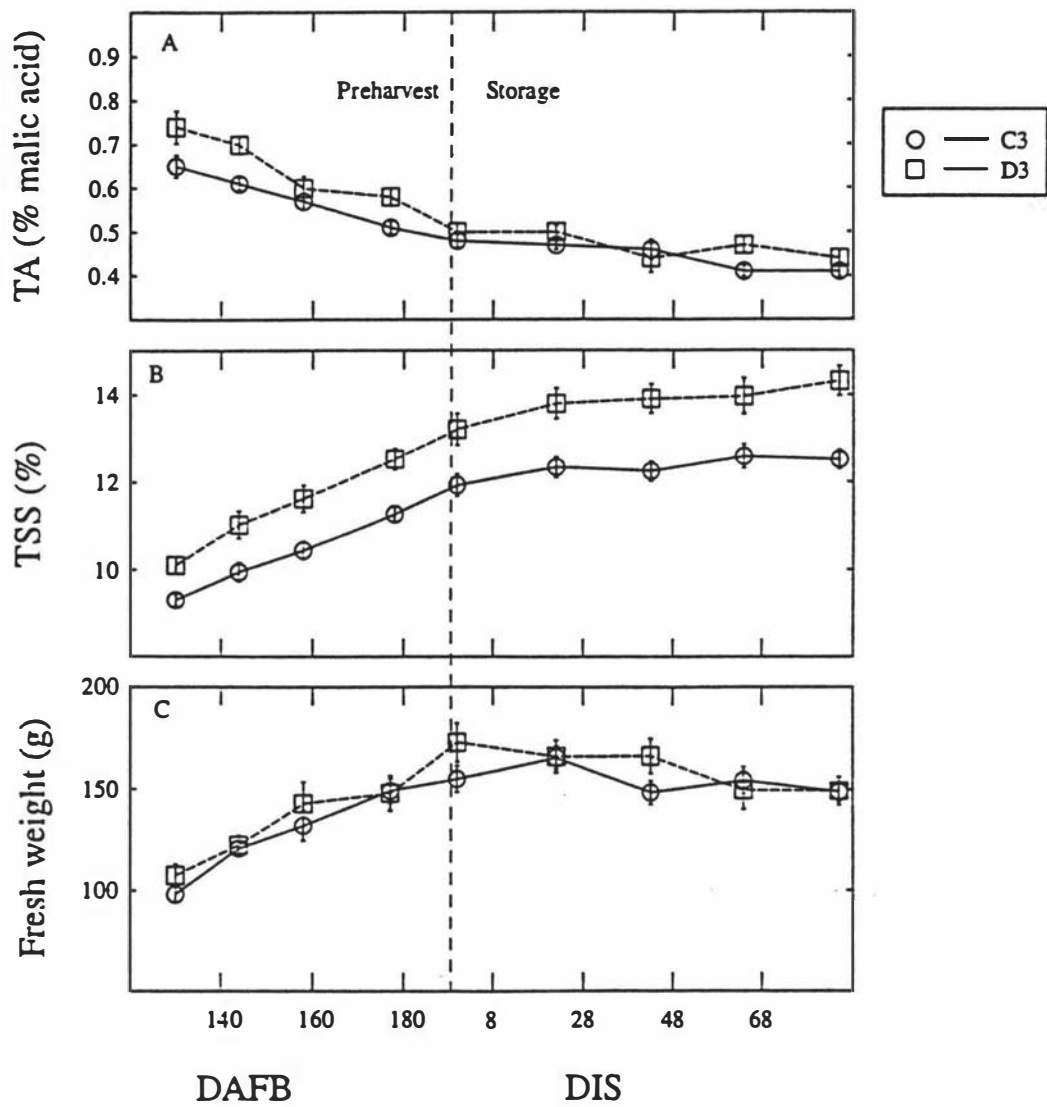


Fig. 26 Titratable acidity (TA), total soluble solids (TSS) and fresh mass for C3 and D3 fruit for days after full bloom (DAFB) and days in storage (DIS). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 9 experimental units (trees). Abbreviations are C3=control, Expt. 3 (n=6), D3=deficit, Expt. 3 (n=3).

4.5.4 Fruit sugar concentration

Figures 27 and 28 show higher concentrations ($P < 0.05$) of sucrose, sorbitol and total soluble sugars in D3 fruit than in C3 fruit at final harvest. As there was no difference in sampled fruit weight (Fig. 26C) at this time, the differences in sugar concentration are not due to dilution. All sugars increased during the first 21 days in

storage (DIS). Thereafter, sugar levels decreased to 42 DIS with glucose, sorbitol, fructose and total sugars rising again to 84 DIS. Sucrose concentrations remained constant to 63 DIS in the D3 fruit but rose sharply at 84 DIS (Fig. 27A) whereas sucrose concentrations in the C3 fruit remained approximately constant from 63 DIS. Similar trends in sugar concentration changes during storage were reported by Ackermann et al. (1992) in 'Glockenapfel' apples, and by Chan et al. (1972) in 'McIntosh' apples. Ebel et al. (1993) reported an increase in the level of both TSS and starch in fruit from deficit irrigation treatments. Landsberg and Jones (1981) reported an increase in the conversion of starch to sugars under deficit irrigation. A greater increase in sucrose level during storage in the D3 fruit when compared to C3 (Fig. 27A) may indicate a higher level of starch to sucrose conversion in these fruit although there are no data to substantiate this. Conversion of sucrose to fructose during storage appears favoured in fruit from the D3 trees, as the fructose level recorded at the end of storage was higher in these trees when compared to C3, whereas at harvest no significant difference in fructose concentration existed between treatments (Fig. 27C). The reduction in sucrose, fructose and total soluble sugars at 42 and 63 DIS may be attributed to the catabolism of sugars by respiration (Knee and Smith, 1989). Increased sugar levels at 84 DIS indicate starch hydrolysis in fruit during storage (Knee and Smith, 1989). Sorbitol concentrations in both treatments increased similarly during storage (Fig. 27D). Increased sorbitol during storage may be due to anaerobic conversion of fructose (Ackermann et al., 1992). No consistent differences in glucose concentration existed, either preharvest, or during storage.

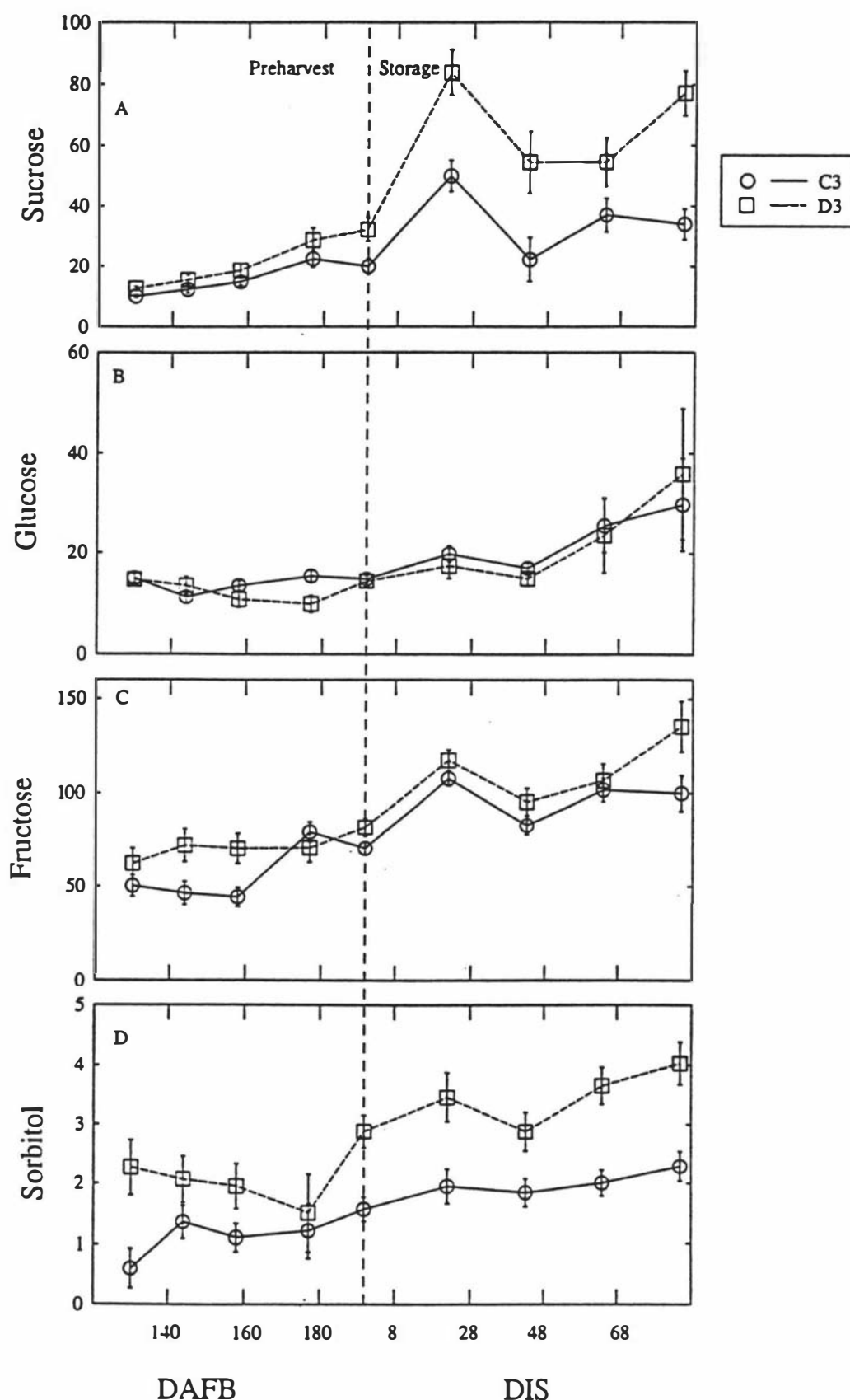


Fig. 27 Concentration ($\text{mg}\cdot\text{g}^{-1}$ fresh weight) of fructose, sucrose glucose, and sorbitol for C3 and D3 fruit for days after full bloom (DAFB) and days in storage (DIS). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 9 experimental units (trees). When pooled experimental error differed between treatments due to different n values per treatment the maximum error has been presented. Abbreviations are C3=control, Expt. 3 ($n=6$), D3=deficit, Expt. 3 ($n=3$).

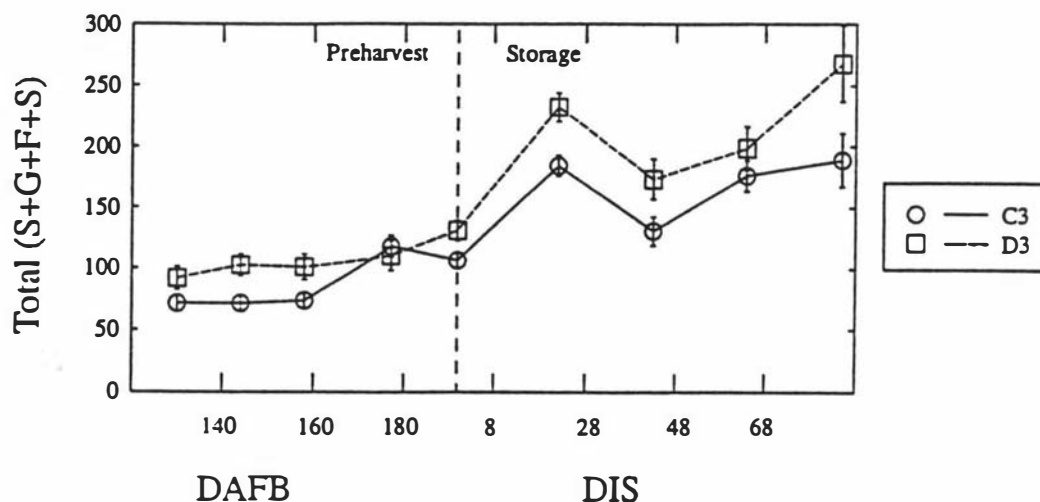


Fig. 28 Concentration ($\text{mg}\cdot\text{g}^{-1}$ fresh weight) of total soluble sugars (fructose, sucrose glucose, and sorbitol) for C3 and D3 fruit for days after full bloom (DAFB) and days in storage (DIS). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 9 experimental units (trees). Abbreviations are C3=control, Expt. 3 ($n=6$), D3=deficit, Expt. 3 ($n=3$).

4.5.5 Fruit mineral concentration

Calcium concentrations were the same in D3 and C3 fruit (Fig. 29A). This is expected since Ca^{2+} uptake into the fruit predominantly occurs in the early stages of fruit expansion (Ferguson and Watkins, 1989). This is probably prior to the development of water deficit in the D3 treatment. No significant changes in Ca^{2+} concentration during storage was observed with time or between treatments.

Spraying of CaCl_2 is common commercial practise in New Zealand and may further minimise the impact that deficit irrigation might have on fruit Ca^{2+} concentration. Regular CaCl_2 sprays were applied to experimental trees in this study. Low values of Ca^{2+} measured at 192 DAFB (Fig. 29A) are inconsistent with all the other values. We therefore assume there has been an analytical error in the Ca^{2+} determination at this time.

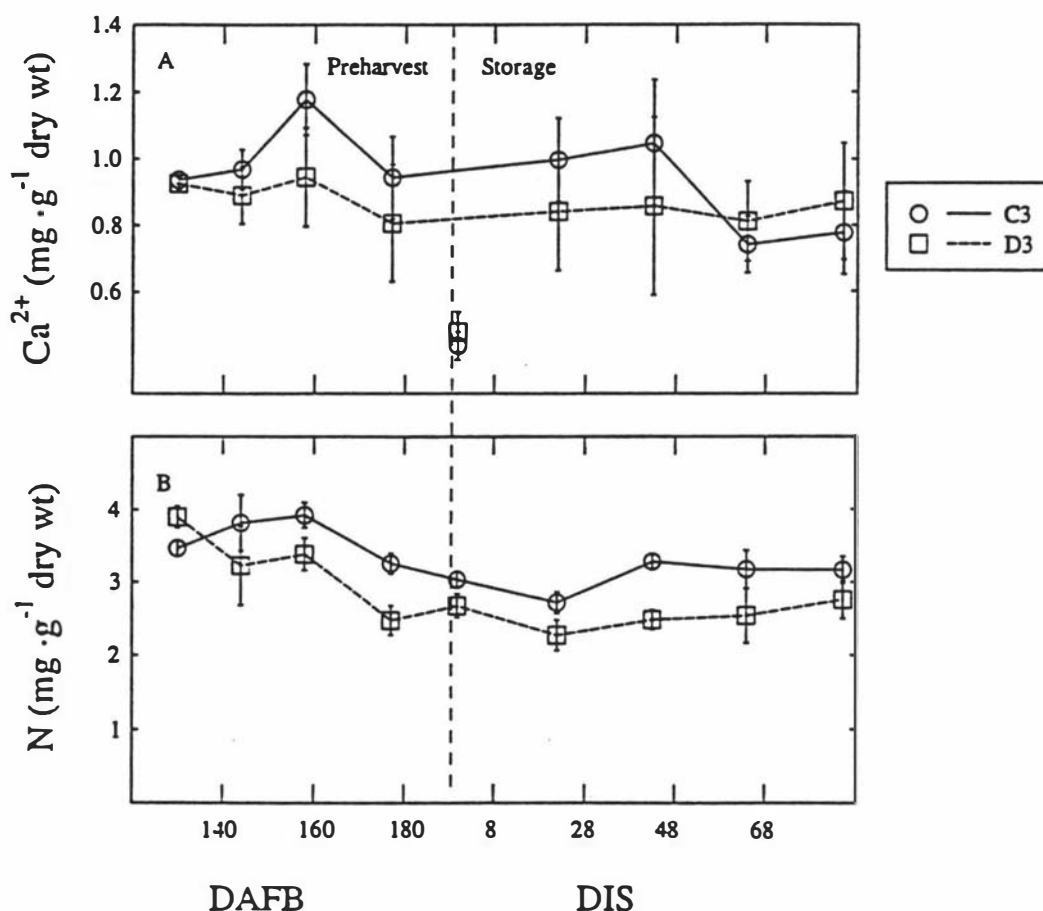


Fig. 29 Concentration of calcium and nitrogen for C3 and D3 fruit for days after full bloom (DAFB) and days in storage (DIS). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 9 experimental units (trees). Abbreviations are C3=control, Expt. 3 (n=6), D3=deficit, Expt. 3 (n=3). An analytical error has been assumed responsible for the outlier at 192 DAFB as no rational explanation for this anomaly can be offered.

A significant reduction in N content of the D3 fruit, compared to C3, was observed at some sampling times both preharvest and during storage (Fig. 29B). Nitrogen levels are important to the storage quality of apples (Bramlage, 1993) with a reduced N level being advantageous in general (section 4.4.7). No differences were observed between treatments for the concentration of Mg^{2+} , P, and K^{+} during storage (Data not shown).

In conclusion, these data suggest that fruit attributes which are modified

preharvest due to tree water deficit, also show treatment differences during the storage period. Differences in the conversion of sugars between treatments may indicate differences in enzymatic activity both pre- and post-harvest. For example an increased level of sucrose accumulation in the D3 fruit during the storage period may indicate that the activity of acid invertase, a sucrose metabolizing enzyme, has been reduced, or that the activity of either sucrose synthase and/or sucrose-phosphate synthetase is increased (Yamaki and Ishikawa, 1986). Elaboration on this, however, is beyond the scope of my data. The lack of storage disorders observed for either treatment indicates that deficit irrigation does not increase the susceptibility of fruit to storage disorders.

4.6 Fruit water relations

In recent years much research has been carried out on the water relations of the vegetative portion of apple trees (Jones et al., 1991; Wang and Stutte, 1992; Wang et al., 1995; Yoon, 1995). These studies have attempted to evaluate the level of osmotic adjustment which may take place in the leaves, roots or stems of apple trees under water stress. Jones et al. (1985) stated that the most obvious organ demonstrating osmotic adjustment is the fruit. However, studies on the water relations of apple fruit are scarce. Research on other fruit water relations include studies on tomato (Ho et al., 1987), cotton fruit (Van Iersel and Oosterhuis, 1995), grape (Matthews et al., 1987), citrus (Syvertsen and Albrigo, 1980) and Asian pear (Behboudian et al., 1994a).

Osmotic adjustment is defined as a reduction in water potential which is accompanied by a similar decline in osmotic potential. This results in the maintenance of turgor within the organ under investigation. Pavel and DeJong (1995) found that the most important component of fruit osmotic potential of apple is soluble carbohydrates with decreasing fruit osmotic potential (becoming more negative) over the growing season as sugar concentration increases. Pavel and DeJong (1995) state that fructose contributes most to solute potential in 'Golden Delicious' and 'Cox's Orange Pippin' fruit. Ho et al. (1987) investigated fruit osmotic adjustment in tomato in relation to fruit composition. They found that K^+ ions play an important role in osmotic potential of these fruit. Ho et al. (1987) also suggested that organic acids may contribute to fruit solute potential.

Information on the influence of fruit composition on fruit water relations is limited. Even less is available on the response of fruit water relations to water deficit conditions. Recent studies on the influence of water deficit on fruit water relations and

composition include that of Behboudian et al. (1994a) who studied Asian pears and Failla et al. (1992) who studied changes in fruit composition of apple under DI and speculated on the influence this may have on fruit water relations. Ho et al. (1987) compared plants grown in nutrient solutions having different electrical conductivities indicating different osmotic potentials whose low values may mimic water deficit conditions.

The following section investigates the influence of plant water deficit on fruit water relations and explores the occurrence of osmotic adjustment in apple fruit in relation to fruit composition, specifically fruit sugar concentration.

4.6.1 Fruit water potential and its components

Fruit water potential (Ψ_{fw}), osmotic potential (Ψ_{fs}), and turgor potential (Ψ_{fp}) were evaluated throughout the season in Experiments 2 and 4 using hygrometer equipment (Figs. 30, 31, 32, and 33). In Experiment 4 diurnal values of fruit water relations were also measured (Figs. 37, 38, and 39).

Figure 30 illustrates the components of fruit water potential measured during Experiment 2. For D2 fruit Ψ_{fw} was reduced ($P < 0.10$) compared to C2 at 93 and 121 DAFB (Fig. 30A). Osmotic potential was also similarly reduced (Fig. 30B) resulting in the maintenance of Ψ_{fp} (Fig. 30C). This suggests the possibility of osmotic adjustment in apple fruit under DI.

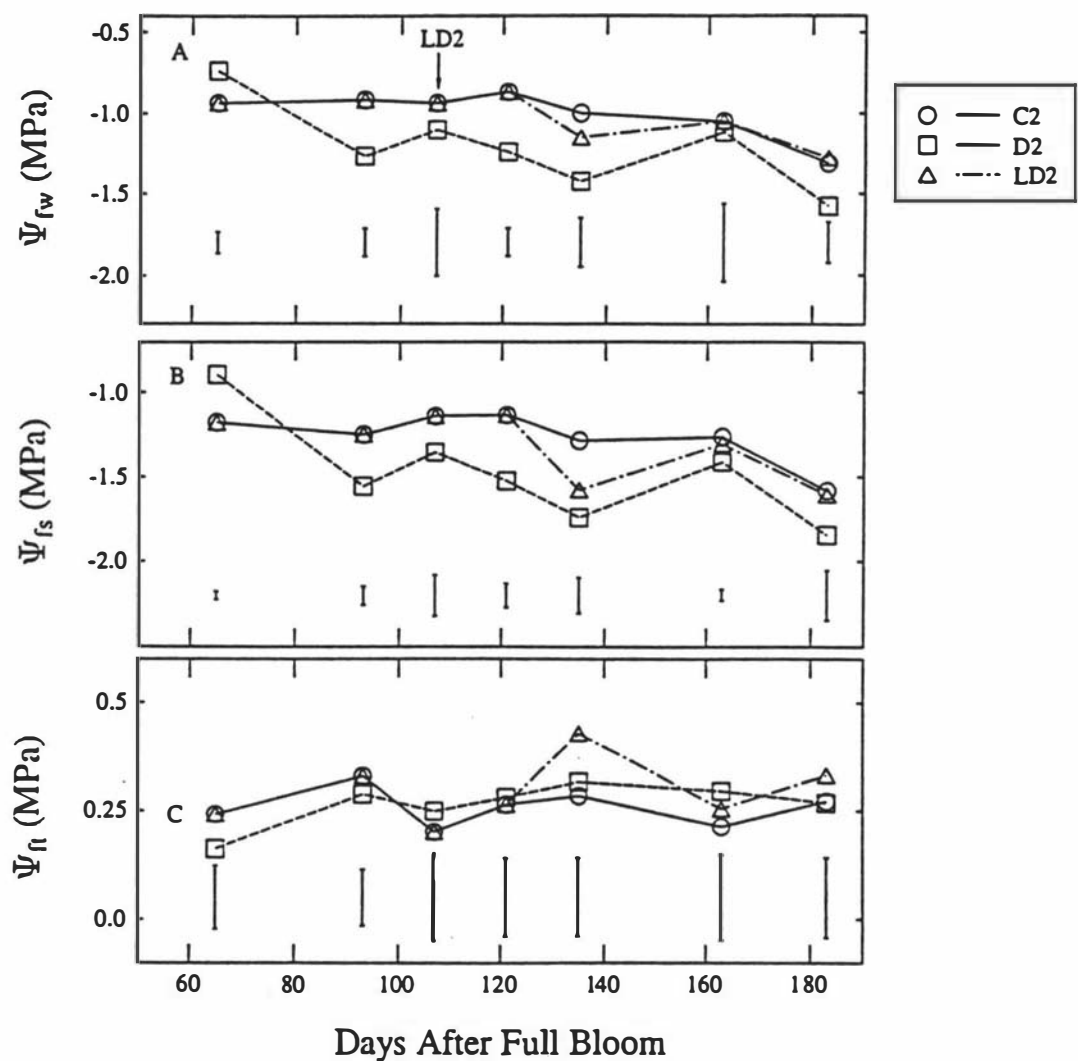


Fig. 30 Fruit water potential (Ψ_{fw}) (A), osmotic potential (Ψ_{fs}) (B), and turgor potential (Ψ_n) (C) measured at midday during the season for C2, D2 and LD2 in Expt. 2. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 from 120 DAFB) experimental units (trees). Abbreviations are C2=control, (n=2), D2=deficit, (n=2), and LD2=late deficit, (n=2). Arrows indicate the beginning of LD2.

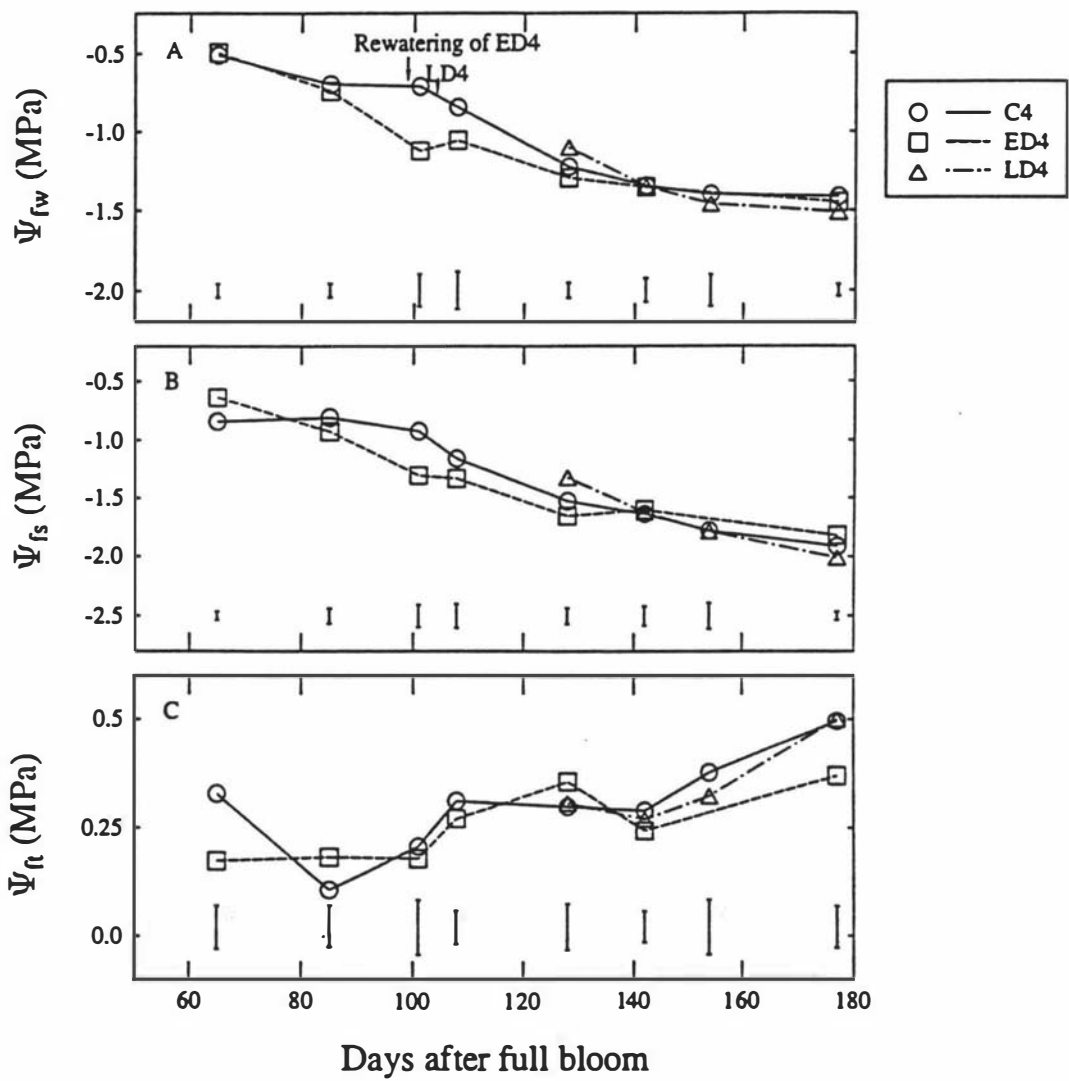


Fig. 31 Fruit water potential (Ψ_{fw}) (A), osmotic potential (Ψ_{fs}) (B), and turgor potential (Ψ_{fp}) (C) measured at predawn during the season for C4, ED4 and LD4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 8 (or 12 from 128 DAFB) experimental units (trees). Abbreviations are C4=control, Expt. 4 (n=4), ED4=early deficit, Expt. 4 (n=4), and LD4=late deficit, Expt. 4 (n=4). Arrows indicate time of rewatering of the ED4 trees and the beginning of the LD4.

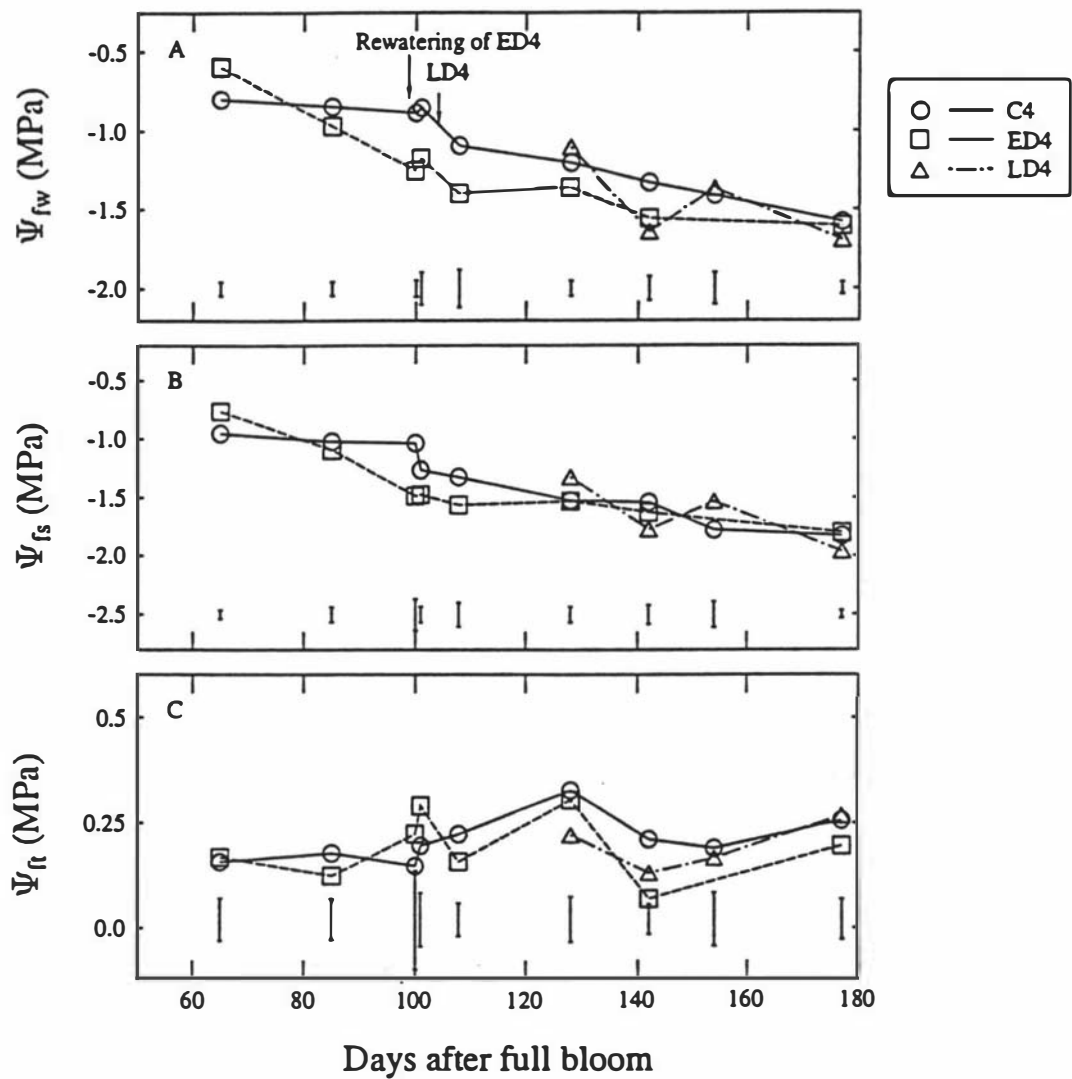


Fig. 32 Fruit water potential (Ψ_{fw}) (A), osmotic potential (Ψ_{fs}) (B), and turgor potential (Ψ_t) (C) measured at midday during the season for C4, ED4 and LD4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 8 (or 12 from 128 DAFB) experimental units (trees). Abbreviations are C4=control, Expt. 4 (n=4), ED4=early deficit, Expt. 4 (n=4), and LD4=late deficit, Expt. 4 (n=4). Arrows indicate time of rewatering of the ED4 trees and the beginning of the LD4.

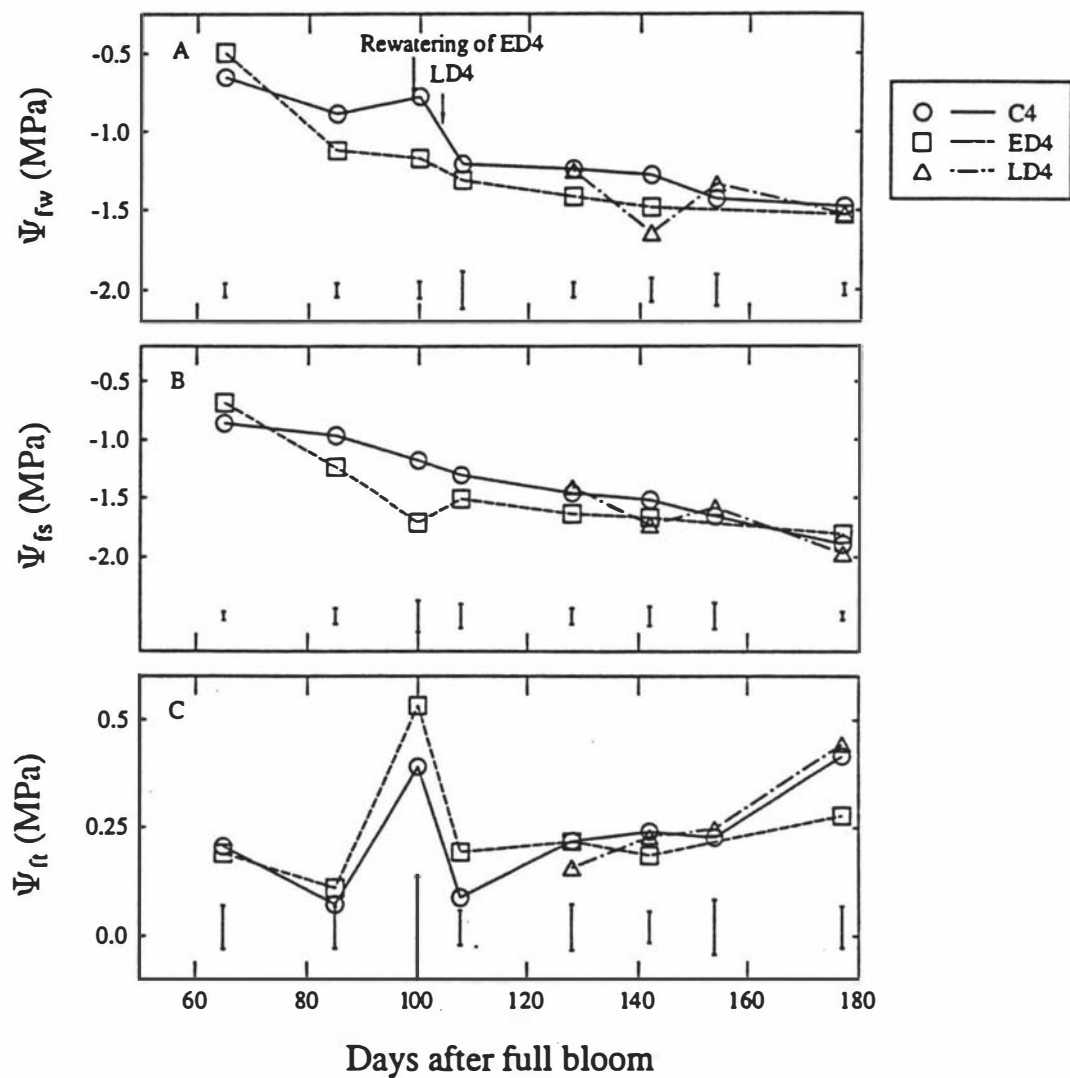


Fig. 33 Fruit water potential (Ψ_{fw}) (A), osmotic potential (Ψ_{fs}) (B), and turgor potential (Ψ_t) (C) measured at dusk during the season for C4, ED4 and LD4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 8 (or 12 from 128 DAFB) experimental units (trees). Abbreviations are C4=control, Expt. 4 (n=4), ED4=early deficit, Expt. 4 (n=4), and LD4=late deficit, Expt. 4 (n=4). Arrows indicate time of rewatering of the ED4 trees and the beginning of the LD4.

Similar results are presented for Experiment 4 for components of fruit water potential measured diurnally (Fig. 31 (predawn), Fig. 32 (midday), and Fig. 33 (dusk)) with values of Ψ_{fw} in ED4 fruit generally being lower than for C4 fruit during the stress period (Figs. 31, 32, and 33; Appendix 2, Table 1 for P values). An exception being at 65 DAFB, just after the beginning of the water deficit period (Figs. 31, 32, and 33). Differences between treatments were apparent irrespective of the time of day. As was the case for Experiment 2, in Experiment 4 a reduction in Ψ_{fw} was coupled with the reduction in Ψ_{fs} which resulted in the maintenance of turgor in DI fruit at levels equivalent to the controls (Figs. 31C, 32C, and 33C; Appendix 2, Table 1 for P values) during the stress period. Periodic reduction in turgor of ED4 compared to C4 was measured following rewatering of the ED4 fruit (Appendix 2, Table 1 for P values). This did not result in a reduction in final fruit size of the ED4 compared to C4. Full recovery of Ψ_{fw} in the ED4 fruit did not occur until 42 days after rewatering. These 1995 data support the 1994 data that suggests turgor maintenance via a reduction in Ψ_{fs} occurs in apple fruit if water deficit is induced during the early part of the growing season.

Water deficit induced during the later stages of fruit growth did not result in consistent differences in water potential components between LD2 and C2 and LD4 and C4 fruit in either Experiments 2 or 4 respectively (Figs. 30, 31, 32, and 33; Appendix 2, Table 1 for P values). These results are in agreement with those reported by Behboudian et al. (1994a) who showed that a water deficit late in the season minimally affected fruit water relations of Asian pear. This may be due to the relative strength of the near mature fruit as a sink for water and carbohydrates. Because Ψ_{fs} of all fruit gets lower through the season as fruit ripen (Figs. 30B, 31B, 32B, and 33B) fruit become

more effective competitors for available water. Thus, fruit water relations may be unaffected despite a reduction in the Ψ_1 of the tree.

4.6.2 Fruit sugar composition and its relation to fruit water relations.

Evidence for osmotic adjustment in apple leaves has been previously presented (Lakso et al., 1984; Fanjul and Rosher, 1984; Wang and Stutte, 1992; Wang et al., 1995). Sorbitol, the major sugar present in the leaves of apple (Wang and Stutte, 1992), is known to increase in leaves of water stressed apples (Wang and Stutte, 1992; Wang et al., 1995). Wang and Stutte (1992) and Fanjul and Rosher (1984) observed that sugar accumulation in leaves was important in apple leaf osmotic adjustment.

Osmotic adjustment in fruit, however, has been a matter of conjecture. Some work has been done on the contribution of various compounds to osmotic potential. Pavel and DeJong (1995) state that fructose contributed the most to solute potential of 'Golden Delicious' and 'Cox's Orange Pippin' apple fruit. Sucrose makes the next largest contribution in 'Cox's Orange Pippin', however, both glucose and sucrose are important components of the solute potential in 'Golden Delicious'. Pavel and DeJong (1995) calculated from Berüter's (1989) data that sugars contribute about 46% early in the season and approximately 86% later in the season to fruit solute potential of apple. Behboudian et al. (1994a) measured an increase in fruit sugar concentration at the end of an early-season water deficit in Asian pear. We may, therefore, expect that, similar to leaves, both the concentration and composition of fruit sugars are modified under DI and relate to changes in Ψ_{fw} and Ψ_{fs} .

An increase in total sugar concentration was measured during an early-season water deficit in the D2 and ED4 fruit from Experiments 2 and 4 (Fig. 34) ($P < 0.10$ at 93 DAFB, $P < 0.05$ at 121 DAFB and $P < 0.02$ at 134 DAFB in D2; $P < 0.001$ at 100

and 101 DAFB in ED4). This corresponds to the general reduction in Ψ_{fs} at this time (Figs. 30, 31, 32, and 33). As the reduction in Ψ_{fs} is similar to that observed for Ψ_{fw} , Ψ_{fp} is maintained during the early season DI. The evaluation of individual sugars indicates that increases in total sugar concentrations are due to increased levels of glucose, fructose, and sorbitol during the stress period in both 1994 and 1995 (Fig. 35 and 36).

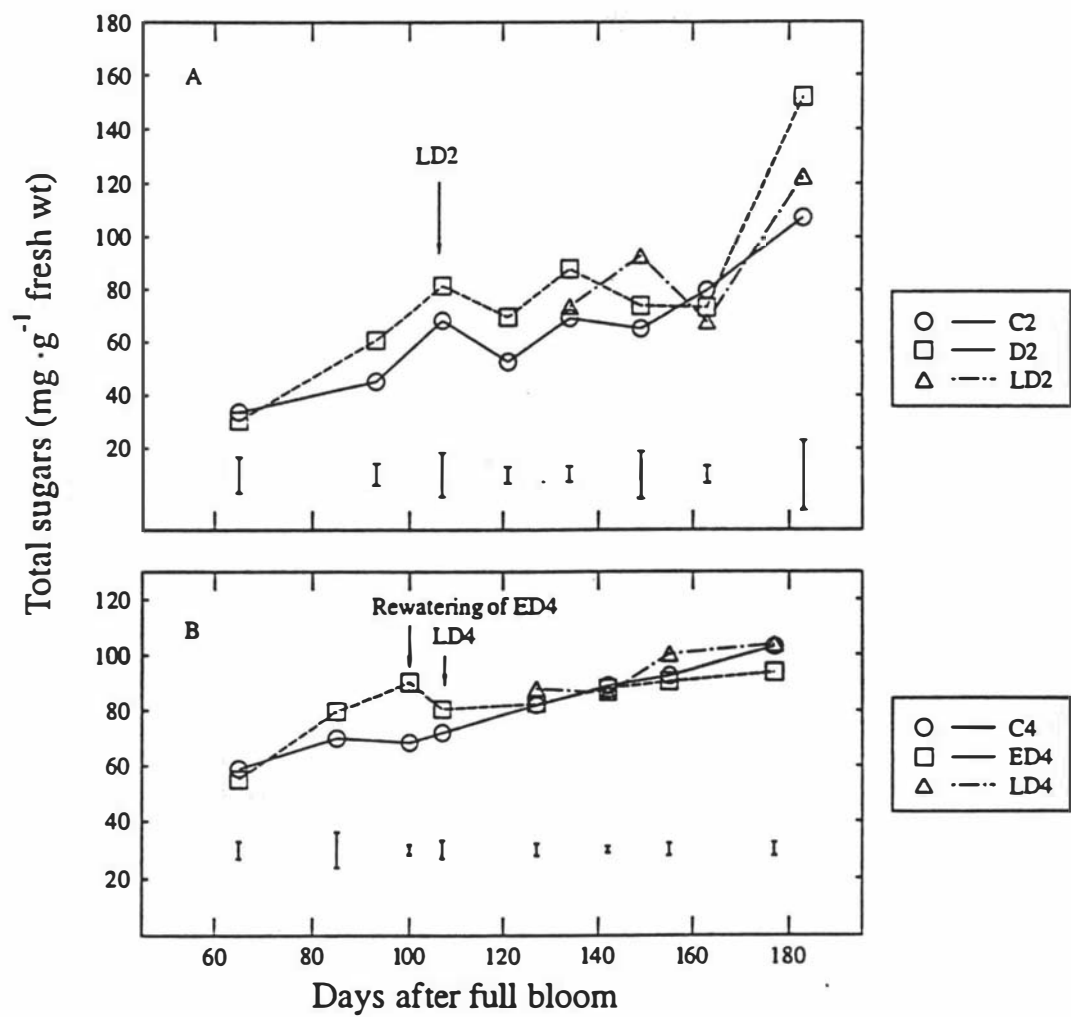


Fig. 34 Mean total sugar concentration for fruit of Expt. 2 (A) and Expt. 4 (B). Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 from 134 DAFB), and 8 (or 12 from 128 DAFB) experimental units (trees) for A and B respectively. Abbreviations are C2=control, Expt. 2 (n=2), D2=deficit, Expt. 2 (n=2), LD2=late deficit, Expt. 2 (n=2). C4=control, Expt. 4 (n=4), ED4=early deficit, Expt. 4 (n=4), and LD4=late deficit, Expt. 4 (n=4). Arrows indicate the beginning of the LD2 treatment, time of rewatering of the ED4 treatment and the beginning of the LD4 treatment.

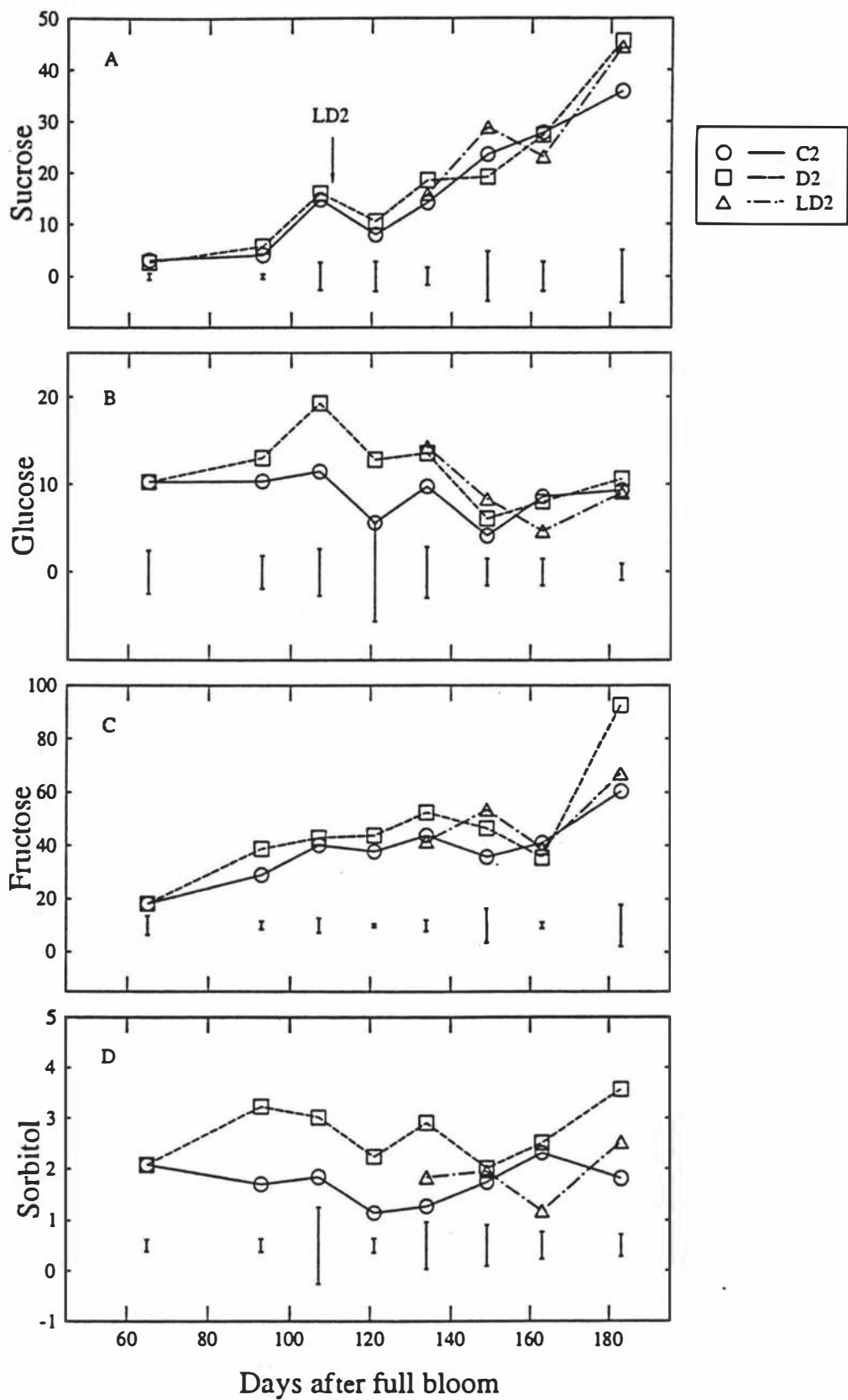


Fig. 35 Mean concentration of sucrose (A), glucose (B), fructose (C), and sorbitol (D) (mg g⁻¹ fresh wt) for Expt. 2. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 4 (or 6 from 134 DAFB) experimental units (trees). Abbreviations are C2=control (n=2), D2=deficit (n=2), and LD2=late deficit (n=2). Arrows indicate the beginning of the LD2 treatment.

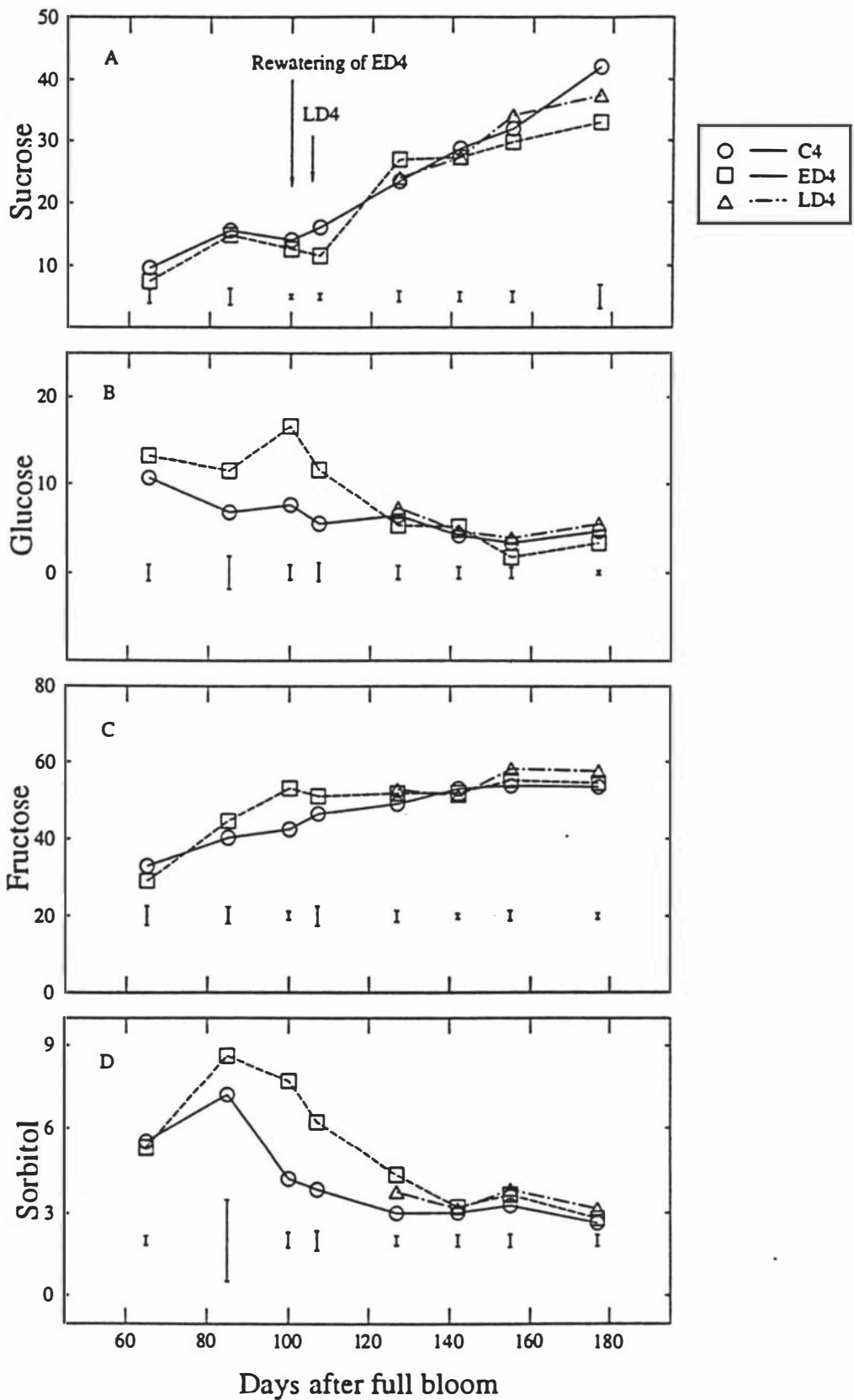


Fig. 36 Mean concentration of sucrose (A), glucose (B), fructose (C), and sorbitol (D) (mg g^{-1} fresh wt) for Expt. 4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 8 (or 12 from 128 DAFB) experimental units (trees). Abbreviations are C4=control ($n=4$), ED4=early deficit ($n=4$), and LD4=late deficit ($n=4$). Arrows indicate the time of rewatering of the ED4 treatment and the beginning of the LD4 treatment.

Other compatible solutes such as K^+ and organic acids have also been reported as instrumental in osmotic adjustment of tomato fruit (Ho et al., 1987) and may play a role in the osmotic adjustment in the fruit of apple (Pavel and DeJong, 1995). Failla et al. (1992) found that under water deficit conditions, induced during the early part of the growing season, the concentration of K^+ , Ca^{2+} , and Mg^{2+} was increased in apple fruit. A water deficit induced later in the season only increased K^+ levels. Data for Ca^{2+} , Mg^{2+} , and K^+ (Fig. 22D, 23D, and 25D) showed no consistent or significant differences between treatments for Experiment 4. Results for Experiment 2 (Figs. 22B, 23B, and 25B) are also similar, but at final harvest fruit K^+ concentration was significantly higher in the D2 fruit than C2 or LD2 (Fig. 25B). The K^+ concentration prior to this was not different between treatments. Additionally, Ca^{2+} was higher ($P < 0.05$) in D2, than in C2 fruit at 121 DAFB. But again, these differences were not consistent over the stress period. Titratable acidity, measured as percent malic acid, tended to be higher in fruit of the D2 and ED4 treatments during the stress period (Fig. 19, B and D). This may indicate that organic acids make a contribution to apple fruit solute potential.

Multiple regression analysis of the individual sugars (sucrose, glucose, fructose, and sorbitol), K^+ , Ca^{2+} , Mg^{2+} , and malic acid on Ψ_{fs} indicates that sucrose contributes most to the total R^2 for the model. Other significant contributors to R^2 include glucose, K^+ , malic acid, and sorbitol (Table 9). The large contribution of sucrose to the total R^2 may be due to the relative increase in sucrose concentration as the season progresses compared to changes in other solutes. Figure 36 shows that sucrose concentration increases more than any other sugar during the season and that fructose, although the most abundant sugar, shows a minimal increase during the season. The Ψ_{fs} becomes more negative as the season progresses predominantly due to increased sugar

concentration (Fig. 34). The increase in sucrose concentration predominantly accounts for the increase in total sugar concentration from 85 DAFB as fructose concentration shows minimal change after this time. The significant contribution of both glucose and sorbitol to the Ψ_{fs} may be because both these sugars show an increase during the ED4 stress period (Fig. 36, B and D) when Ψ_{fs} of the ED4 fruit was more negative than the C4 treatment (Fig. 31B, 32B, and 33B). The same may be true for TA (Fig. 19). Morgan (1980) indicates K^+ may be an important osmotic constituent. The K^+ concentration is indicated as a contributor to Ψ_{fs} in Table 9. However, changes in fruit K^+ concentration during the season is minimal, and no difference between treatments is apparent (Fig. 25).

Rewatering of the ED4 fruit resulted in a gradual decline in total sugar concentration so that at final harvest the sugar concentration was lower than either C4 or LD4 fruit. This may be due to dilution of sugar concentration (Chalmers et al., 1985).

Table 9. The partial R² contribution and total R² for multiple variable regression of various solutes on Ψ_{fs} and the contribution of each solute to R² for Experiment 4.

Solute	Partial R ² contribution
Sucrose	0.38 *
Glucose	0.075 *
K ⁺	0.035 *
Malic acid	0.013 *
Sorbitol	0.0142 *
Ca ²⁺	0.0014 ns
Mg ²⁺	0.0007 ns
Fructose	0 ns
Total R ²	0.52

ns and * indicate no significant contribution to the model or significance at *P* < 0.05.

An estimated contribution of individual solutes to the observed difference in Ψ_{fs} between ED4 and C4 treatments during the ED4 stress period was calculated using van't Hoff's equation (Salisbury and Ross, 1992, p. 21) as follows:

$$\Psi_{fs} = -miRT$$

- where
- Ψ_{fs} = osmotic potential (bars)
 - m = molality of the solution (moles of solute/1000g H₂O)
 - i = a constant that accounts for ionization of the solute and/or other deviations from perfect solutions.
 - R = the universal gas constant (0.0831 litre bars/mol degree)
 - T = absolute temperature (degree K)

Table 10 gives the contribution of individual sugars and malic acid to the difference in Ψ_{fs} between treatments in Experiment 4. Only solutes that showed increased

concentration in the ED4 fruit during the ED4 stress period are included.

Table 10. The contribution of individual solutes to the decreased Ψ_{fs} observed in the ED4 fruit during the stress period.

DAFB	Ψ_{fs} difference between C4 and ED4. (MPa)	Solute	Contribution to difference in Ψ_{fs} (MPa)
85	0.153	Glucose	0.06
		Malic acid	0.081
		Total contribution	0.141
100 and 101	0.491	Glucose	0.119
		Fructose	0.150
		Sorbitol	0.02
		Malic acid	0.03
		Total contribution	0.319
108	0.206	Glucose	0.081
		Sorbitol	0.013
		Malic acid	0.010
		Total contribution	0.104

Table 10 indicates that an increase in solutes that were measured accounts for some of the reduction in Ψ_{fs} measured in the ED4 fruit during a water deficit. Discrepancies between calculated Ψ_{fs} differences and measured values should be due to other solutes that were not measured but may have contributed to the difference in Ψ_{fs} between treatments.

Fruit size may have an influence on fruit sugar concentration as larger fruit give a lower concentration of sugars due to a dilution effect. In Experiment 2 no significant reduction in fruit size was observed in the D2 fruit until 135 DAFB (Fig. 15B). A trend of increased total sugar concentration was, however, measured from 93 DAFB (Fig.

34A). In Experiment 4, fruit from the ED4 treatment were smaller than the C4 fruit during the deficit period (Fig. 15D).

The data on fruit water relations show that despite a reduction in tree water status, Ψ_{fp} is generally maintained. The importance of turgor maintenance for organ growth has been repeatedly emphasized (Goode and Higgs, 1973; Morgan 1980; Hsiao et al., 1976; Hsiao, 1993). In Experiment 2, fruit size of D2 was significantly reduced compared to C2 and LD2 from 135 DAFB despite maintenance of turgor. In the 1995 season, fruit size was significantly reduced in the ED4 fruit during an early-season water deficit while Ψ_{fp} was maintained. Osmotic adjustment, therefore, does not result in the maintenance of growth in apple fruit under deficit irrigation. Munns (1988) challenged the current thinking on the role of turgor maintenance and osmotic adjustment in plant growth. One of the overall conclusions reached in Munns (1988), is that all studies on plants in a drying soil that have followed growth as well as osmotic adjustment, reveal that osmotic adjustment does occur while growth is also decreased. This is in agreement with the data here. The direct evidence for the necessity of turgor for growth has still to be demonstrated (Sinclair and Ludlow, 1985). Factors such as cell wall elasticity may allow turgor maintenance in fruit cells with a reduction in cell size (Dainty, 1976). This may have been the mechanism for size reduction and turgor maintenance in the D2 and ED4 fruit. However, the scope of my data does not allow substantiation of this.

4.6.3 Diurnal fruit water relations

Fruit, like leaves are reported to demonstrate diurnal fluctuations in water potential (Chapman, 1971). Maximum Ψ_{fw} were generally recorded predawn (Figs. 37A, 38A, 39A). During the day, fruit water potential generally dropped. However, differences were minimal and not significant in many cases (Appendix 2, Tables 2, 3,

and 4). This is unlike leaves which demonstrate large diurnal variation in Ψ_1 (Figs. 5 and 6).

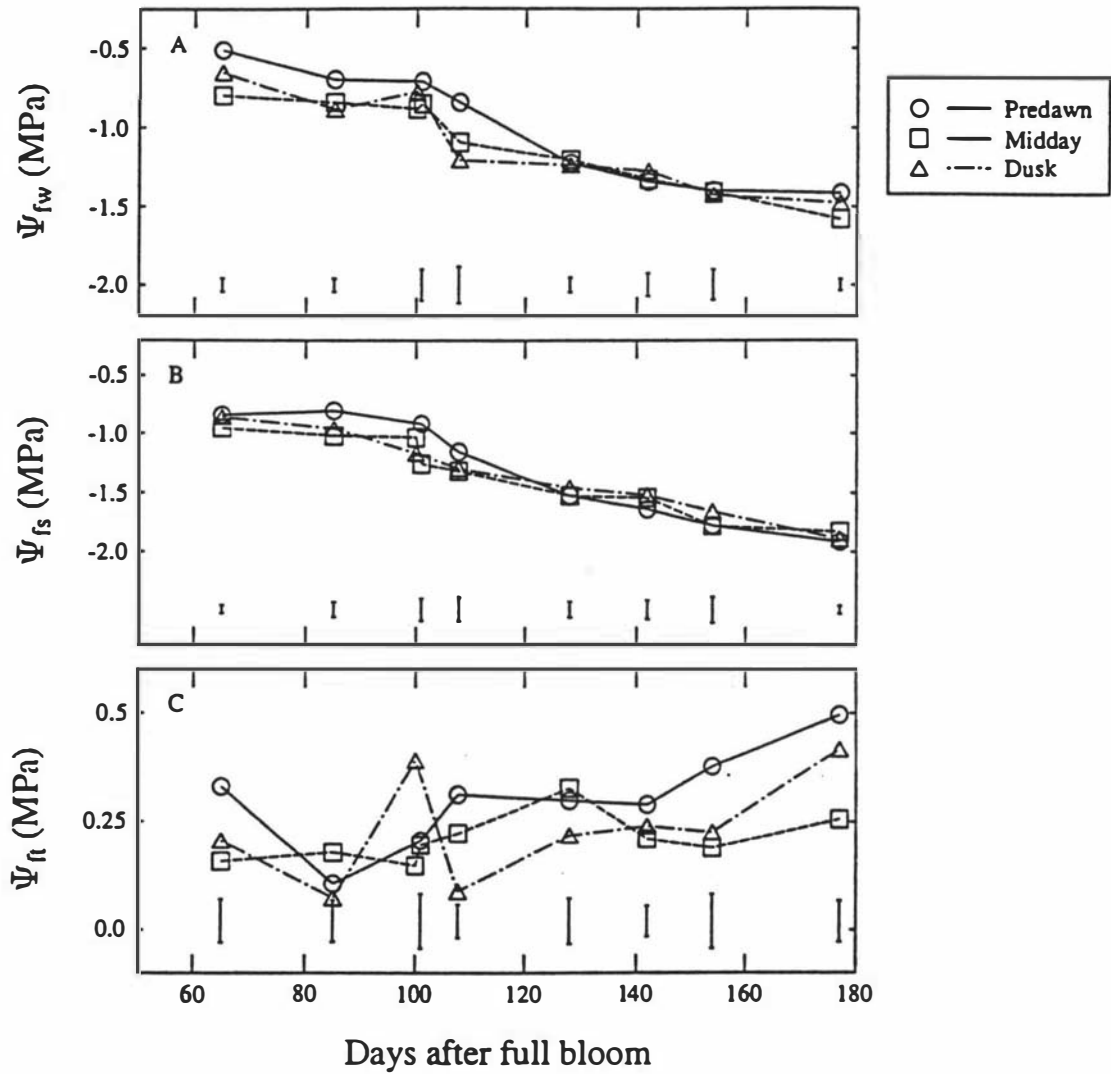


Fig. 37 Fruit water potential (Ψ_{fw}) (A), osmotic potential (Ψ_{fs}) (B), and turgor potential (Ψ_t) (C) measured on C4 (n=4) at predawn, midday and dusk throughout the season in Expt. 4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 8 (or 12 from 128 DAFB) experimental units (trees).

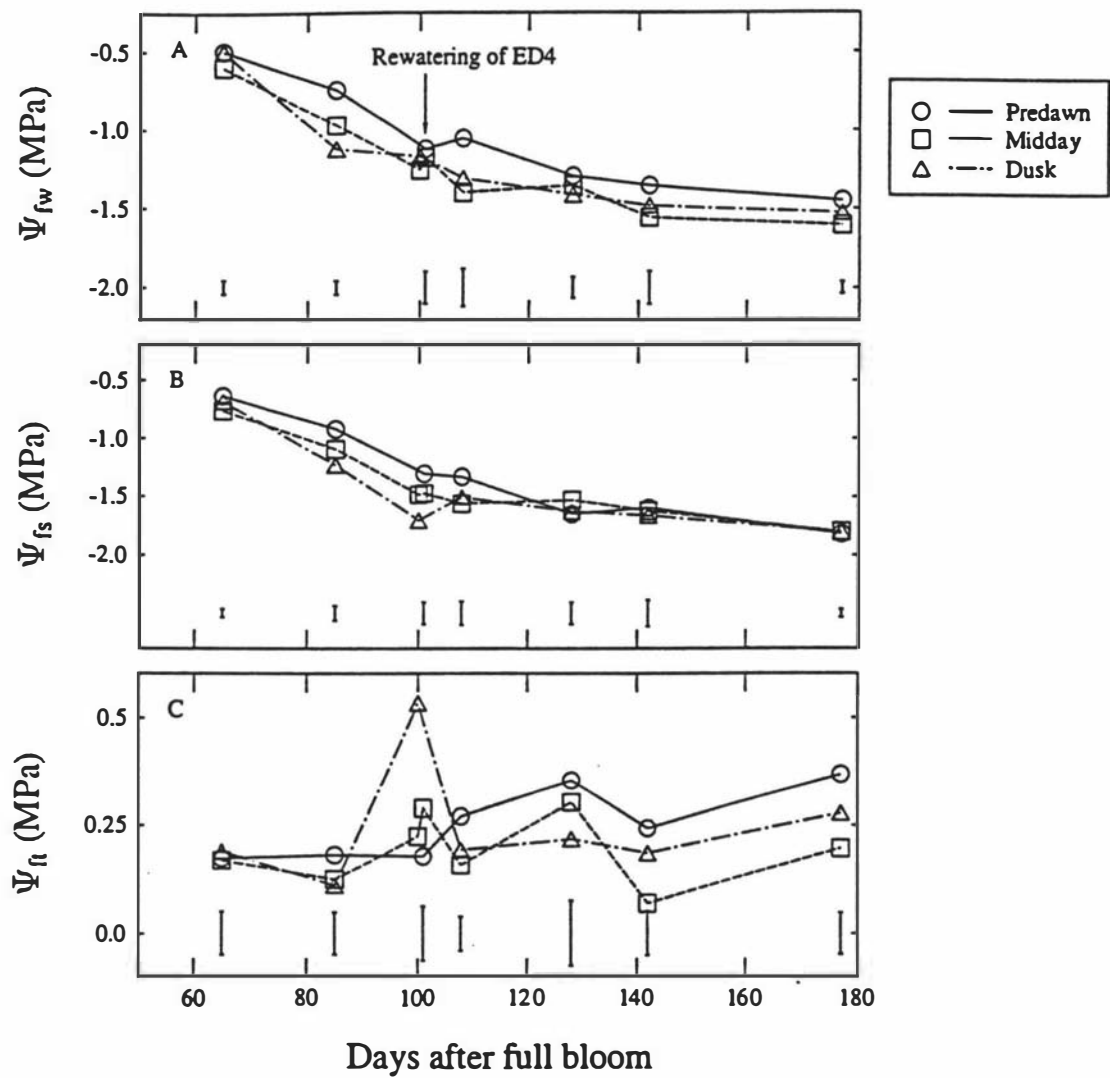


Fig. 38 Fruit water potential (Ψ_{fw}) (A), osmotic potential (Ψ_{fs}) (B), and turgor potential (Ψ_{fp}) (C) measured on ED4 (n=4) at predawn, midday and dusk throughout season in Expt. 4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 8 (or 12 from 128 DAFB) experimental units (trees). Arrows indicate time of rewatering of the ED4 treatment.

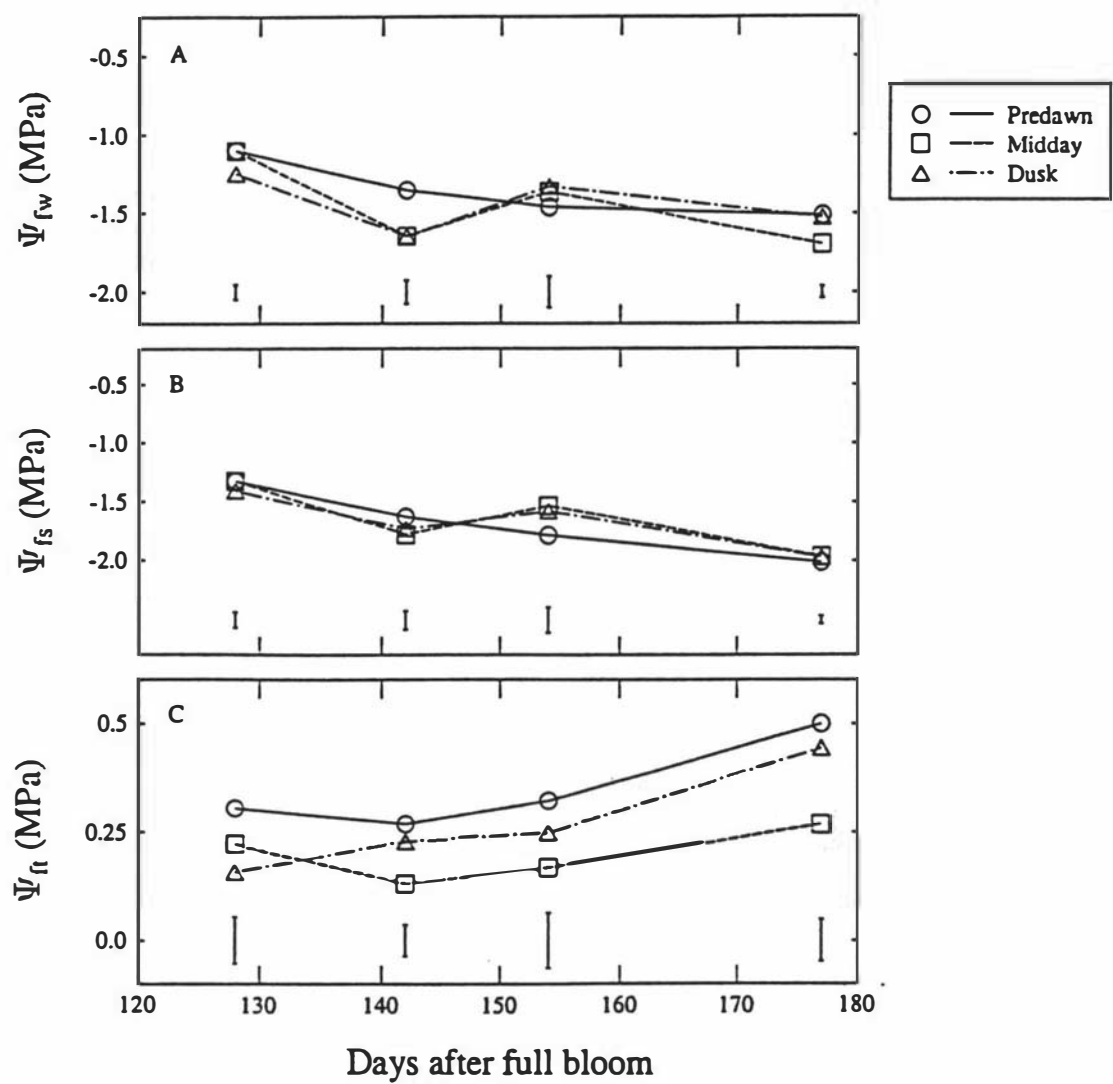


Fig. 39 Fruit water potential (Ψ_{fw}) (A), osmotic potential (Ψ_{fs}) (B), and turgor potential (Ψ_{ft}) (C) measured on LD4 (n=4) at predawn, midday and dusk throughout season in Expt. 4. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 8 (or 12 from 128 DAFB) experimental units (trees).

Turgor potential showed minimal difference between treatments throughout the season when measurements were taken at the same time of the day (Fig. 31C, 32C, and 33; Appendix 2, Table 1). Turgor potential showed some diurnal fluctuations irrespective of treatment with midday Ψ_{fp} generally being the lowest and predawn Ψ_{fp} the highest towards the end of the season (Figs. 37C, 38C, and 39C). Measurements of Ψ_{fp} in the C4 and ED4 fruit during the early part of the season were inconsistent with time of day. Berüter (1989) reported fluctuations in Ψ_{fp} with time of day and demonstrated a maximum value during the early morning and a minimum at approximately midday which is in agreement with my data. Non-significant diurnal fluctuations of Ψ_{fs} (Figs. 37, 38 and 39; and Tables 2, 3 and 4 of Appendix 2) are in line with non-significant differences observed in sugar concentration with time of day (Fig. 40).

The values of Ψ_{fw} (Figs. 30, 31, 32, and 33) were generally higher than Ψ_l at midday (Fig. 2), however, pre-dawn values of Ψ_{fw} tended to be lower than pre-dawn Ψ_l (Figs. 37, 38, and 39 compared to Fig. 4). This further indicates that fruit show less diurnal fluctuation in water relations than leaves. A higher Ψ_{fw} than Ψ_l has been reported for apple and Asian pear (Chapman, 1971; Behboudian et al., 1994a). As fruit transpiration is usually negligible, most of the water loss from fruit occurs as it is drawn out of the fruit into the xylem (Klepper, 1968). The higher water potential in the fruit compared to the leaf could be partially due to a high resistance to water movement out of fruit to leaves which are the main site of transpiration. Therefore, despite some water loss from the fruit to the rest of the tree the fruit still maintain Ψ_{fw} at levels higher than that of the leaves at midday.

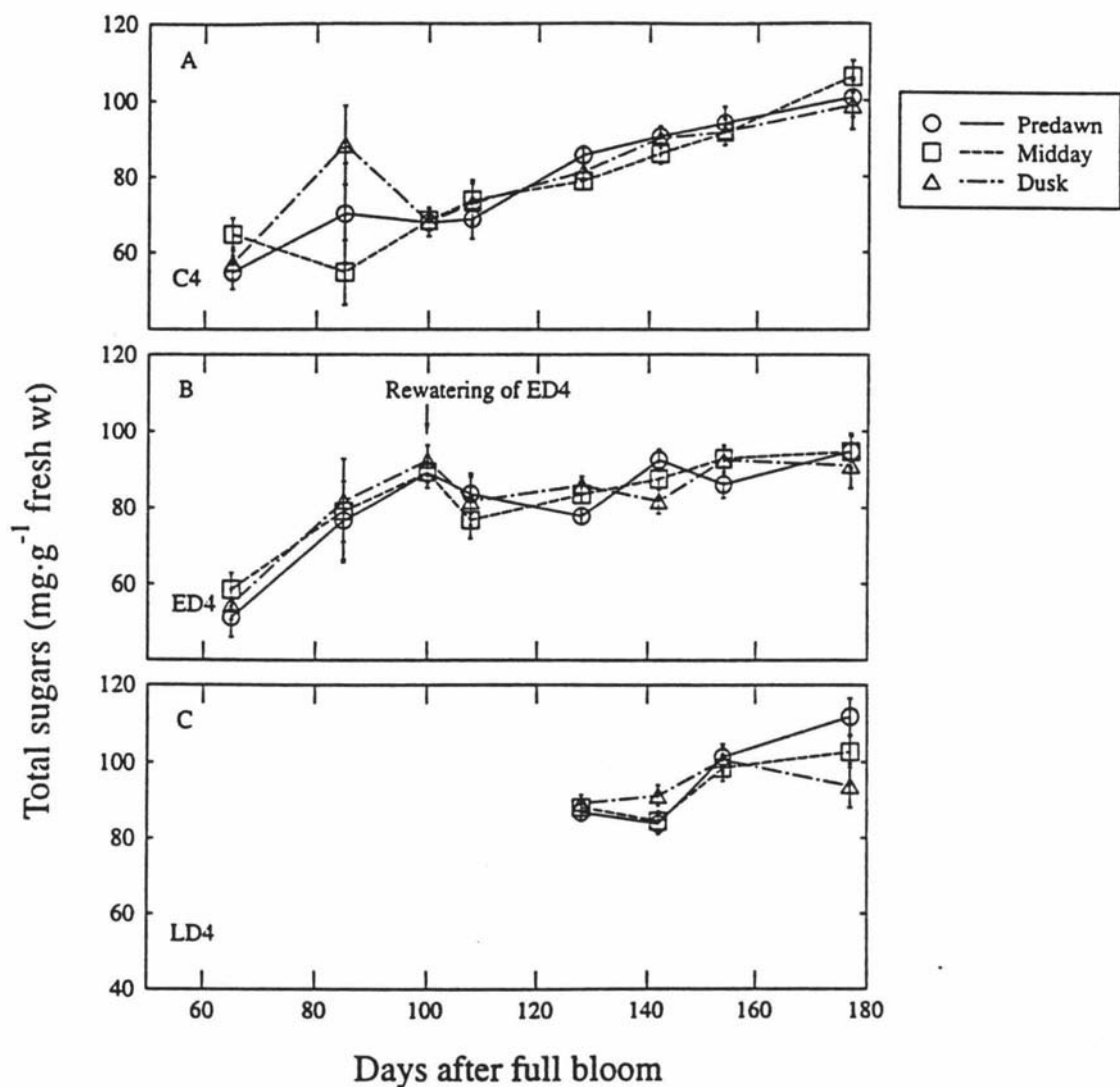


Fig. 40 Mean total sugar concentration of C4 (A), ED4 (B), and LD4 (C) measured at predawn, midday and dusk throughout season. Standard error bars of treatment means for each measurement time are based on the pooled experimental error of 8 (or 12 from 128 DAFB) experimental units (trees). Arrows indicate time of rewatering of the ED4 treatment.

Data presented in this section show that apple fruit are strong sinks for water within the plant. As they mature they are able to maintain their Ψ_{fw} under DI while leaves show a reduction in this parameter. Early in the season, however, fruit water relations are influenced by deficit irrigation, and fruit undergo some osmotic adjustment

which is predominantly due to increased sugar concentrations. Despite osmotic adjustment, fruit growth may still be reduced. Osmotic adjustment, which occurs in apple fruit under conditions of an early-season water deficit, does not maintain fruit growth during a period of water deficit.

5 GENERAL CONCLUSION

As world water resources become increasingly scarce, efficient water use has become a high priority in many areas of the world, for example, the Loire valley in France (Cointepas, 1993), California in the USA (Anon, 1995), Australia (Braun and Buss, 1990), and the Western Cape Province of South Africa (Lötter et al., 1985). To maximise the efficiency of irrigation, a comprehensive understanding of the impact of plant water status on fruit yield and quality is required. The primary objective of this study was to investigate the impact of reduced plant water status on fruit composition, growth and water relations of 'Braeburn' apple. Plant parameters such as carbon assimilation and vegetative growth were also monitored. Plant water deficit was induced at different times during the growing season, with fruit attributes and plant physiological responses being measured throughout.

In this study, plant water status has had a minimal influence on the vegetative growth of the trees due to the timing of the deficit irrigation treatments. The fruit set and cell division phases of fruit growth which are reportedly sensitive to water deficit (Powell, 1974; Hsiao et al., 1976) occur at the same time as predominant shoot growth and, therefore, water deficit at this time was avoided. Both photosynthesis and stomatal conductance were generally reduced under reduced plant water status.

Fruit size was minimally affected under late-season DI. When water deficit was induced early and maintained throughout the season, fruit size was reduced. However, an early-season stress followed by rewatering gave no difference in fruit size at final harvest. Growth of 'Braeburn' apple appears resilient to periodic water deficit indicating that short term reductions in irrigation will not detrimentally influence crop yield. Return bloom may be reduced under an early-season water deficit, but is unaffected by

a late- season DI. Fruit quality parameters such as TSS may be enhanced under a late-season water deficit. Data presented in this thesis suggest that a late-season water deficit has a minimal influence on fruit size, while some quality parameters may be enhanced and savings in irrigation water may constitute an advantage. An early-season water deficit appears less desirable, as return bloom may be reduced. Rewatering of trees subjected to early-season DI may result in the reduction of TSS at final harvest. Fruit mineral concentration does not show consistent differences between treatments. Plant water status does not appear to influence the storage quality of 'Braeburn' apples.

Early-season water deficit lowers both Ψ_{fw} and Ψ_{fs} which may be associated with increased sugar and acid levels within fruit. Despite turgor maintenance, growth was reduced during the stress period. These data indicate that turgor maintenance does not necessarily maintain growth, and that despite osmotic adjustment being demonstrated, fruit size is reduced. A late-season water deficit had a minimal impact on water relations of the fruit.

Overall a water deficit induced during the early part of the season followed by rewatering may save water but gives no improvement in fruit quality or may reduce it through the reduction in sugar and TSS levels. A late-season water deficit, however, may enhance fruit quality at harvest through an increase in TSS whilst conserving irrigation water. A reduction in fruit size which accompanies deficit irrigation throughout the season makes this treatment undesirable.

This research has focused solely on the 'Braeburn' cultivar which is a late maturing, large-fruited apple. For completeness, similar studies need to be carried out on other apple cultivars to determine whether or not these results apply. For example, although fruit size was not reduced under a late-season deficit in this study, other apple

cultivars may be more susceptible to a late-season stress and show reduced fruit size. Additionally, a small reduction in fruit size of 'Braeburn' will have a minimal influence on the market value of the fruit. However, size reduction in smaller-fruited cultivars such as 'Gala' may be more important. This needs to be investigated prior to implementing a late-season deficit in other cultivars. As 'Braeburn' matures late in the growing season, there is limited opportunity for implementation of a post-harvest water deficit to control autumn shoot growth. In early-maturing cultivars a post-harvest water deficit may allow additional control of vegetative growth.

Late-season application of DI has not been researched sufficiently. However, the results presented in this thesis indicate that a management strategy which takes advantage of the frequently occurring late-season drought in many important horticultural regions of New Zealand may be beneficial. Further investigation into the impact of a late-season deficit on other apple cultivars is required.

In DI research more emphasis has been placed on the water relations of the plant, than on those of the fruit. This thesis has explored the changes in water relations components of apple fruit under water deficit conditions. However, questions such as the role of cell wall elasticity in turgor maintenance remain unanswered. Water relations data presented in this research indicate that fruit turgor maintenance, thought to be important for fruit growth, does not eliminate the reduction in fruit growth under early-season DI. Thus, the relationship between turgor and fruit growth under DI deserves further investigation. Changes in fruit composition were evaluated destructively in this study. The development of techniques that may allow *in situ* measurements of solute change in fruit both diurnally and throughout the season would be valuable in a study such as this. The possibility of using TDR equipment for solute evaluation is one

possibility.

Although not a key research theme in this thesis the dynamics of root growth under DI also deserves further investigation. With new techniques such as the Computerized Video Imaging Minirhizotron System developed by the Environment Group, HortResearch, Palmerston North, such studies are becoming feasible.

A recent news article in the popular media (N. Z. One Network News, 9 Feb 1996) documented the findings of K. Arrow, Stanford University, USA. He reported that if the global population continues to increase at its current rate we will have exhausted all available fresh water reserves world wide in 30 years. If this prediction is accurate the enormous importance of efficient water use becomes a matter of necessity. It is the responsibility of this generation to ensure fresh water, the essence of life, is available for future generations.

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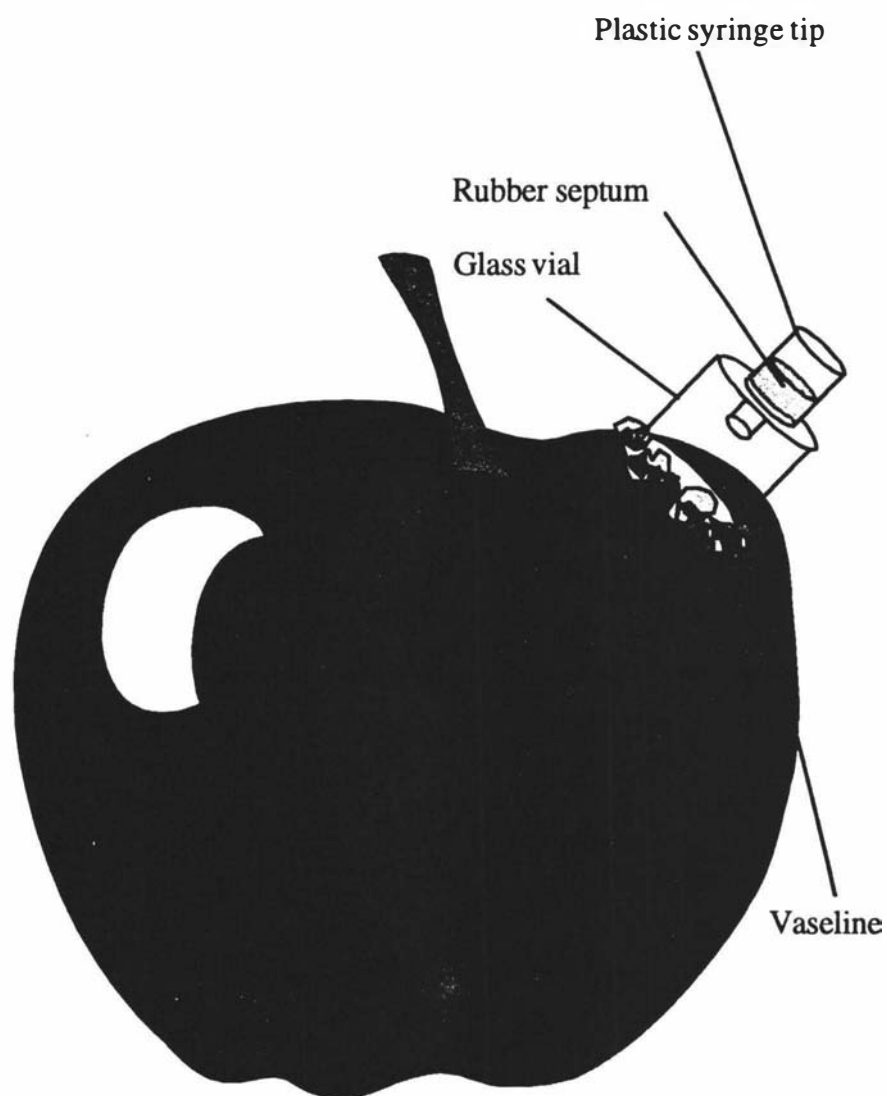
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APPENDIX 1

Placement of vial on fruit for ethylene measurements in Expt. 2



APPENDIX 2. Statistical details for section 4.6.

Table 1. P values of differences in Ψ_{fw} , Ψ_{fs} , and Ψ_{fp} between treatments for Experiment 4.

DAFB	Time	Ψ_{fw}		Ψ_{fs}		Ψ_{fp}	
		C4 ED4 ^z	C4 LD4 ^y	C4 ED4	C4 LD4	C4 ED4	C4 LD4
85	5am	ns		0.0364		ns	
	12pm	0.072		ns		ns	
	8pm	0.003		0.012		ns	
100	12pm	0.002		0.057		ns	
	8pm	0.002		0.030		ns	
101	5am	0.030		0.031		ns	
	12pm	0.066		0.021		ns	
108	5am	ns		ns		ns	
	12pm	0.092		ns		ns	
	8pm	ns		ns		0.092	
128	5am	ns	0.0901	ns	ns	ns	ns
	12pm	0.052	ns	ns	0.051	ns	ns
	8pm	0.088	ns	ns	ns	ns	ns
142	5am	ns	ns	ns	ns	ns	ns
	12pm	0.096	0.0096	ns	0.060	0.040	ns
	8pm	ns	0.052	ns	0.090	ns	ns
154	5am		ns		ns		ns
	12pm		ns		ns		ns
	8pm		ns		ns		ns
177	5am	ns	0.090	0.091	0.060	0.08	ns
	12pm	ns	0.050	ns	0.020	ns	ns
	8pm	ns	ns	ns	ns	ns	ns

^z P values for difference between C4 and ED4

^y P values for difference between C4 and LD4

Table 2. *P* values for comparison of diurnal fruit water relations data for C4, Experiment 4.

DAFB	Values compared (time)	<i>P</i> value for comparison of Ψ_{fw}	<i>P</i> value for comparison of Ψ_{fs}	<i>P</i> value for comparison of Ψ_{fd}
85	5am-12pm	0.041	0.036	ns
	12pm-8pm	ns	ns	ns
	5am-8pm	0.011	0.036	ns
100	12pm-8pm	ns	ns	ns
101	5am-12pm	ns	ns	ns
108	5am-12pm	ns	ns	ns
	12pm-8pm	ns	ns	0.03
	5am-8pm	0.050	ns	0.002
128	5am-12pm	ns	ns	ns
	12pm-8pm	ns	ns	ns
	5am-8pm	ns	ns	ns
142	5am-12pm	ns	ns	ns
	12pm-8pm	ns	ns	ns
	5am-8pm	ns	ns	ns
155	5am-12pm	ns	ns	0.05
	12pm-8pm	ns	ns	ns
	5am-8pm	ns	ns	ns
177	5am-12pm	0.007	ns	0.002
	12pm-8pm	0.072	ns	0.031
	5am-8pm	0.007	ns	ns

Table 3. *P* values for comparison of diurnal fruit water relations data for ED4, Experiment 4

DAFB	Values compared (time)	<i>P</i> value for comparison of Ψ_{fw}	<i>P</i> value for comparison of Ψ_{fs}	<i>P</i> value for comparison of Ψ_{fp}
85	5am-12pm	0.0037	0.08	ns
	12pm-8pm	0.033	ns	ns
	5am-8pm	0.0001	0.005	ns
100	12pm-8pm	ns	ns	ns
101	5am-12pm	ns	ns	ns
108	5am-12pm	0.06	ns	0.069
	12pm-8pm	ns	ns	ns
	5am-8pm	ns	ns	ns
128	5am-12pm	ns	ns	ns
	12pm-8pm	ns	ns	ns
	5am-8pm	ns	ns	ns
142	5am-12pm	ns	ns	0.03
	12pm-8pm	ns	ns	ns
	5am-8pm	ns	ns	ns
177	5am-12pm	0.011	ns	0.02
	12pm-8pm	ns	ns	ns
	5am-8pm	0.011	ns	ns

Table 4. P values for comparison of diurnal fruit water relations data for LD4, Experiment 4.

DAFB	Values compared (time)	P value for comparison of Ψ_{fw}	P value for comparison of Ψ_{fs}	P value for comparison of Ψ_{fp}
128	5am-12pm	ns	0.013	ns
	12pm-8pm	0.050	ns	ns
	5am-8pm	0.04	ns	0.06
142	5am-12pm	ns	ns	0.01
	12pm-8pm	ns	ns	0.07
	5am-8pm	ns	ns	ns
155	5am-12pm	ns	ns	ns
	12pm-8pm	ns	ns	ns
	5am-8pm	ns	ns	ns
177	5am-12pm	0.003	ns	0.003
	12pm-8pm	0.006	ns	0.01
	5am-8pm	ns	ns	ns