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

This thesis is presented in partial fulfilment of the requirements of the degree of Doctor of Philosophy in Horticultural Science at Massey University, Palmerston North, New Zealand.

Tessa Marie Mills

1996
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 al
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.
ACKNOWLEDGEMENTS

I have been most fortunate to have Dr M. Hossein Behboudian as my chief supervisor. Hossein, aside from being an expert in this field of research and a widely published and respected scientist, is a generous and compassionate person who has the academic and personal well being of his students at heart. Dr Brent Clothier, my second supervisor has also given me invaluable assistance. He has a broad understanding of many research areas and always makes a supreme effort to review my written work thoroughly. I feel privileged to have had such excellent supervision throughout my PhD studies. I must also thank the rest of the Environment Group, HortResearch, Palmerston North for providing me with an interesting and fun place to work. HortResearch has not only given me the opportunity to pursue my PhD but I have had the advantage of excellent computer and statistical support services. Nihal DeSilva warrants special mention as he bore the brunt of my numerous statistical queries.

Help from the Massey University Fruit Crops Unit and Plant Growth Unit staff has been invaluable. Without the technical expertise provided by Ray Johnson, Shane Max, Hugh O'Donald, Giles Russel and Deane Pegler my experimental work would not have run smoothly. At times when things were not going well it was these people who helped fix it up. Chris Rawlingson and Colin Tod also gave me considerable technical support. I have really enjoyed working in the Plant Science Department. Everyone is friendly and caring making the environment very positive and supportive.

Final thanks must go to my husband, Ralph. His love, encouragement and exceptional cooking skills means that my home life is very happy. Ralphs contribution is very special to me. To Mum and Dad thanks for knowing I could do it and to Jo and Laurie, thanks for not being too honest about what I was getting myself into.
TABLE OF CONTENTS

ABSTRACT .......................................................... i

ACKNOWLEDGEMENTS .................................................. iii

LIST OF ABBREVIATIONS AND SYMBOLS ........................................ ix

FIGURE CAPTIONS ...................................................... xi

LIST OF TABLES ........................................................... xxvi

1 INTRODUCTION .......................................................... 1

2 LITERATURE REVIEW ....................................................... 5
  2.1 Introduction - The physiology of deficit irrigation ...................... 5
  2.2 The physiological responses of deciduous fruit crops to reduced
      plant water status. ................................................. 8
      2.2.1 The evaluation of plant water status ................................ 8
      2.2.2 Plant responses to water deficit .................................. 10
          2.2.2.1 Osmotic adjustment ....................................... 10
          2.2.2.2 Stomatal conductance ..................................... 13
          2.2.2.3 Carbon assimilation ..................................... 13
          2.2.2.4 Tree growth. ............................................. 16
2.2.4.1 Leaf area .................................. 16
2.2.4.2 Root growth ................................ 17
2.2.4.3 Shoot growth ................................ 18
2.2.4.4 Trunk growth ................................ 18

2.2.3 Effects of plant water deficit on crop yield and fruit quality ........................................ 19

2.2.3.1 Crop yield ................................... 19
2.2.3.1.1 Fruit number ................................ 19
2.2.3.1.2 Fruit size .................................. 21

2.2.3.2 Fruit quality under deficit irrigation .......... 22
2.2.3.2.1 Fruit firmness ............................... 22
2.2.3.2.2 Total soluble solids ......................... 23
2.2.3.2.3 Titratable acidity ........................... 24
2.2.3.2.4 Fruit colour ................................ 24
2.2.3.2.5 Fruit soluble sugar concentration ......... 25
2.2.3.2.6 Fruit ethylene evolution .................... 26
2.2.3.2.7 Fruit storage disorders as affected by deficit irrigation ................................ 27
2.2.3.2.8 Fruit mineral concentration ................ 27

2.3 Seasonal timing of deficit irrigation. ................. 29
2.3.1 Early-season deficit irrigation. .......................... 30
2.3.2 Late-season deficit irrigation. .......................... 30
2.3.3 Deficit irrigation throughout the fruit growing season. 31
2.3.4 Postharvest deficit irrigation. .......................... 31
3 GENERAL MATERIALS AND METHODS ........................................... 34

3.1 Experimental setup ....................................................... 34

3.1.1 Orchard soil .............................................................. 34

3.1.2 Experiment 1 (1992-93) .................................................... 34

3.1.3 Experiment 2 (1993-94) .................................................... 35

3.1.4 Experiment 3 (1993-94) .................................................... 37

3.1.5 Experiment 4 (1994-95) .................................................... 37

3.2 Determination of soil water content ....................................... 39

3.3 Meteorological data ......................................................... 40

3.4 Evaluation of plant parameters ........................................... 41

3.4.1 Plant water status ......................................................... 41

3.4.2 Photosynthesis and stomatal conductance ............................... 41

3.4.3 Determination of tree size and growth ................................ 42

3.4.4 Evaluation of return bloom ............................................. 43

3.4.5 Evaluation of $^{13}$CO$_2$ discrimination ................................ 43

3.5 Fruit harvest and quality assessment .................................... 43

3.5.1 Harvest protocol ......................................................... 43

3.5.1.1 Experiment 1 .......................................................... 43

3.5.1.2 Experiment 2 .......................................................... 44

3.5.1.3 Experiment 3 .......................................................... 44

3.5.1.4 Experiment 4 .......................................................... 45

3.5.2 Fruit quality analysis ..................................................... 45
4 RESULTS AND DISCUSSION

4.1 Development and maintenance of plant water deficit
   4.1.1 Soil water content
   4.1.2 Plant water potential

4.2 Carbon Assimilation under reduced plant water status
   4.2.1 Photosynthetic rate
   4.2.2 Stomatal conductance
   4.2.3 Diurnal patterns of Pn and g_s under water deficit
   4.2.4 Discrimination against $^{13}$CO$_2$

4.3 Vegetative growth
   4.3.1 Shoot growth
   4.3.2 Leaf area
   4.3.3 Trunk growth
   4.3.4 Root growth
   4.3.5 Return Bloom

4.4 Fruit Quality
   4.4.1 Fruit size
   4.4.2 Fruit firmness
   4.4.3 Total soluble solids
   4.4.4 Titratable acidity
   4.4.5 Colour
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.4.6 Fruit ethylene evolution</td>
<td>104</td>
</tr>
<tr>
<td>4.4.7 Mineral concentration</td>
<td>105</td>
</tr>
<tr>
<td>4.5 Storage attributes of fruit grown under deficit irrigation</td>
<td>113</td>
</tr>
<tr>
<td>4.5.1 Titratable acidity</td>
<td>113</td>
</tr>
<tr>
<td>4.5.2 Total soluble solids</td>
<td>113</td>
</tr>
<tr>
<td>4.5.3 Fruit weight</td>
<td>114</td>
</tr>
<tr>
<td>4.5.4 Fruit sugar concentration</td>
<td>115</td>
</tr>
<tr>
<td>4.5.5 Fruit mineral concentration</td>
<td>118</td>
</tr>
<tr>
<td>4.6 Fruit water relations</td>
<td>121</td>
</tr>
<tr>
<td>4.6.1 Fruit water potential and its components</td>
<td>122</td>
</tr>
<tr>
<td>4.6.2 Fruit sugar composition and its relation to fruit water relations.</td>
<td>128</td>
</tr>
<tr>
<td>4.6.3 Diurnal fruit water relations</td>
<td>136</td>
</tr>
<tr>
<td>5 GENERAL CONCLUSION</td>
<td>143</td>
</tr>
<tr>
<td>6 LITERATURE CITED</td>
<td>147</td>
</tr>
<tr>
<td>APPENDIX 1</td>
<td>168</td>
</tr>
<tr>
<td>APPENDIX 2</td>
<td>169</td>
</tr>
</tbody>
</table>
LIST OF ABREVIATIONS 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)  \( \Psi_{fw} \)
Fruit Osmotic Potential (MPa)  \( \Psi_{fs} \)
Fruit Turgor Potential (MPa)  \( \Psi_{fp} \)
Leaf Water Potential (MPa)  \( \Psi_I \)

Days After Full Bloom  DAFB
Days In Storage  DIS
Experiment  Expt.
Figure  Fig.
Hour  h
| Internal CO₂ Concentration (μmol·mol⁻¹) | Cᵢ  |
| Irradiance (W·m⁻²) | Ir  |
| Metre | m  |
| Photosynthetic Rate (μmol·m⁻²·s⁻¹) | Pn  |
| Probability | P  |
| Ratio $^{13}$C:$^{12}$C | $\delta^{13}$C  |
| Regulated Deficit Irrigation | RDI  |
| Seconds | s  |
| Soil volumetric water content (m³·m⁻³) | $\theta$  |
| Stage 1 harvest | S1  |
| Stage 2 harvest | S2  |
| Standard error | SE  |
| Stomatal Conductance (mmol·m⁻²·s⁻¹) | $g_s$  |
| Time Domain Reflectometry | TDR  |
| Titratable Acidity (% malic acid) | TA  |
| Total Soluble Solids (% Brix) | TSS  |
| Transpiration (mmol·m⁻²·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≥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. 2 Midday leaf water potential (Ψ1) 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≥7); D2=deficit, Expt. 2 (n≥4); LD2=late deficit, Expt. 2 (n≥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 ≥ 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 (Ψ₁) 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.

Fig. 5  Diurnal leaf water potential (Ψ₁) 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 ($\Psi_f$) 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.

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=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. 9 Internal CO2 (Ci) 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.

Fig. 10 Diurnal Photosynthetic rate (Pn) and irradiance (Ir) 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 (gs) 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 \( n=4 \), \( D_1 = \text{deficit} \) (\( n=11 \) up to 170 DAFB (stage 1 harvest) when \( n=6 \) and at 180 DAFB (stage 2 harvest) where \( n=5 \)); \( C_2 = \text{control}, \) Expt. 2 (\( n\geq 7 \)); \( D_2 = \text{deficit, Expt. 2 (} n\geq 4 \)); \( LD_2 = \text{late deficit, Expt. 2 (} n\geq 7 \)); \( C_3 = \text{control, Expt. 3} (n=6); D_3 = \text{deficit, Expt. 3} (n=3); \) \( C_4 = \text{control, Expt. 4} (n=4); \) \( ED_4 = \text{early deficit, Expt. 4} (n=4); \) and \( LD_4 = \text{late deficit, Expt. 4} (n=4) \). 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 \( C_1 = \text{control} (n=10 \) up to 170 DAFB (stage 1 harvest) when \( n=6 \) and at 180 DAFB (stage 2 harvest) when \( n=4 \), \( D_1 = \text{deficit} (n=11 \) up to 170 DAFB (stage 1 harvest) when \( n=6 \) and 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 \( C_1 = \text{control, Expt. 1 (} n=10 \) up to 170 DAFB (stage 1 harvest) when \( n=6 \) and at 180 DAFB (stage 2 harvest) when \( n=4 \), \( D_1 = \text{deficit, Expt. 1 (} n=11 \) up to 170 DAFB (stage 1 harvest) where \( n=6 \) and 180 DAFB (stage 2 harvest) where \( n=5 \)); \( C_2 = \text{control, Expt. 2 (} n=2 \)); \( D_2 = \text{deficit, Expt. 2 (} n=2 \)); \( LD_2 = \text{late deficit, Expt. 2 (} n=2 \)); \( C_3 = \text{control, Expt. 3 (} n=6 \)); \( D_3 = \text{deficit, Expt. 3 (} n=3 \)); \( C_4 = \text{control, Expt. 4 (} n=4 \)); \( ED_4 = \text{early deficit, Expt. 4 (} n=4 \));
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) 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. 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.
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=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).
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. 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).

Fig. 27  Concentration (mg·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 (mg·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).
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.

Fruit water potential ($\Psi_{fw}$) (A), osmotic potential ($\Psi_{fs}$) (B), and turgor potential ($\Psi_{fp}$) (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.

Fruit water potential ($\Psi_{fw}$) (A), osmotic potential ($\Psi_{fs}$) (B), and turgor potential ($\Psi_{fp}$) (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.

Fruit water potential ($\Psi_{fw}$) (A), osmotic potential ($\Psi_{fs}$) (B), and turgor potential ($\Psi_{fp}$) (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 ($\Psi_{fw}$) (A), osmotic potential ($\Psi_{fs}$) (B), and turgor potential ($\Psi_{fp}$) (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.

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.

Fig. 37 Fruit water potential (Ψfw) (A), osmotic potential (Ψfs) (B), and turgor potential (Ψfp) (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 (Ψfw) (A), osmotic potential (Ψfs) (B), and turgor potential (Ψfp) (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 ($\Psi_{fw}$) (A), osmotic potential ($\Psi_{fs}$) (B), and turgor potential ($\Psi_{fp}$) (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).

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.
LIST OF TABLES

Table 1. The partial $R^2$ contribution and total standardised $R^2$ 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.

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 are C4=control, Expt. 4; ED4=early deficit, Expt. 4; LD4=late deficit, Expt. 4.

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 Experiments 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.

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 $P < 0.05$. 
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 different letters are significantly different at $P < 0.05$.

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 different letters are significantly different at $P < 0.05$.

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 different letters are significantly different at $P < 0.05$.

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 different letters are significantly different at $P < 0.05$.

Table 9. The partial $R^2$ contribution and total $R^2$ for multiple variable regression of various solutes on $\Psi_{fs}$ and the contribution of each solute to $R^2$ for Experiment 4.
Table 10. The contribution of individual solutes to the decreased $\Psi_{fs}$ observed in the ED4 fruit during the stress period.