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Water use of macadamia trees is dynamically regulated by the presence or absence of fruit

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ABSTRACT

Macadamia, an oil rich fruit producing tree, is characterized by a predominantly isohydric water management strategy, enforced by means of strict stomatal control. However, the presence of fruit, a significant sink, increases both the net assimilation rate (A) and stomatal conductance (g_s) in macadamia and a range of other crops. It is, however, unclear if increases in A and g_s at a leaf level in the presence of fruit would lead to increased canopy transpiration (E_c) in macadamia. This study therefore aimed to demonstrate that the presence of fruit leads to an increase in A, g_s and E_c. In order to examine the effect of fruit on leaf gas exchange, the study used fruiting and non-fruiting branches, in combination with phloem-girdling to extrapolate possible effects of fruit on leaf gas exchange to a canopy level. Measurements of leaf gas exchange were made on four different treatments including non-fruiting (NF), fruiting (F), girdled non-fruiting (GNF), and girdled fruiting (GF) branches, over a 7-month period in a mature commercial macadamia orchard. Independent estimates of E_c, using sap flow measurements, were made across two seasons in the same orchard. No significant differences in light saturated net assimilation rate (A_{max}) and g_s were observed between GF branches and non-girdled treatments approximately 2-months after girdling, whilst A_{max} and g_s of GNF were significantly reduced during the same period. Fruit removal on GF branches, resulted in a significant reduction in both A_{max} and g_s compared to F and NF treatments. There were also no significant differences in g_s between F and NF branches throughout the trial, suggesting that increases in g_s, in the presence of fruit can be scaled to a canopy level. The presence of fruit led to an ~25% increase in g_s at air vapour pressure deficits (VPD_{air}) > 1.50 kPa, which translated into ~20% higher E_c during fruiting compared to non-fruiting periods. This increase occurred irrespective of changes in canopy size and weather and was largely attributed to significantly higher E_c in response to air vapour pressure deficit within the 0.0 – 3.0 kPa range. Crop load therefore needs to be considered when developing water use models for irrigation scheduling in macadamia orchards.

Abbreviations

A	net CO_2 assimilation rates
A_{max}	light saturated net assimilation rate
C_i	intercellular CO_2 concentration
E_c	canopy transpiration
E	transpiration
ET_o	reference evapotranspiration
F	fruiting branches
GF	phloem-girdled fruiting branches
GNF	phloem-girdled non-fruiting branches
g_s	stomatal conductance
K_t	transpiration crop coefficients
LAI	leaf area index
NF	non-fruiting branches
NIH	nut in husk
NSL	non-stomatal-limitations
REML	Restricted Maximum Likelihood estimation
RH	air relative humidity
PAR	photosynthetically active radiation
R_s	solar radiation
T_{air}	air temperature
VEPAC	Variance Estimation, Precision & Comparison methodology
VPD_{leaf}	leaf to air vapour pressure deficit

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VPD_{air} air vapour pressure deficit
ψ_{pd} pre-dawn leaf water potential

1. Introduction

Macadamia trees (*Macadamia* F. Muell) exhibit isohydric behaviour, with strict stomatal control to maintain a nearly constant minimum midday leaf water potential under high evaporative demand, leading to relatively low net CO_2 assimilation rates (*A*) (Smit et al., 2020) compared to other fruit tree crops (Flore and Lakso, 1989). This contrasts with anisohydric behaviour, that allow a greater decline in water potential (Klein, 2014). Sade and Moshelion (2014) suggested that fruit trees may shift flexibly towards isohydrodynamic behaviour, in accordance with fruit load. This may be particularly relevant for predominantly isohydric oil storing tree crops, which includes macadamia and olive, who may need to shift behaviour to meet whole-tree photo-assimilate demand at critical times, such as the oil accumulation stage. This shift has implications for irrigation scheduling at different times during the production season, especially when schedules are derived from water use models.

High fruit loads were associated with increased water extraction in grapevines (Naor et al., 1997), peaches (Lopez et al., 2008) and pears (Marsal et al., 2008), with *A* and stomatal conductance (g_s) 40 % higher in fruiting trees as compared to trees were fruit was removed (Syvertsen et al., 2003). In apples, deflowered trees had 65 % lower *A*, following the cessation of shoot growth in comparison to trees carrying the heaviest crop load (Palmer et al., 1997). Naor et al. (2013) observed higher g_s in fruiting olive trees which was more pronounced during periods of high assimilate demand. In apples, fruit presence reduced g_s sensitivity to vapor pressure deficit of the air (VPD_{air}; Pretorius and Wand, 2003). Despite the vast number of studies on stomatal responses to environmental and internal factors, mechanistic understanding of this process is lacking (Hölttä et al., 2017). Currently used empirical (Ball et al., 1987; Leuning, 1995) and optimisation models (Sperry et al., 2017; Wolf et al., 2016) explain stomatal behaviour based largely on the premise that g_s optimizes carbon uptake relative to water loss via transpiration (*E*). Dewar et al. (2022) presented evidence for sink feedback on *A* and g_s through sugar regulated non-stomatal limitations (NSL) and turgor-regulated phloem unloading. The presence of a strong sink (such as an oil storing nut) likely causes an increase in *A* through increased g_s. However, optimal stomatal control to meet the higher demand of sugars will likely be achieved by balancing CO_2 supply with the increase in NSL caused by the decline in leaf turgor due to increased water loss as a result of the increase in g_s. Although there are numerous reports of plant growth regulator-mediated and physical control of g_s, the role of biochemical control of g_s, where sucrose acts as metabolic link between mesophyll photosynthesis and stomatal movement cannot be ignored (Kottapalli et al., 2018; Lawson and Matthews, 2020; Lima et al., 2018).

The continuous transport of assimilates from source leaves to sinks, is therefore essential to prevent the down-regulation of photosynthesis. In trees, which consist of an intricate matrix of fruiting and non-fruiting branches (i.e. proximal and distal sinks), and where phloem loading can be both passive and active process in tissues accumulating large amount of non-structural carbohydrates, such as oil accumulating fruit (Lalonde et al., 2003; Turgeon, 2010a, 2010b), long distance transport of assimilates from source to sink would have to occur to maintain leaf gas exchange to meet whole tree assimilate demand. This would be especially important in non-fruiting branches.

Studying the effect of source-sink relations on leaf gas exchange is, however, difficult when considering the complexity of source-sink dynamics within tree canopies. As a result, many studies have used branch isolation methods, which include cincturing or phloem-girdling of a single branch (Iglesias et al., 2002; Poirier-Pocovi et al., 2018; Schaper and Chacko, 1993; Urban et al., 2004; Williams et al., 2000). Phloem-girdling allows source-sink relationships to be altered by preventing the export of substances, including photoassimilates, out of the single stem or branch. The impact of the accumulation of photo-assimilates on *A* and g_s, as a result of feedback inhibition can then be determined, which can be extrapolated to a larger canopy. Furthermore, through fruit and leaf removal, branch isolation can be used successfully to generate hypothetical scenarios of the impact sink strength on *A* and g_s. It should, however, be noted that it is not only the transport of assimilates that is blocked by phloem-girdling and this action may also impact hormone transport and the distribution of hormones within the plant (Goren et al., 2004).

Smit et al. (2020) found that both *A* and g_s of macadamias varied in response to VPD_{air} throughout the crop's phenological cycle, with both increasing relative to VPD_{air} as sink strength of developing fruit increased. These results were obtained from completely randomized spot measurements of leaf gas exchange on branches bearing fruit and branches not bearing fruit, which suggests that changes in stomatal behaviour in response to sink strength occur at a canopy level. Given the well-defined relationship between *A* and g_s (Ball et al., 1987; Leuning, 1995), this study hypothesized that *A* and g_s would be higher in both fruiting and non-fruiting branches in the presence of developing fruit, and that downregulation of *A* and g_s can be expected upon fruit removal. Furthermore, it was hypothesized that because leaf level increases in g_s during nut filling occurs across the whole canopy, this would translate into increases in canopy transpiration (E_c) relative to atmospheric evaporative demand. It is important to establish this in macadamia, as Iglesias et al. (2002) suggests that sink effects on *A* are not readily observable in all species and under all conditions. The study therefore aimed to establish that long distance transport of assimilates occurs in macadamias by using branch isolation methods on both vegetative and reproductive branches and if leaf level upregulation of g_s occurs in the presence of fruit and whether this leads to an increase in E_c or not.

2. Materials and methods

2.1. Orchard description, weather variables and fruit growth

The trial was conducted in a mature bearing orchard located approximately 35 km west of Nelspruit in the Schagen Valley, Mpumalanga, South Africa (25°21′50.36″ S, 30°46′46.47″ E, approximately 900 m.a.s.l.). This orchard consisted of irrigated macadamia trees (cv. HAES 695, 'Beaumont' grafted on 'Beaumont' rootstocks, *M. tetraphylla* x *M. integrifolia*) planted in 2005 (11 years old at the start of the trial) at an 8 × 4 m spacing. Weather data, including air temperature (T_{air}), air vapour pressure deficit (VPD_{air}), solar radiation (R_s), wind speed and direction, air relative humidity (RH) and rainfall, was collected at 20 min intervals, using a WS-GP1 Delta-T (Delta-T Devices Ltd, Cambridge, United Kingdom) automatic weather station, which was installed over a dry short grass surface within 100 m of the orchard. Reference evapotranspiration (ET_o) was calculated as described by Allen et al. (1998) and Pereira et al. (2015). Data quality control was performed as suggested by Allen (2008). Tree canopy dimensions, including height, width and breadth were measured throughout the trial. Measurements of leaf area index (LAI) were performed randomly throughout the duration of the trial using a Decagon AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, WA, USA).

Fruit growth was monitored over two consecutive seasons, including the season before the trial (2016 – 2017) and during the trial (2017 – 2018). During both seasons, 20 nuts were randomly harvested across the orchard on a weekly basis from 1 week post anthesis (2016/10/10 in the first season and 2017/10/12 in the second season) up to approximately 19 weeks post anthesis (2017/02/27 in the first season and 2018/02/23 in the second season, which was eight weeks before harvest, on 2017/04/30 in the first season and 2018/04/27 in the second season. Measurements of fruit included nut in husk (NIH) fresh mass and NIH diameter. The data was used to establish when fruits became significant sinks, which was assumed to occur as soon as individual nut mass increased in a linear fashion, as found by Trueman and Turnbull (1994).

2.2. Sink manipulation trial - leaf gas exchange

Ten macadamia trees close to the centre of the orchard and within the same planting row, were selected for treatments. Four treatments, each consisting of twenty replicates, were randomly allocated to the ten selected trees. The treatments included phloem-girdled non-fruiting branches (GNF), non-fruiting branches (NF), phloem-girdled fruiting branches (GF) and fruiting branches (F). All branches were at least 0.5 m in length, with 15 to 20 leaves per branch. Non-fruiting branches were purely vegetative and bore no fruits or racemes. Fruiting branches bore two or more nuts per branch. Girdling was performed in the 2017–2018 season approximately 8 weeks post anthesis (2017/12/12), and post premature nut drop (4 weeks post anthesis), by carefully removing a strip of bark (approximately 4.0 cm wide) from the base of each branch without damaging underlying xylem tissue. This was close to the end of the exponential growth phase of the fruit and at this point fruit were considered to be significant sinks as oil accumulation had started. The selected branches for each treatment were situated on the outside of the canopy, ensuring that leaves were acclimated to a sun-exposed environment. Furthermore, to determine the true influence of sink strength on leaf gas exchange, all the nuts on branches of the GF treatment were removed, approximately two months (2018/02/03) after the commencement of the trial.

Measurements of leaf gas exchange commenced on 2017/12/12 and were performed using a LI-6400 XT photosynthesis system (LI-COR, Lincoln, Nebraska, USA). Measurements were made during seven data collection campaigns from 2017/12/12 (early fruiting period) to 2018/06/30 (after harvest). During the week in early February 2018 when fruit were removed from the GF treatment, gas exchange was measured before fruit removal (2018/02/03), and for two days after fruit removal (2018/02/04 and 2018/02/05) to assess the rapidity of responses at leaf level. The measured parameters included, amongst others, light saturated net CO_2 assimilation rate (A_{max}), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i). Sensors inside the leaf cuvette monitored photosynthetically active radiation (PAR) and leaf temperature. For all spot measurements, the CO_2 concentration was maintained at 400 μmol mol^{-1}, the flow rate was 400 μmol s^{-1}, PAR was maintained between 1500 and 2000 μmol m^{-2} s^{-1} (LI-6400 XT LED light source) and relative humidity was maintained at >50 % to prevent stomatal oscillations.

Measurements were made on randomly selected mature, hardened-off leaves, on each labelled treatment branch, and typically situated on the outside of the canopy, within 2 m from the soil surface. Measurements were made between 09:00 h and 16:00 h on the sun-exposed face of the canopy, on either the western or eastern side of the row. All leaves measured during the spot measurement campaign were fully sun-exposed (PAR > 1000 μmol m^{-2} s^{-1}) immediately before measurements. Spot measurements made under these conditions (termed A_{max}) were typically recorded as soon as A stabilized (total time in chamber <2 min). Selected daytime (08:00 h – 17:00 h) weather variables during each of the measurement days, together with the presence or absence of fruit on each date, are provided in Table 1.

2.3. Canopy transpiration

Sap flow measurements were conducted across two seasons from 2016/08/10 to 2018/08/08, on four trees in the centre of the orchard. Sap flow measurements were performed using the heat ratio method as described by Burgess et al. (2001) and Taylor et al. (2013), with specific details in Smit et al. (2020). Canopy transpiration (E_c, mm) was calculated using the ground area allocated to each experimental tree within the experimental orchard (i.e. 32 m^2). Average E_c as reported in this study consisted of hourly averaged E_c for each of the individually measured trees (N = 4). Transpiration crop coefficients (K_t) were calculated by dividing E_c by ET_o, as defined by Villalobos et al. (2013). To avoid any confounding of whole tree water relations by girdling wounds, sap flow measurements were conducted on separate, ungirdled trees. The influence of sink strength on E_c was thus assessed in relation to the normal phenologically-determined presence or absence of fruit on the tree during the time of measurement. For transpiration measurements, the non-fruiting period in both seasons was taken as 1 May – 31 October (the period from after harvest to the end of the fruit drop period) and the fruiting period was taken as 1 November – 30 April (the period from the end of the fruit drop period to harvest). All nuts were harvested by hand upon maturity on 2017/04/30 and 2018/04/27.

Table 1
Average (± standard deviation) daytime (8:00 – 17:00 h) weather variables including air temperature (T_{air}), air vapour pressure deficit (VPD_{air}) and total solar radiation (R_s) for each of the leaf gas exchange measurement days. N is the number of leaf gas exchange measurements per treatment. The presence (yes) or absence (no) of fruit during each of the seven leaf gas exchange measurement dates is also shown.

Measurement Date	Treatment	*N*	Presence of fruit	T_{air} (°C)	VPD_{air} (kPa)	R_s (MJ m^{-2} day^{-1})
2017/12/12	GNF	5	No	27.9 ± 6.5	2.09 ± 1.1	27.86
	GF	5	Yes			
	NF	5	No			
	F	5	Yes			
2018/02/03	GNF	26	No	23.3 ± 1.5	0.69 ± 0.2	11.82
	GF	16	Yes			
	NF	23	No			
	F	21	Yes			
2018/02/04	GNF	16	No	23.9 ± 4.4	1.31 ± 0.6	22.17
	GF	15	No			
	NF	30	No			
	F	22	Yes			
2018/02/05	GNF	16	No	22.3 ± 2.7	0.93 ± 0.8	10.47
	GF	10	No			
	NF	18	No			
	F	17	Yes			
2018/03/19	GNF	25	No	24.1 ± 3.6	0.94 ± 0.4	15.47
	GF	21	No			
	NF	23	No			
	F	23	Yes			
2018/04/18	GNF	19	No	22.0 ± 3.8	1.56 ± 0.7	10.06
	GF	16	No			
	NF	18	No			
	F	20	Yes			
2018/06/30	GNF	8	No	20.6 ± 6.7	1.89 ± 1.0	11.50
	GF	11	No			
	NF	16	No			
	F	14	No			

GNF - Phloem-girdled non-fruiting branches GF - Phloem-girdled fruiting branches.
NF - Non-fruiting branches F - Fruiting branches.

Measurements of pre-dawn leaf water potential (ψ_{pd}) were made on trees instrumented with sap flow sensors using a Scholander pressure chamber (Model 600, PMS Instrument Company, Albany, OR, USA). These measurements assessed tree water status and were used to eliminate water stress as a confounding factor in any of the results. Measurements of ψ_{pd} were made on 60 days throughout the trial. Water stress in macadamias is suggested to occur at ψ_{pd} lower than −0.5 MPa to −0.7 MPa (Stephenson et al., 2003). A mean value of −0.13 ± 0.04 MPa was determined for the duration of the trial. During the 2016/2017 season diurnal sun leaf water potential (ψ_{sun}) was measured on three leaves per measurement tree.

2.4. Statistical analysis

To analyse the influence of sink treatments on A_{max} and g_s, data from each of the measurement dates and treatments was compared using repeated measures ANOVA with Restricted Maximum Likelihood estimation (REML) in the Variance Estimation, Precision & Comparison methodology (VEPAC) of Statistica (TIBCO Software Inc. Version 13.3).

The individual tree replicates were a random variable so that $N = 10$. Using LSD multiple comparisons, the treatment means were regarded as statistically different if $p \leq 0.05$.

To analyse the response of E_c to T_{air}, VPD_{air}, R_s and ET_o during fruiting and non-fruiting periods, data from all measurement dates were grouped into six T_{air} categories spanning 5 °C, eight categories of VPD_{air} spanning 0.5 kPa, four categories of R_s spanning 1.0 MJ m^{-2} h^{-1} and five categories of ET_o spanning 0.1 mm h^{-1}. Using repeated measures ANOVA with REML in the VEPAC of Statistica (TIBCO Software Inc. Version 13.3), a test for differences in E_c during fruiting and non-fruting periods was conducted. The individual tree replicate was a random variable so that $N = 4$. Using LSD multiple comparisons, the treatment means were regarded as different if $p \leq 0.05$.

All raw gas exchange and sap flow data is available, in addition to data analysis files.

3. Results

3.1. Weather and fruit growth

Average daily T_{air} throughout the girdling trial was 19.0 °C, with the highest (21.7 °C) monthly average measured in January 2018 and the lowest (13.9 °C) in June 2018 (Fig. 1A). Daily maximum T_{air} never exceeded 35 °C, with the highest daily maximum (34.2 °C) coinciding with the highest daily average temperature on 25 December 2018. Total rainfall during the assessment period (2017/10/08 – 2018/06/30) was 504 mm, with most of the rainfall occurring in December 2017 (116 mm) and February 2018 (175 mm) (Fig. 1A). Total ET_o for the duration of the trial was 654 mm, with an average daily ET_o of 3.2 mm during this period (Fig. 1B). Daily average VPD_{air} was 0.92 kPa, and rarely exceeded 1.8 kPa (Fig. 1B). Total rainfall and irrigation for this period was 600 mm. This ensured that the trees remained unstressed, as indicated by ψ_{pd} measured throughout the trial which was greater than −0.5 MPa (data not shown).

Throughout two growing seasons an approximate linear increase in

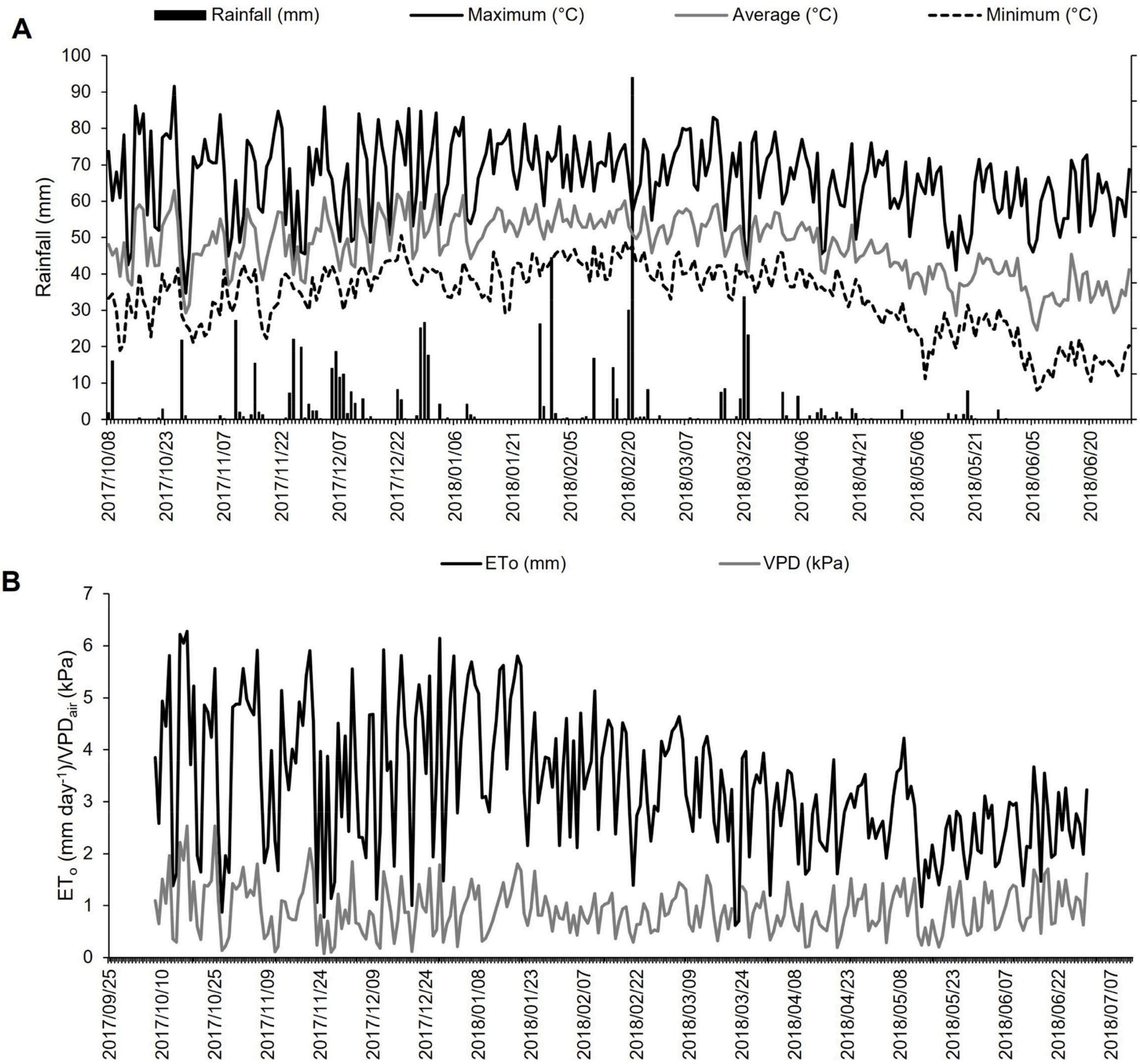

Fig. 1. (A) Daily average, maximum, and minimum air temperature and rainfall, and (B) daily reference evapotranspiration (ET_o) and air vapour pressure deficit (VPD_{air}) for the duration of the trial (2017/10/08 – 2018/06/30).

NIH diameter was observed up to 10 weeks post anthesis. Thereafter the NIH diameter increased at a slower rate, and the final average diameter was 30 mm in both seasons (Fig. 2A). Individual NIH fresh mass followed a sigmoidal pattern, increasing exponentially from 0 to 13 weeks post anthesis, which roughly corresponded to the start of January, where after only a very slight increase was observed for the remainder of fruit development (Fig. 2B). Average individual NIH fresh mass 13 weeks post anthesis was 1.6 g, and only reached an average recorded final fresh mass of 1.7 g approximately 20 weeks post anthesis. Individual NIH diameter and mass did not differ between seasons (Fig. 2A & B). Based on these measurements and existing knowledge of macadamia fruit development (Trueman, 2013), it was estimated that the nuts became a significant reproductive sink when the exponential growth phase of the sigmoidal growth curve began and mass increased in a more or less linear fashion. Based on results by Stephenson et al. (1989), oil accumulation was likely to begin towards the end of the exponential growth phase in the middle of December for both seasons. As a result, all periods between November and the end of April (harvest) were designated high sink strength periods, whilst periods from May to October were designated as low sink strength periods.

3.2. . Sink manipulation effects on leaf gas exchange

Light-saturated net CO_2 assimilation rate (A_{max}) at the start of the trial (2017/12/12) was not significantly different between the treatments, averaging 10.6 μmol CO_2 m^{-2} s^{-1} across all treatments. There were also no significant differences in A_{max} between NF and F treatments throughout the trial (Fig. 3A). Light-saturated net CO_2 assimilation rate of the GNF treatment showed a strong reduction (to 2.7 μmol m^{-2} s^{-1}) relative to all other treatments when measured on 2018/02/03, eight weeks after phloem-girdling. Values for this treatment remained significantly lower than those of the non-girdled treatments for the remainder of the season. Phloem-girdling induced an average seasonal reduction in A_{max} of 84 % in the GNF treatment compared to pre-girdling levels, and an 83 % reduction compared to NF and F treatments from 2018/02/03 to 2018/06/30.

The GF treatment showed similar A_{max} values as NF and F treatments before fruit removal on 2018/02/03 (Fig. 3A). One day after fruit removal, A_{max} of the GF treatment was lower, but not significantly so, compared to the NF and F treatments. On 2018/02/05, two days after fruit removal, A_{max} was significantly lower in the GF treatment than in the NF treatment, but was not significantly different to the F treatment. From 2018/03/19 (approximately six weeks after fruit removal) until the end of the trial on 2018/06/30, the GF treatment exhibited significantly lower A_{max} values compared to both the NF and F treatments, but similar values to the GNF treatment. Fruit removal at harvest (2018/04/27) in the F treatment resulted in a smaller decrease in A_{max} over an eight-week period compared to the NF treatment, which showed a stronger decrease. However, the final values for these treatments on 2018/06/30 were not significantly different.

Similar to A_{max}, g_s was not significantly different between treatments at the start of the trial, averaging 0.13 mol m^{-2} s^{-1} across all treatments (Fig. 3B). Again, no significant difference was observed between the NF and F treatments for the duration of the trial. On 2018/02/03, eight weeks after phloem-girdling, a significant reduction in g_s was observed in the GNF treatment compared to the other treatments. Phloem-girdling induced on average an 84 % reduction in g_s in the GNF treatment over the remainder of the trial compared to the pre-girdling GNF value, and an 83 % lower g_s compared to the NF and F treatments. A continuous reduction of g_s in the GNF treatment was observed from the time of phloem-girdling onwards, and the final value of g_s on 2018/06/30 was very low (0.01 mol m^{-2} s^{-1}).

A significant reduction of g_s in the GF treatment compared to the NF treatment was observed one day after fruit removal (2018/02/04). It should be noted that values of g_s on 2018/02/04 were also lower than on 2018/02/03 for the NF (significantly) and F (not significantly) treatments, with all three treatments returning to similar values on 2018/02/05 as for 2018/02/03. A transient reduction in g_s occurred across all treatments on 2018/02/04, coinciding with peak VPD_{air} and R_s (Table 1), consistent with short term stomatal responses to atmospheric demand. These short-term fluctuations did not alter the longer term treatment effects and trends. In the GF treatment on 2018/03/19, six weeks after fruit removal, g_s was significantly lower compared to the NF and F treatments. This trend continued for 2018/04/18. On both days, g_s values were similar for the GF and GNF treatments. On 2018/06/30, after the commercial harvest (2018/04/27), g_s in the GF treatment did not differ significantly from the values for the NF and GNF treatments, but was lower compared to the F treatment.

No significant differences in C_i were observed on five of the seven measurement days (Fig. 3C). However, on 04/02/2018, one day after fruit removal, Ci was significantly higher in the GNF treatment. On 05/02/2018, C_i of GNF treatment was significantly higher than the NF treatment. The lowest C_i values for all treatments were observed on the final measurement day in June 2028.

3.3. The influence of fruit on canopy transpiration responses to atmospheric drivers

There were small differences in E_c in response to T_{air} during fruiting and non-fruiting periods (Fig. 4A). Within the lower range of 15 – 20 °C, E_c was significantly higher during the non-fruiting period (0.05 mm h^{-1}) compared to the fruiting period (0.03 mm h^{-1}), whilst in the higher ranges of 25 – 30 °C, 30 – 35 °C and 35 – 40 °C transpiration was not significantly different between fruiting periods and non-fruiting periods. Differences between fruiting and non-fruiting periods were more distinct when considering the response of E_c to VPD_{air} (Fig. 4B). Canopy transpiration during fruiting periods was, on average, 0.02 ± 0.01 mm h^{-1} higher than during non-fruiting periods across all VPD_{air} ranges.

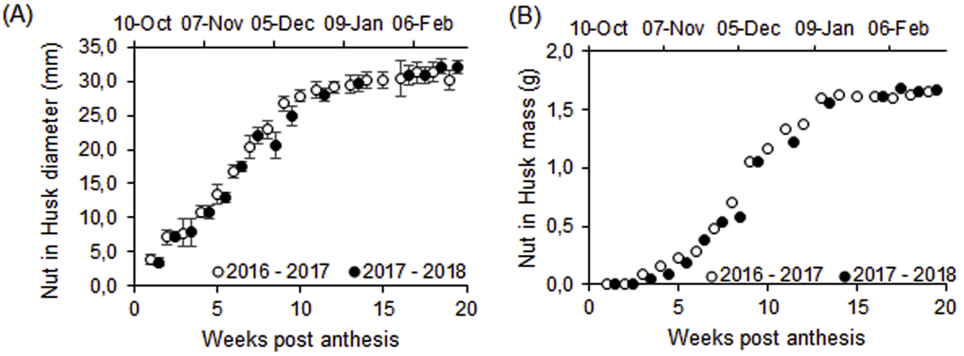

Fig. 2. (A) Average (± standard deviation) nut in husk diameter and (B) average nut in husk fresh mass of 20 randomly collected macadamia fruits from one week post anthesis to 20 weeks post anthesis in the 2016–2017 and 2017–2018 production seasons.

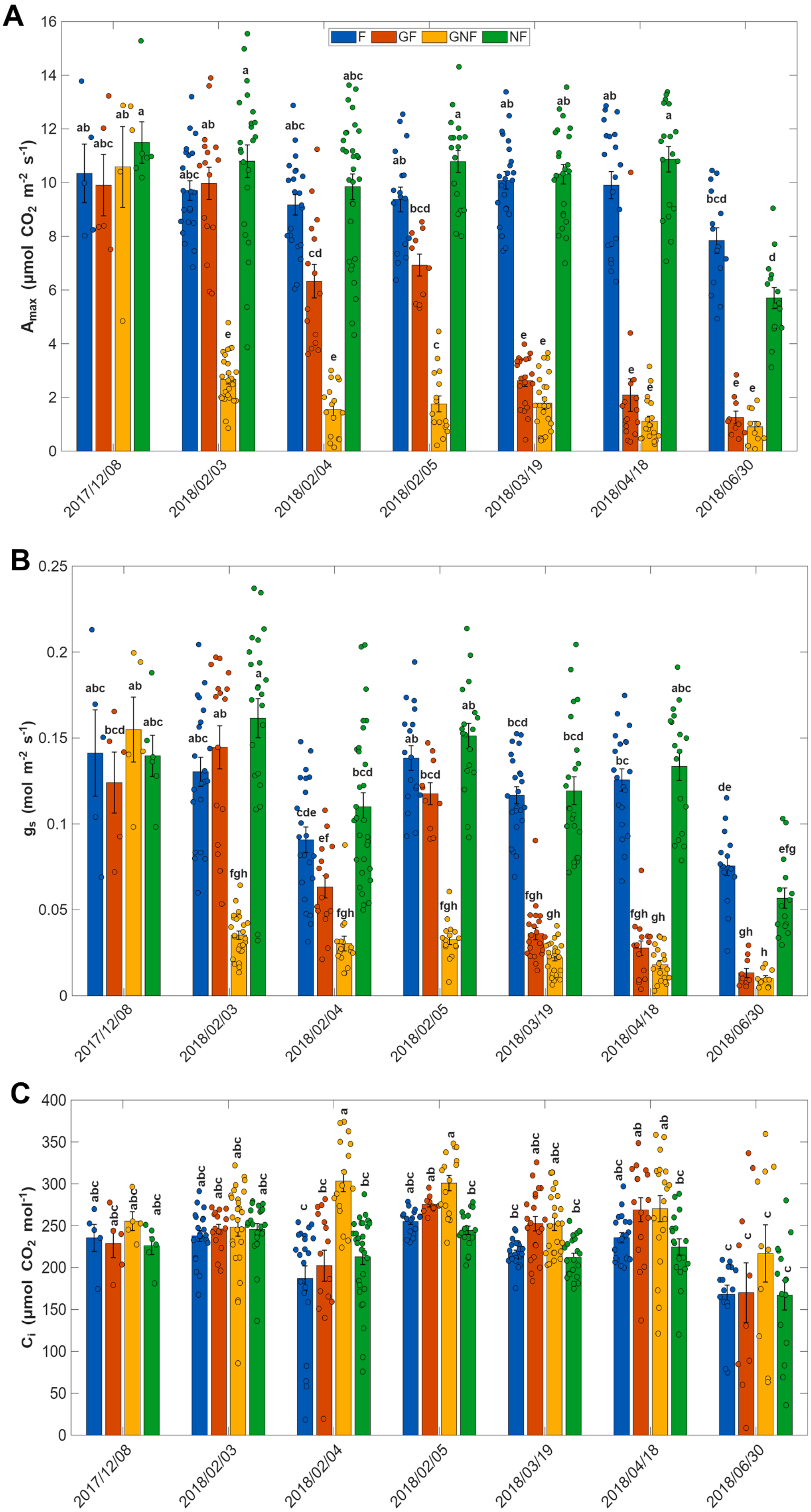

Fig. 3. Average (± standard deviation) (A) light-saturated net CO_2 assimilation rate (A_{max}), (B) stomatal conductance (g_s), and C) internal CO_2 concentration (Ci) measured on seven days during the trial period. Treatments included phloem-girdled non-fruiting branches (GNF), non-fruiting branches (NF), phloem-girdled fruiting branches (GF) and fruiting branches (F). Fruit was removed from GF branches on 3 February 2018. Means followed by the same letter are not significantly different ($p = 0.05$) as analysed using repeated measures ANOVA.

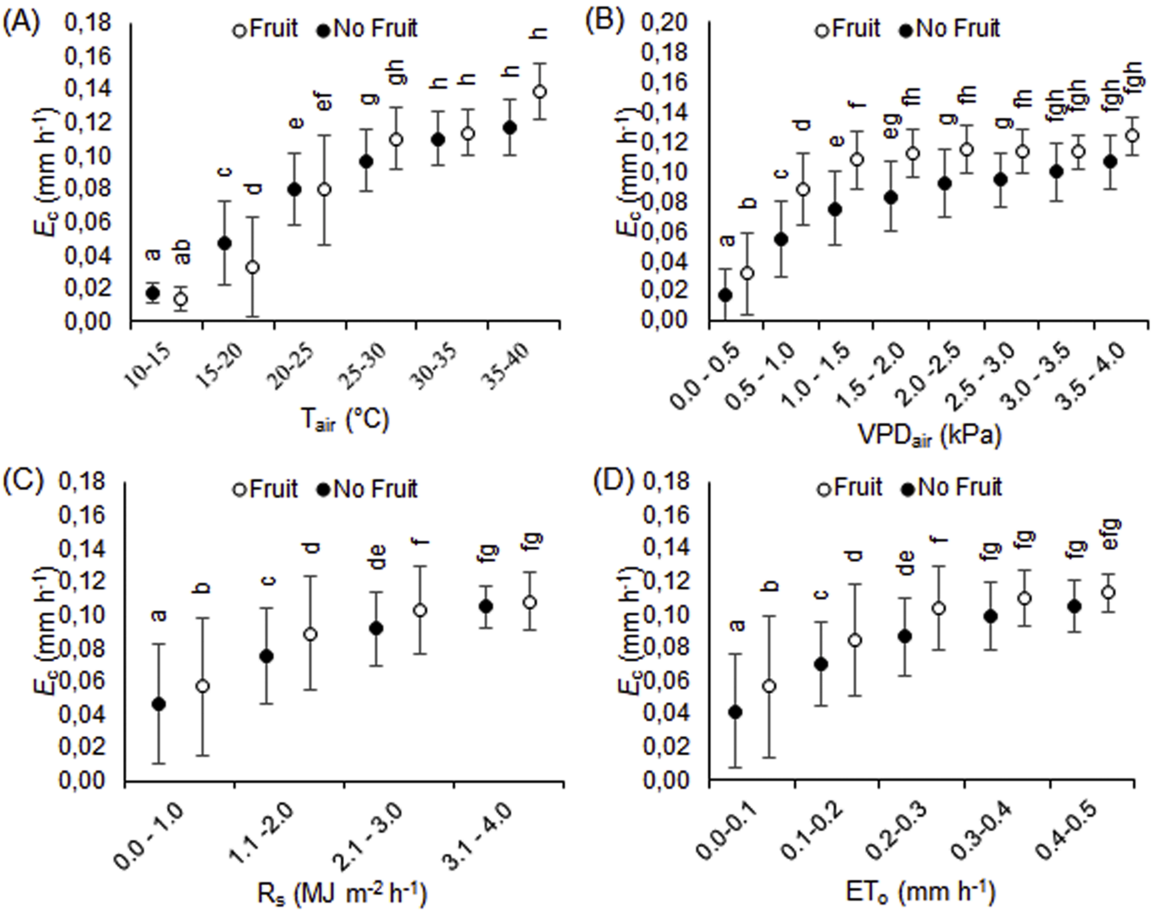

Fig. 4. Response of average daytime (0600 h – 1800 h) hourly canopy transpiration (E_c) to (A) air temperature (T_{air}), (B) air vapour pressure deficit (VPD_{air}), (C) solar radiation (R_s) and (D) reference evapotranspiration (ET_o) during fruiting ($N = 8688$) and non-fruiting ($N = 8717$) periods over two consecutive seasons from 10 August 2016 to 8 August 2018. Means followed by the same letter are not significantly different ($p = 0.05$) as analysed using repeated measures ANOVA.

Within the 0.0 – 3.0 kPa range, E_c during fruiting periods was significantly higher compared to non-fruiting periods, whilst no differences between the two periods were found when VPD_{air} exceeded 3.0 kPa.

Within the 0.0 – 3.0 MJ m^{-2} h^{-1} R_s range, E_c was significantly higher (on average 0.01 ± 0.001 mm h^{-1}) during the fruiting period compared to the non-fruiting period. At R_s above 3.0 MJ m^{-2} h^{-1} no significant differences in E_c were found between fruiting and non-fruiting periods (Fig. 4C). Canopy transpiration was significantly higher (on average 0.02 ± 0.009 mm h^{-1}) during fruiting compared to non-fruiting periods within the 0.0 – 0.3 mm h^{-1} range of ET_o (Fig. 4D). When ET_o exceeded 0.3 mm h^{-1} no significant differences in E_c were found between fruiting and non-fruiting periods.

Given that E_c is impacted by changes in canopy size, growth flushes and pruning, events throughout the course of the study could have contributed to the observed responses of E_c to weather variables. In order to eliminate canopy size as a confounding factor, average diurnal responses of weather variables and E_c were compared for a month before (1–30 April 2018 - fruiting) and a month after (1–31 May 2018 - non-fruiting) commercial harvest (Fig. 5), which occurred on 2018/04/27. During these periods no significant differences in canopy size were observed, with average LAI measured on 2018/04/18 being 4.6 ± 0.5 m^2 m^{-2} and 4.3 ± 0.4 m^2 m^{-2} on 2018/06/03. On 2018/06/16 light hand pruning occurred to ensure better light penetration into the canopy and would have had little impact on LAI. In addition, the small change in average canopy volume by 4 m^3 from 2018/01/17 to 2018/05/01 for a canopy of approximately 80 m^3, suggests that changes in canopy size over a two month period were likely to be negligible, especially as the late summer vegetative flush had hardened off by this stage. Changes in canopy size were therefore unlikely to have contributed to differences in E_c between the fruiting and non-fruiting periods.

Given the large variation in most of the weather variables, there were no statistically significant differences ($p = 0.05$) in daytime T_{air} (Fig. 5A), R_s (Fig. 5B), VPD_{air} (Fig. 5C) and ET_o (Fig. 5D) between the fruiting and non-fruiting months. There were, however, significant differences in daytime E_c between the fruiting and non-fruiting months. During the fruiting month E_c was significantly higher than the non-fruiting month at the following times: 09:00, 10:00, 12:00, 14:00, 15:00, and 16:00 (Fig. 5E), when considering the response of E_c to ET_o. Transpiration at these times was on average 0.03 ± 0.01 mm h^{-1} higher during the fruiting month compared to the non-fruiting month.

When the area under each curve in Fig. 5E was integrated, the average daytime E_c during the fruiting month (April 2018) was 0.85 mm day^{-1}, which was higher than 0.55 mm day^{-1} calculated for the non-fruiting month (May 2018). Total monthly daytime transpiration for April 2018 (fruiting) was 27.5 mm compared to 18.3 mm for May 2018 (non-fruiting), whilst total ET_o for April 2018 was 80 mm and for May 2018 it was 76 mm.

To account for possible variations in weather variables causing the observed variation in transpiration volumes, K_t values were calculated for the sap flow trees, which normalizes transpiration for prevailing weather conditions. Although there was significant variation in daily K_t values (Fig. 6) there was a steady increase in fortnightly values from August until April, following which there was a sharp decline. The average K_t value for April was 0.32, whilst following harvest on 27 April 2028, the K_t value fell to 0.28 in May 2028.

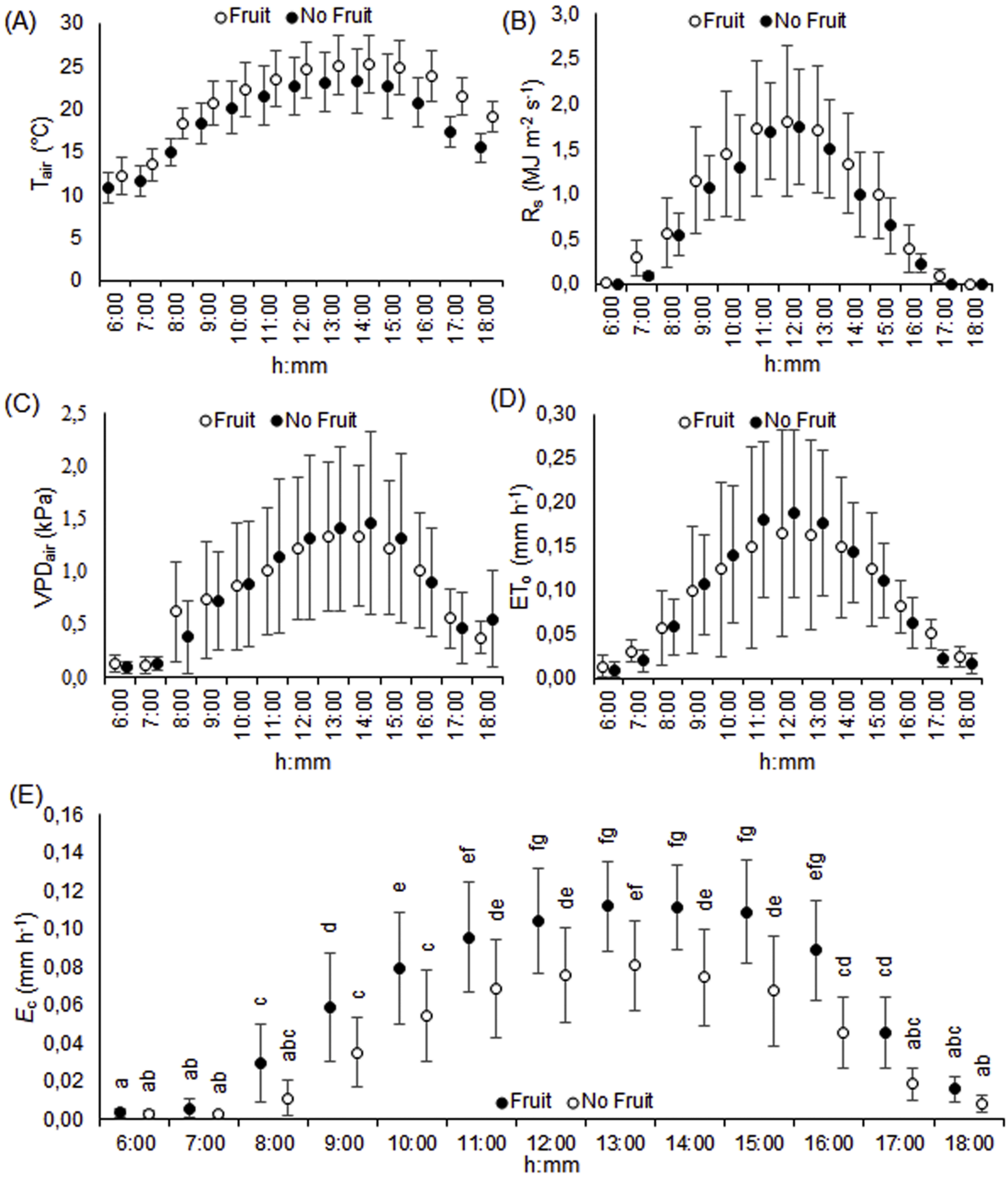

Fig. 5. Average diurnal progression of (A) air temperature (T_{air}), (B) solar radiation (R_s), (C) air vapour pressure deficit (VPD_{air}), (D) reference evapotranspiration (ET_o) and (E) canopy transpiration (E_c) during fruiting ($N = 403$) and non-fruiting ($N = 390$) months of April and May 2018, respectively. Means followed by the same letter are not significantly different ($p = 0.05$) as analysed using repeated measures ANOVA.

4. Discussion

Although Smit et al. (2020) reported an impact of developing macadamia fruit on gas exchange at a leaf level, additional evidence was required to determine if this response could be upscaled to a canopy level and if these changes would lead to an increase in whole tree transpiration, irrespective of microclimate conditions. This is required to understand the impact of developing fruit on seasonal transpiration volumes, which in turn impacts water requirements and water management of macadamia orchards. This is particularly important during the oil accumulation stage, as underestimating water requirements at this time could lead to water stress, which has a negative impact on yield and quality (Stephenson et al., 2003).

Although the upregulation of A_{max}, g_s and E_c in the presence of fruit is a common phenomenon and has been demonstrated in a range of fruit tree crops, including apple (Lenz, 1986; Wünsche et al., 2000), avocado (Silber et al., 2013), date palm (Zhen et al., 2019) and olive (Bustan et al., 2016), fruit load has also been shown to have insignificant effects on A_{max}, g_s and E_c in pear (Naor, 2001) and peach (Mahhou et al., 2005). The exact nature of this phenomenon therefore needs to be determined for macadamia. Acknowledging the complexity of whole tree source-sink dynamics, and difficulties in scaling leaf gas exchange measurements to canopy level, the study used phloem-girdled and non-girdled branches, with and without fruits, to examine the effect of fruits, predominantly during the oil accumulation stage, on macadamia leaf gas exchange. Although the main aim of girdling was to disrupt

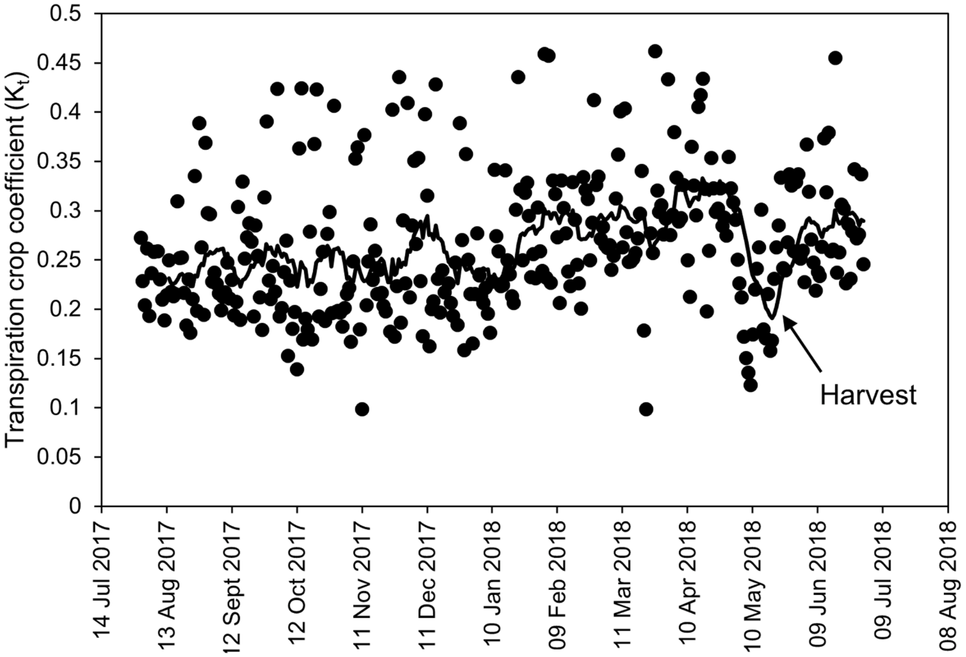

Fig. 6. Daily transpiration crop coefficients (K_t) for the 'Beaumont' macadamia trees instrumented with sap flow equipment for the 2027/18 season. The solid line indicates a 14-day running average. The arrow marks when harvesting of the trees instrumented with sap flow equipment occurred.

assimilate transport, impeding phloem transport will also impact transport of hormones away from the branch, potentially impacting gas exchange. For instance, phloem girdling of eucalyptus shoots increased foliage-derived ABA, reducing g_s (Mitchell et al., 2017), Similarly, girdled soybean shoots showed elevated ABA and jasmonic acid levels. (Castro-Valdecantos et al., 2021).

No significant differences in A_{max} and g_s were observed between girdled fruiting (GF) branches and non-girdled branches (F & NF) approximately two months after phloem-girdling, whilst A_{max} and g_s of girdled non-fruiting (GNF) branches were significantly reduced during the same period as compared to the other treatments. The reduction in A_{max} and g_s was accompanied by significantly higher C_i one month after girdling on a day when g_s was reduced due to high VPD$_{air.}$ This suggests that there were both stomatal and NSL (mesophyll CO_2 conductance and biochemical constraints to the light and dark reactions) to photosynthesis in GNF branches. Before fruit removal, A_{max} and g_s of GF branches were approximately 3.8 times higher than that of GNF branches. The maintenance of comparative A_{max} and g_s in GF branches as compared to F and NF treatments suggests that macadamia fruit are strong enough sinks to prevent the downregulation of photosynthesis as a result of end product feedback inhibition. In addition, the conversion of simple sugars to oil in the macadamia fruit would encourage continued transport of assimilates to the fruit. This is supported by findings in *Lolium perenne,* where enhanced production of lipids resulted in increased carbon capture, which was speculated to result largely from reduced feedback inhibition of photosynthesis (Beechey-Gradwell et al., 2019). The result is that photosynthesis is "blind" to carbon accumulation, thereby ensuring the continued production of photoassimilates. This could partly explain why A_{max} and g_s of GF branches were no different from NF and F branches before fruit removal, but were significantly lower than non-girdled treatments more than a month after fruit removal. These results are further supported by findings in olive and cashew, where both A_{max} and g_s showed no decrease after phloem-girdling of fruit bearing branches (Proietti and Tombesi, 1990; Schaper and Chacko, 1993). In contrast, the lower A_{max} and g_s in GNF is supported by results in girdled branches of apple (Zhou and Quebedeaux, 2003), grape (Roper and Williams, 1989) and mango (Urban et al., 2004) with low sink strength or low crop load, further demonstrating the impact of fruit on A_{max} and g_s.

Although the proposed induction of a sink limitation by fruit removal in girdled branches resulted in the down-regulation of A_{max} and g_s, there were no significant differences in A_{max} and g_s between non-girdled NF and F branches throughout the duration of the trial. The maintenance of high A_{max} and g_s, during fruiting periods was therefore not limited to branches containing the sink, but also occurred in branches containing no direct sink (i.e. non-fruiting branches). In coffee, Cannell (1971) demonstrated that there are large transfers of assimilates throughout the tree, which buffer the increased whole tree assimilate demand brought about by developing fruit. In a phloem-girdling study in macadamia to determine factors impacting fruit set, abscission and dry matter accumulation, Trueman and Turnbull (1994) found that the number of fruit set on ungirdled branches was independent of leaf number, suggesting that fruit can obtain carbohydrates from elsewhere on the tree. When combined with evidence from this study, it confirms that branches are not autonomous in their carbon requirements but are dependent on the tree as a whole. This also implies that if assimilates can be transported over long distances, albeit to a range of sinks and not limited to developing fruit, an upregulation of leaf gas exchange, in the presence of a strong sink, would not be limited to leaves or branches in close proximity to fruit, but could apply to the canopy as a whole. If fruit were only supported by distal source leaves, it would imply that NF branches would have lower A_{max} and g_s than F branches due to the differences in sink demand between the two branches. This was not the case and provides further evidence for branch dependence on other tree parts in macadamia, as suggested for coffee by Vaast et al. (2005). Similar whole tree responses have been found in apple (Wünsche et al., 2005) and date palm (Zhen et al., 2019), with g_s on fruiting trees being substantially higher than non-fruiting trees.

The upregulation of g_s in both F and NF branches during fruit bearing periods resulted in an increase in E_c relative to non-fruiting periods, which was particularly noticeable in the response of macadamia E_c to increases in VPD$_{air}$, R$_s$ and ET$_o$, over two consecutive seasons, during fruiting compared to non-fruiting periods. This isohydrodynamic response to crop load was reflected in midday Ψ_{sun} during the oil accumulation period which averaged −1.32 MPa, as opposed to −0.86 MPa during early fruit growth. Higher g_s during periods of high assimilate demand resulted in less strict control of Ψ_{sun}. When comparing macadamia E_c before and after commercial harvest, E_c was ~20 % higher during fruiting compared to non-fruiting periods. This large difference in E_c can be explained by the approximately 25 % higher g_s measured during fruiting as compared to non-fruiting periods, when VPD_{air} was <3.0 kPa. This is in agreement with the variable response of g_s to increases in leaf to air vapour pressure deficit (VPD_{leaf}) during high and low fruit load periods demonstrated by Smit et al. (2020) and suggests that when assimilate demand is high, stomata will remain open for longer resulting in increased transpiration relative to evaporative demand., as seen in the change in K_t values before and after harvest. Similar increases in E_c as a result of fruiting were found in apples (Lenz, 1986), avocado (Silber et al., 2013) and olive (Bustan et al., 2016), with E_c in fruit bearing trees being significantly higher than that of non-fruiting trees under the same set of environmental conditions. Silber et al. (2013) attributed the increase in E_c in fruiting trees to the higher g_s in these trees and suggested that irrigation should be adjusted for actual crop load.

The major constraint to establishing causality between the upregulation of E_c and increased fruit load or sink strength across multiple seasons, is the dominating effect of changes in weather and canopy size, which significantly impact canopy E_c. As a result, the diurnal course of a range of weather variables and transpiration was examined in April and May 2018, which was approximately one month before and one month after commercial harvest, during which changes in canopy size were negligible. With the exception of T_{air}, which was on average 2.9 °C higher over the course of the daylight hours in April 2018 as compared to May 2018, the other weather variables were fairly similar before and after harvest. However, average diurnal E_c during April 2018 remained consistently higher from 0700 h to 1800 h compared to May 2018, with the distinct difference being the presence or absence of fruit. The analysis of K_t values for the month before and after harvest provided further support for the hypothesis that the increases in E_c observed in April 2018 were unrelated to weather variations, as average K_t for April during the fruit bearing period was 0.32, as compared to 0.26 in the fruitless May period. A similar drop in crop coefficient (K_c) values following harvest was observed in both apples and pears by Girona et al. (2011), which was attributed to the removal of fruit.

We therefore propose that strong assimilate demand from developing fruit, particularly during oil accumulation, reduces end product feedback on photosynthesis. This may promote wider stomatal apertures across the canopy via hydraulic or biochemical signalling, sustaining carbon supply to reproductive sinks and elevating whole-tree water use despite typically isohydric stomatal control.

5. Conclusions

It was hypothesised that the variable responses of g_s to the presence of oil storing fruit in macadamia would result in an increase in canopy transpiration. Through phloem-girdling studies, it was demonstrated that the presence of fruit increases both A_{max} and g_s and that branches are not autonomous in their carbohydrate requirements, suggesting that even in non-fruiting branches g_s remains high when fruit are present on the tree. There thus seems to be upregulation of canopy conductance in response to the assimilate demand from developing fruit at the tree level. By analysing the response of E_c to various environmental factors before and after harvest and actual E_c before and after harvest, it was evident that the increase in g_s in response to the presence of fruit translated into increased E_c. Irrigation scheduling based on a constant K_t (adjusted for canopy size) fails to account for this increased water demand. In summer rainfall regions, where precipitation often declines during this period, unadjusted K_t values could induce water stress, potentially impairing flower initiation.

Given the observational basis of this study, it is suggested that future studies aim to quantify and track assimilate production, and export and storage within sink and source leaves and tissues, to establish when and how changes in leaf gas exchange occur in macadamia trees. Furthermore, given the significance of the results in this study, it would be of great value to both researchers and irrigators if crop phenological and physiological parameters are accounted for in water use models, to improve water management, especially during fruit bearing periods. In addition, ways in which crop load can be easily measured or predicted need to be developed to allow adjustment for variable crop load.

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CRediT authorship contribution statement

Theunis G Smit: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Nicky J Taylor:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Stephanie J.E. Midgley:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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