The effect of wind run on transpiration and leaf temperature of *Leucospermum conocarpodendron* on the Cape Peninsula

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Abstract

Parts of the Cape Floristic Region are subject to exceptionally high levels of wind in certain seasons, however it has recently been recorded that the Western Cape has experienced a reduction of 25.7% in wind run between the years 1974 – 2005. Shifts in wind run across the globe may significantly affect whole plant physiology through changes in transpiration which can influence mass-flow mediated movement of nutrients in winter as well as leaf temperature. The objectives of this study were to establish whether (a) decreased wind run could reduce transpiration in winter when vapour pressure deficit is low and (b) leaf temperature approaches damaging levels during low wind run conditions in *Leucospermum conocarpodendron* on the Cape Peninsula over a given time period. High levels of vapour pressure deficit (>1.5 kPa.24hr^{-1}) did not occur simultaneously with high levels of wind run (>250 m.24hr^{-1}) and therefore the effects that these factors have on transpiration could be separated. Variable rates of transpiration corresponded with reduced wind run under low vapour pressure deficit conditions in winter, therefore decreased wind run may have the potential to reduce transpiration. However, transpiration is highly sensitive to minor fluctuations in vapour pressure deficit during low wind run conditions. Variable leaf temperatures corresponded with low wind run and low vapour pressure deficit conditions, therefore decreased wind run may have the potential to increase leaf temperatures. However, leaf temperature is highly sensitive to low wind run and low vapour pressure deficit conditions. Low wind run conditions, currently predicted for the future, does not pose a threat to transpiration, nutrient uptake and leaf temperature of *Leucospermum conocarpodendron* plants on the Cape Peninsula.

1. Introduction

Transpiration and leaf temperature are determined by multiple factors (Campbell and Norman 1998), one of which is wind (Grace 1977). Plant ecologists have stressed the importance of wind in moulding floras of mountains and coasts (Salisbury and Ross 1992), and the benefit of shelter to agricultural crops has frequently been demonstrated. Even though parts of the Cape Floristic Region (CFR) are subject to exceptionally high levels of wind in certain seasons, there is a dearth of knowledge on the effect of wind on transpiration and leaf temperature.

The CFR is home to approximately 9000 plant species, of which c.6300 are endemic to the region (Goldblatt and Manning 2002). The region has been identified as a global conservation priority as a result of agriculture, forestry, urbanisation, alien plant invasions and climate change (Bomhard et al. 2005; Bond et al. 2003; Gritti et al. 2006; Midgley et al. 2002). Bomhard et al. (2005) suggested that 2% of Proteaceae endemic to the CFR will become extinct by the year 2050 and the proportion of 'Critically Endangered' taxa will increase from 1% to 7% as a direct result of climate change. However, the current debate on the impact of climate change (Acocks 1953; Bomhard et al. 2005; Hoffman et al. 2011; Midgley et al. 2002; 2003) on the highly speciose CFR gives limited consideration to less obvious factors such as wind (Hoffman et al. 2011).

It has recently been recorded that the Western Cape has experienced a reduction of 25.7% in wind run (the total amount of travelled wind over a period of time) between the years 1974 – 2005 (Hoffman et al. 2011). Shifts in wind run across the globe may significantly affect the hydrological cycle and whole plant physiology (Mc Vicar et al. 2012) in four main ways. Firstly, if evaporative demand declines then it is possible that more moisture will become available for plant growth, infiltration and runoff despite the widespread increase in temperature impacting species distribution and ecosystem function (Hoffman et al. 2011). Secondly, a reduction in wind run may decrease transpiration which may, in turn, reduce nutrient acquisition through mass flow meditated movement of nutrients towards the rhizosphere during winter when water is available and vapour pressure deficit (VPD) is low (Hoffman et al. 2011; Yates et al. 2010). Thirdly, transpiration is directly proportional to photosynthesis which itself is proportional to primary productivity (Drake et al. 1997). Lastly, decreased wind run together with increased temperatures and a reduction in rainfall could potentially exacerbate heat stress of plants during the summer drought (Hoffman et al. 2011), especially plants with large leaves (Caldwell 1970). The fynbos biome supports species with a wide range of leaf sizes. If large leaved species, such as *Leucospermum conocarpodendron* (L.), become vulnerable under these conditions then the species composition of the fynbos biome may change. It is

necessary for important management decisions in the CFR to include wind run in vegetation predictions because variable wind run in space and time may have consequential effects on the growth and survival of native vegetation, as well as vegetation structure and community dynamics in a complex flora.

1.1 The Drivers of Transpiration

Transpiration can be calculated using the variables that determine the heat-energy balance of a leaf surface according to the following equations.

The radiant-energy flux absorbed by a leaf surface (Q_{abs}) is determined by the total absorbed radiation and leaf emissivities (Salisbury and Ross 1992):

$$Q_{abs} = eQ_V + e'Q_{th}$$

where, eQ_V is the total absorbed radiation in the photosynthetically active region, $e'Q_{th}$ is the total absorbed radiation outside the photosynthetically active region and e and e' are the leaf emissivities in the two spectral regions. The net radiation at a leaf surface (Q) is determined by Q_{abs} and the energy emitted by a leaf (Stefan-Boltzmann law) (Salisbury and Ross 1992):

$$Q = Q_{abs} - e'\sigma T^4$$

where, e' is the emissivity of the leaf for long-wave radiation, σ is the Stefan-Boltzmann constant (5.673×10^{-8} $W.m^{-2}.K^{-4}$) and T is the absolute temperature of the leaf. However, if the factors influencing the magnitude of Q are kept constant then changes in Q can be attributed to changes in sensible heat-energy transfer by convection and conduction at a leaf surface (H) and latent heat-energy flux of water vapour (transpiration) at a leaf surface (V) (Salisbury and Ross 1992):

$$Q = H + V$$

Changes in H can be attributed to changes in the difference between air and leaf temperature (ΔT) and changes in boundary layer conductance (g_a) (Salisbury and Ross 1992):

$$H = \Delta T C_p \rho . g_a$$

where, C_p is the specific heat capacity of dry air ($\approx$1.000 $J.kg^{-1}.K^{-1}$) and ρ is the density of dry air (1.205 $kg.m^{-3}$ at 20°C and 1 atm). Changes in V can be attributed to changes in VPD (the difference between vapour pressure within the substomatal cavity of the leaf and vapour pressure of the air; Δp) and leaf conductance which involves stomatal conductance (g_s) and g_a (Salisbury and Ross 1992):

$$V = \frac{\Delta p C_p \rho (g_s + g_a)}{y}$$

where, y is the psychrometric constant (66.6 $Pa.K^{-1}$). Changes in g_a can be attributed to changes in wind run (u) because changes in leaf dimension (l) are constant in a single species (Grace 1977):

$$g_a = \frac{\sqrt{l}}{u}$$

1.2 Aims and Hypotheses

The main objectives of the study were to establish whether (a) decreased wind run could reduce transpiration in winter when VPD is low and (b) leaf temperature approaches damaging levels during low wind run conditions (Hoffman et al. 2011). To achieve this, records of wind run were correlated with diurnal and nocturnal sap flux density during low VPD conditions in winter and wind run was correlated with leaf temperature. Sap flux density was used as an indicator of transpiration. The study was conducted on *L. conocarpodendron* plants in the Cape Peninsula over a given time period. It was hypothesized that wind run is the dominant driver of transpiration when VPD is low and therefore wind run should be the dominant driver of nocturnal transpiration because VPD is relatively lower at night when air temperature is lower. This suggests that decreased wind run should reduce transpiration under low VPD conditions in winter and reduced wind run should result in increased leaf temperature.

2. Methods and Materials

2.1 Study Site

The study site is located in Camps Bay, Western Cape, South Africa within the Table Mountain National Park (33°57'38.64"S, 18°23'13.98"E; elevation of 198 m). The region supports a Mediterranean-type climate, characterised by hot dry summers (December – February) and cool wet winters (June – August). Over the course of the study the maximum average air temperature was 30.76 °C and the minimum average air temperature was 9.52 °C, while the total amount of rainfall was 482.09 mm (Fig. 1). *L. conocarpodendron* is a tree approximately 5 m in height with hairy wedge-shaped leaves approximately 60 mm long with 3 – 10 apical teeth (Manning 2007). A micrometeorological station was installed at the study site and also measured sap flux density and leaf temperature of *L. conocarpodendron* plants continuously from the beginning of March 2012 to the end of September 2012.

2.2 Micrometeorological Station

A Campbell Scientific (Logan, Utah, USA) micrometeorological station was installed in the intercanopy. Wind speed and direction was measured at approximately 4 m above the ground with a wind sentry anemometer and vane, respectively (Model 03001). Air temperature and relative humidity was measured with a shaded, ventilated CS500 sensor. Photosynthetically active radiation (PAR) was measured with a quantum sensor (LI190SB). Rainfall was measured with a tipping bucket rain gauge (TE525). Soil moisture and temperature sensors were buried 10 cm below the soil surface in relatively open passages within the vegetation. Data were recorded at 10 second intervals with 15 minute averages and stored on CR800 and CR1000 dataloggers.

2.3 Sap Flow Probes and Leaf Temperature Thermocouples

Sap flux density was measured with Granier-type (Granier 1987) constant heat thermal dissipation sap velocity probes (TX77099, Dynamax, Houston, USA). A 2 cm by 2 cm patch of bark and phloem were removed from the base (approximately 0.5 m above the ground) of a healthy stem (approximately 20 cm in diameter) and the probes were directly and radially inserted into predrilled holes in the xylem (Clearwater et al. 1999; West et al. 2008). Insulation protected the probes from rainfall and passive thermal gradients (West et al. 2008).

The probes consisted of a pair of 3 cm long, 2 mm thick, stainless steel probes each containing a copper-constantan T-type thermocouple in the centre of the probe (West et al. 2008). The contact

point of a thermocouple produces a small open-circuit voltage (the Seebeck voltage) as a function of temperature (Potter 1996, West et al. 2008). The downstream probe contained a constantan heater element coiled around the steel needle and was supplied with a constant power output (0.2 W) (Clearwater et al. 1999; Davis et al. 2012; Ping et al. 2004). The upstream probe was an unheated, reference probe (Davis et al. 2012). The constantan end of the two thermocouples were connected to give a temperature difference between the heated and reference probes to measure the ambient temperature of the xylem (Clearwater et al. 1999; Davis et al. 2012; Ping et al. 2004). As the sap travelled downstream, heat dissipation increased from the downstream probe. The temperature difference between the probes declined asymptotically with increasing sap velocity (Clearwater et al. 1999). The temperature difference was converted to sap flux density using the program, Baseliner (available online[1]), which in turn used the following empirical equation developed by Granier (1985; 1987):

$$J_s = 0.0119\left(\frac{\Delta T_0}{\Delta T} - 1\right)^{1.23}$$

where J_s is sap flux density ($g.cm^{-2}.s^{-1}$). ΔT is the temperature difference between the heated and unheated probes and ΔT_0 is the temperature difference obtained under zero sap flow conditions.

Leaf temperature thermocouples were handmade and attached to the northward side of the leaves using epoxy adhesive. The leaf temperature data was converted to ΔT (temperature difference between the air and the leaf).

2.4 Replication

A total of seven sap flow probes were inserted into five trees with tree 1 and 7 possessing two sap flow probes each and the rest of the trees possessing one sap flow probe each. The CR1000 datalogger incorporated sap flow probes 1 – 5 and the CR800 datalogger incorporated sap flow probes 6 and 7. Four leaf temperature thermocouples were installed on trees 1 and 7 and an average for each tree was calculated. The present study only incorporates data collected from sap flow probe 1 as a result of equipment failure for the other probes.

2.5 Statistical Analysis

Correlations between sap flux density/leaf temperature and environmental variables were generated (Microsoft Excel 2007; STATISTICA, v10, StatSoft, Inc., 2011). The year was divided into three

[1] <http://c-h2oecology.env.duke.edu/site/resources.html>

seasons (summer, winter and spring) when the seasons were considered. A tree model (Appendix 1) was conducted in the statistical program R (version 2.15.1, R core team, 2012) to indicate recursive portioning of explanatory variables (wind speed, VPD and PAR) when considering sap flux density using the package, "tree" (Ripley 2012). The tree model indicates a series of splits from the top of the tree. This was aimed at finding an explanatory variable that resulted in the greatest change in explained deviance. The variable that occupies the first split on the tree and possesses the longest branches is the variable that has the greatest relative influence on sap flux density.

3. Results

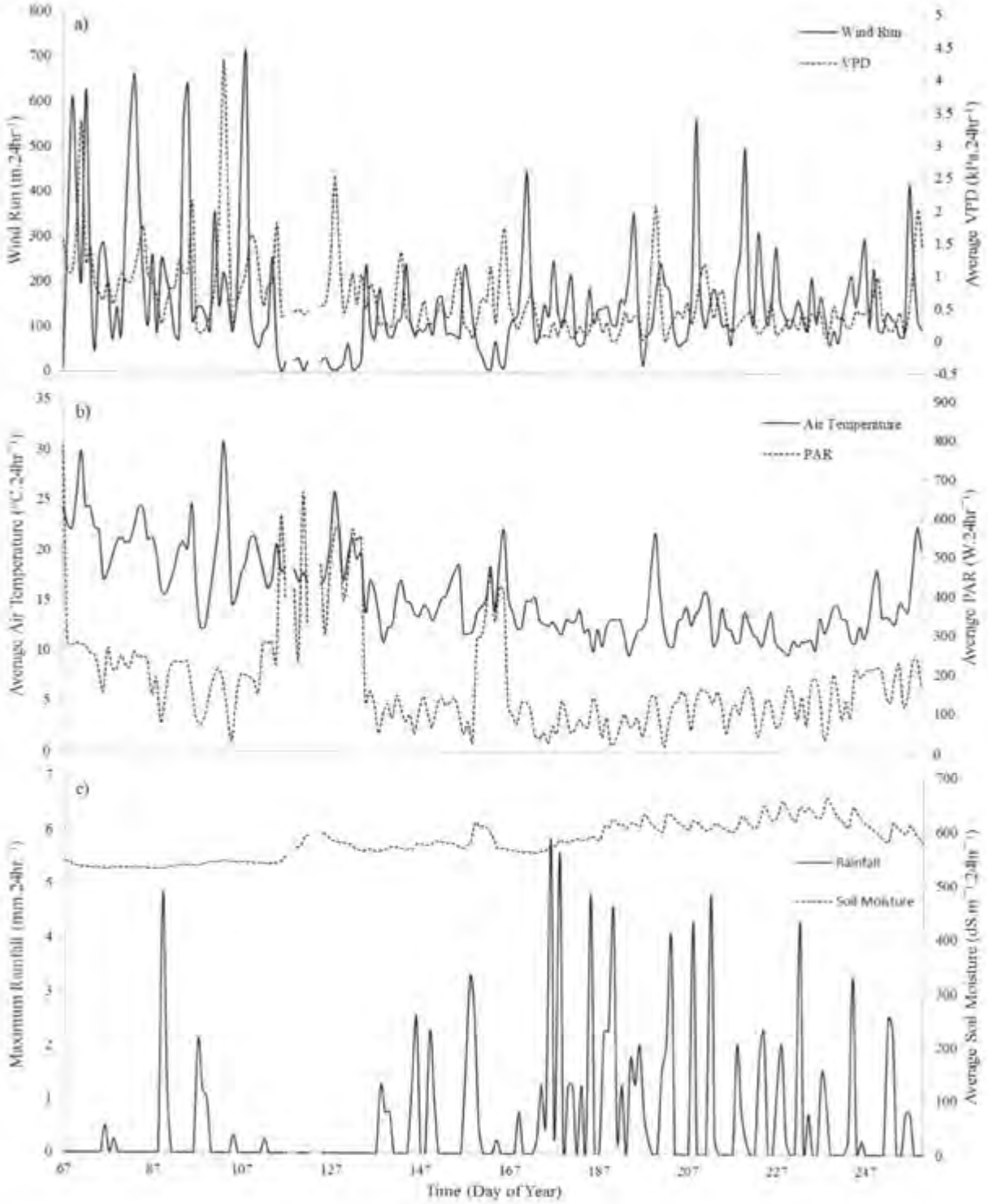

Fig. 1. Daily micrometeorological fluctuations of wind run and vapour pressure deficit (VPD) (a), air temperature and photosynthetically active radiation (PAR) (b) and rainfall and soil moisture (c) over the course of the study (months March – September).

There was substantial variation in wind run, VPD, air temperature, PAR, rainfall and soil moisture over the course of the study (Fig. 1). Wind run did not exceed 706.47 m.24hr^{-1} and VPD did not exceed 4.29 kPa.24hr^{-1} (Fig.1a). These maximum values both occurred in April (Fig. 1a). The maximum average air temperature was 30.76 °C in April and the minimum average air temperature was 9.52 °C in July (Fig. 1b). PAR peaked at the end of April and beginning of May and again at the end of May and beginning of June (Fig. 1b). Air temperature and PAR gradually decreased during winter (Fig. 1b). The total amount of rainfall was 482.09 mm (Fig. 1c). Rainfall and soil moisture increased during winter (Fig. 1c).

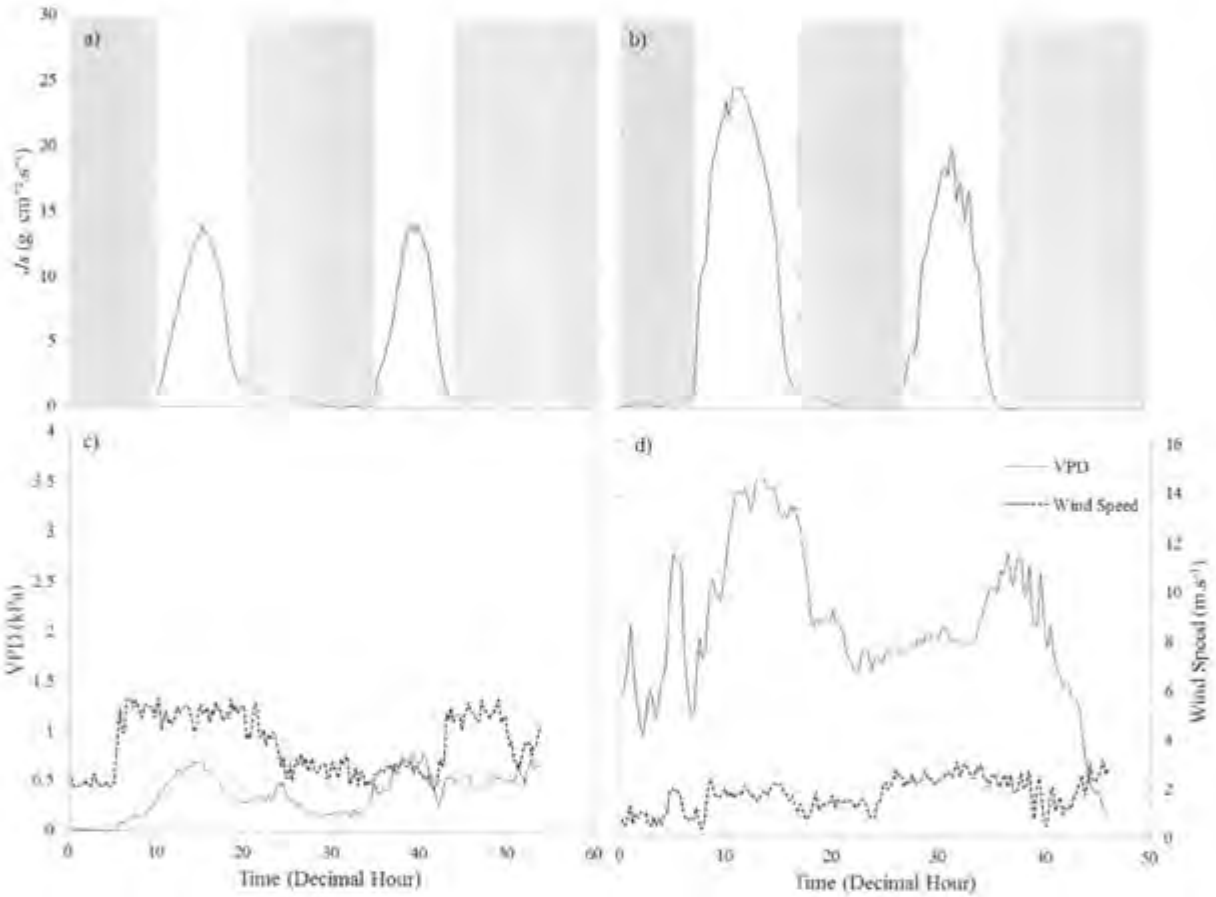

Fig. 2. Diurnal rates of sap flux density and nocturnal rates of sap flux density (J_s) indicated by the grey boxes (a; b). Vapour pressure deficit (VPD) when wind speed is maintained at low levels (c; d) and all other environmental variables are kept constant.

The diurnal sap flux density of the plant was reduced when VPD was less than 0.79 kPa (Fig. 2a and 2c) and the diurnal sap flux density of the plant was increased when VPD reached a maximum value of 3.18 kPa (Fig. 2b and d). This suggested that a decrease in VPD decreased the rate of diurnal sap

flux density when wind speed was maintained at low levels (<4 $m.s^{-1}$), whereas an increase in VPD increased the rate of diurnal sap flux density when wind speed was maintained at low levels. However, a change in VPD did not change the rate of nocturnal sap flux density (Fig. 2).

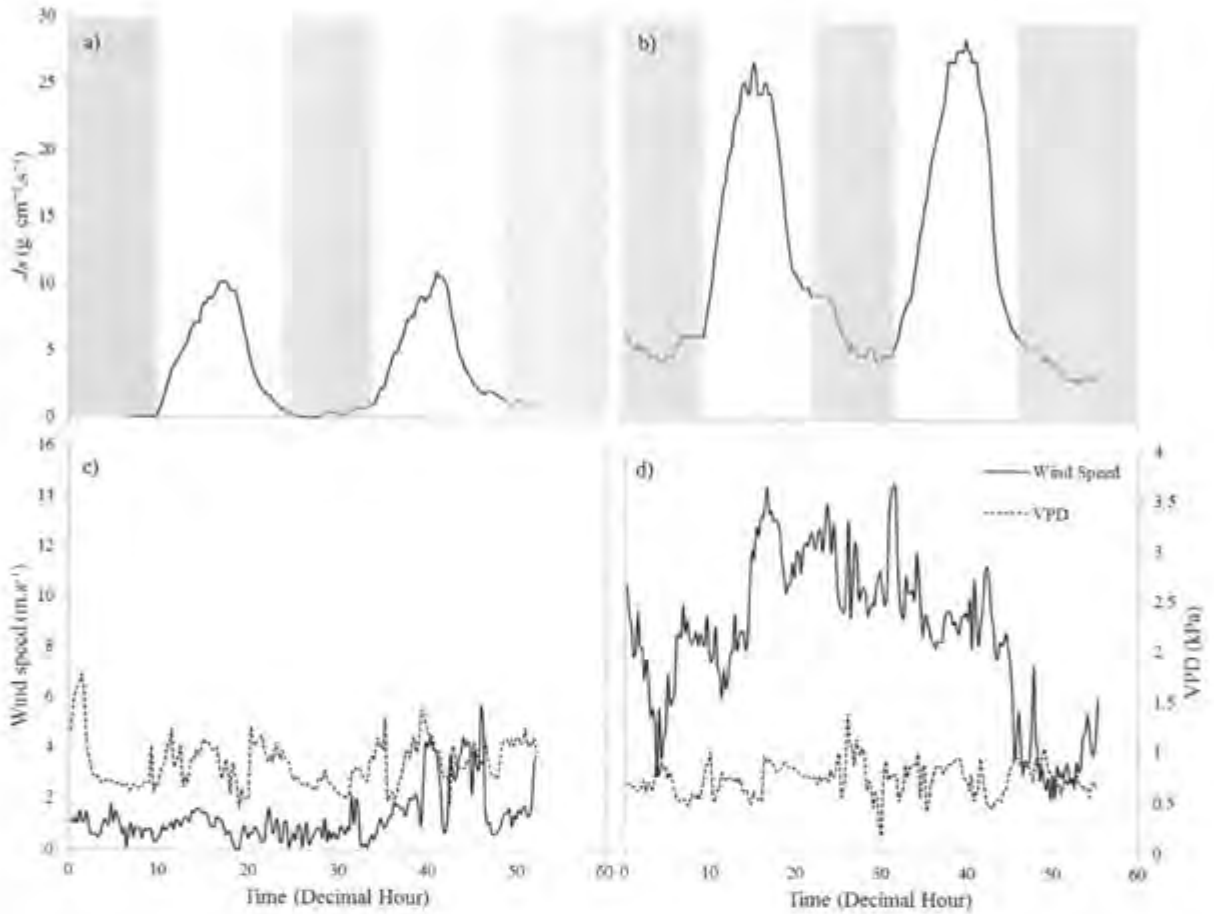

Fig. 3. Diurnal rates of sap flux density (J_S) and nocturnal rates of sap flux density indicated by the grey boxes (a; b). Wind speed when vapour pressure deficit (VPD) is maintained at low levels (c; d) and all other environmental variables are kept constant.

The diurnal and nocturnal sap flux density of the plant was reduced when wind speed was less than 5.68 $m.s^{-1}$ (Fig. 3a and c) and the diurnal and nocturnal sap flux density of the plant was increased when wind speed reached a maximum value of 14.24 $m.s^{-1}$ (Fig. 3b and d). This suggested that a decrease in wind speed decreased the rate of diurnal and nocturnal sap flux density when VPD was maintained at low levels (<1.4 kPa), whereas an increase in wind speed increased the rate of diurnal and nocturnal sap flux density when VPD was maintained at low levels. Although the rate of sap flux did not increase substantially at night due to a reduction in stomatal conductance, there was a notable

increase in sap flux density at night when wind speed was increased and VPD was maintained at low levels.

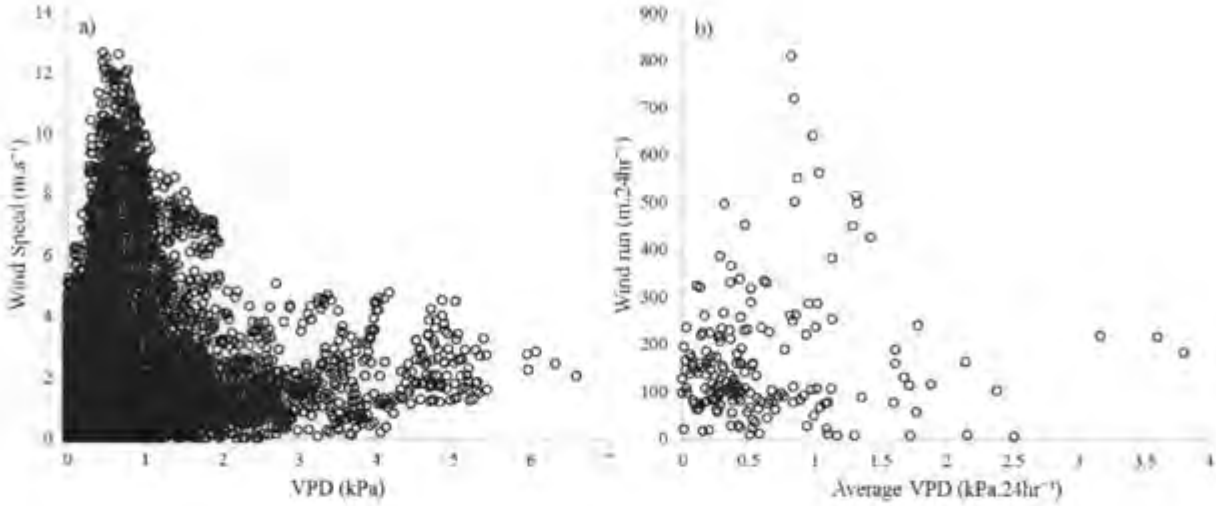

Fig. 4. The relationship between wind speed and vapour pressure deficit (VPD) (a) and the relationship between wind run and average VPD per day (b).

Days occupying high levels of VPD did not include days occupying high levels of wind run and days occupying high levels of wind run did not include days occupying high levels of VPD (Fig. 4a and b). Low levels of VPD were considered to be less than 1.5 kPa.24hr^{-1} and low levels of wind run were considered to be less than 250 m.24hr^{-1} (Fig. 4b; Appendix 1).

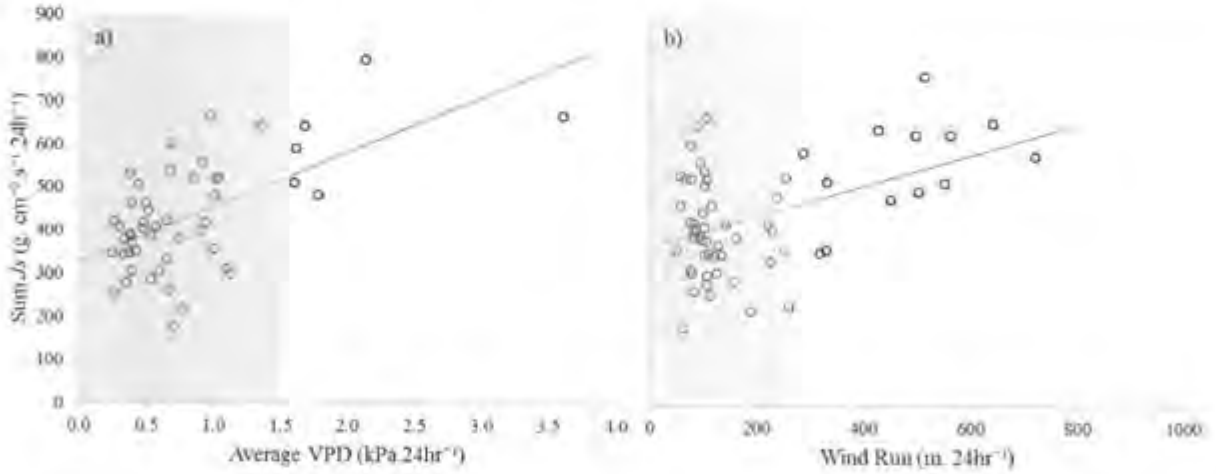

Fig. 5. The relationship between sum sap flux density (J_s) and average vapour pressure deficit (VPD) under low wind run conditions (<250 m.24hr^{-1}) during winter (< day 244) ($p < 0.0001$; $r = 0.59$; $t = 5.06$; $N = 50$) (a). The relationship between sum sap flux density and wind run under low VPD

conditions (<1.5 kPa.24hr^{-1}) during winter ($p < 0.001$; $r = 0.46$; $t = 3.98$; $N = 60$) (b). The grey boxes indicate low VPD (Fig. 5a) and low wind run (Fig. 5b). The outlier in Fig. 5a has been investigated and is real.

A positive relationship existed between sap flux density and VPD under low wind run conditions (<250 m.24hr^{-1}) (Fig. 5a). This suggested that an increase in VPD increased the rate of sap flux density under low wind run conditions. A positive relationship existed between sap flux density and wind run under low levels of VPD (<1.5 kPa.24hr^{-1}) (Fig. 5b). This suggested that an increase in wind run increased the rate of sap flux density under low VPD conditions, however there was substantial variability in sap flux density at both low levels of wind run and VPD (Fig. 5b).

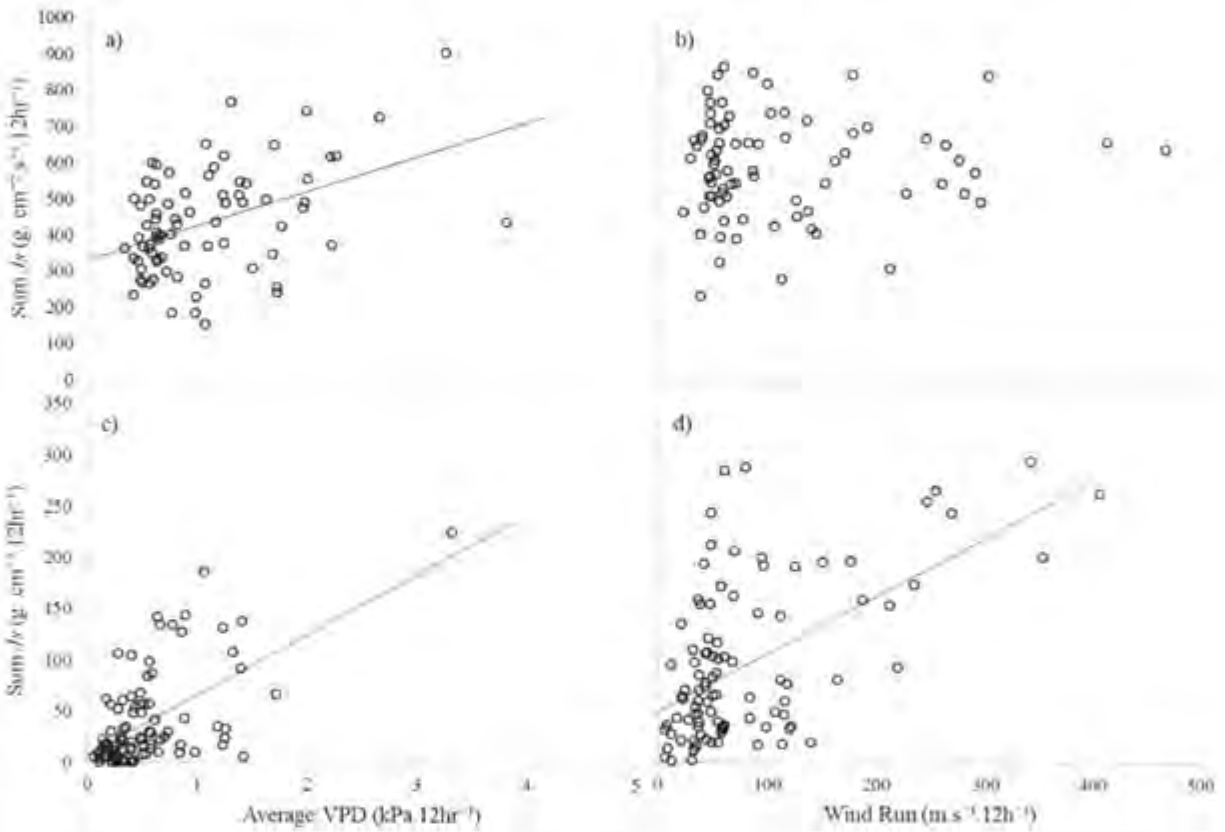

Fig. 6. The relationship between sum sap flux density (J_s) and average vapour pressure deficit (VPD) during the day ($p < 0.0001$; $r = 0.44$; $t = 4.30$; $N = 78$) (a) and at night ($p < 0.0001$; $r = 0.59$; $t = 7.10$; $N = 96$) (c). The relationship between sum sap flux density and wind run, during the day (b) and at night ($p < 0.0001$; $r = 0.57$; $t = 6.72$; $N = 97$) (d). The outlier in fig. 6c has been investigated and is real.

A stronger positive relationship existed between sap flux density and VPD during the day than at night (Fig. 6a and c) and a stronger positive relationship existed between sap flux density and wind run at night than during the day (Fig. 6a and d). The tree model suggested that wind speed, VPD and PAR significantly affected the outcome of sap flux density (Appendix 2). In addition, the tree model suggested that VPD was the dominant driver of diurnal sap flux density and wind speed was the dominant driver of nocturnal sap flux density (Appendix 2).

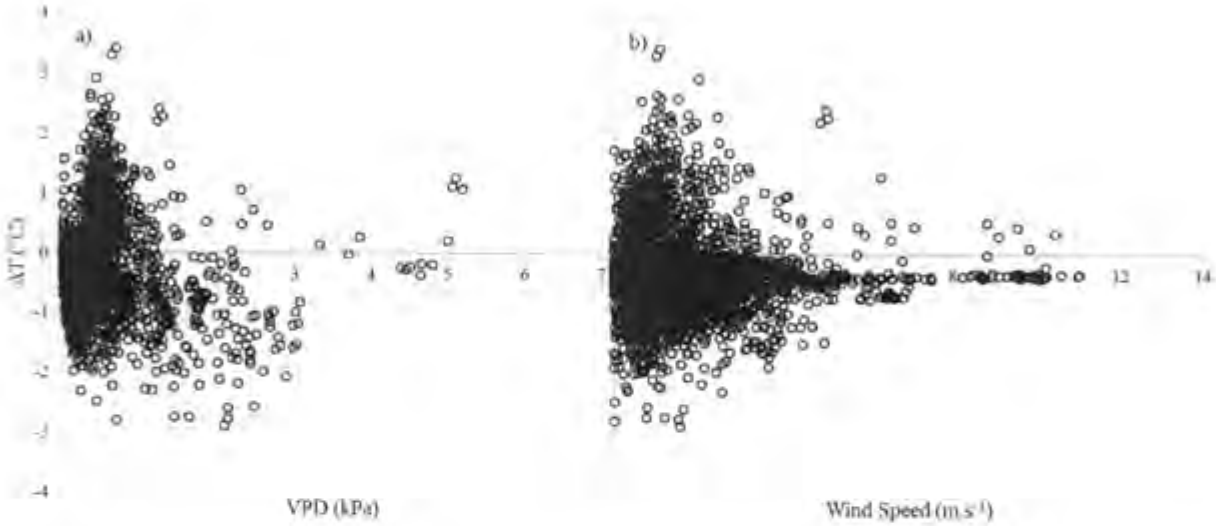

Fig. 7. The relationship between ΔT and vapour pressure deficit (VPD) during the day (a) and the relationship between ΔT and wind speed during the day (b).

There was no relationship between ΔT and VPD (Fig. 7a) and there was no relationship between ΔT and wind speed (Fig. 7b). Nevertheless, there was substantial variability in ΔT at low levels of VPD and wind speed (Fig. 7a and b).

4. Discussion

The main objectives of the study were to establish whether (a) decreased wind run could reduce transpiration in winter when VPD is low and (b) leaf temperature approaches damaging levels during low wind run conditions (Hoffman et al. 2011). Records of wind run were correlated with diurnal and nocturnal sap flux density during low VPD conditions in winter and wind run was correlated with leaf temperature. The study was conducted on *L. conocarpodendron* plants on the Cape Peninsula over a given time period.

An increase in transpiration corresponded with an increase in VPD when all other environmental variables were kept constant (Fig. 2). The air surrounding the leaves did not contain much vapour at high levels of VPD, creating a higher evapotranspirational gradient between the leaves and the surrounding air (Salisbury and Ross 1992). An increase in transpiration also corresponded with an increase in wind run when all other environmental variables were kept constant (Fig. 3). Here the boundary layer thickness was reduced which increased the conductance of the leaf surface (Grace 1977; Hoffman et al. 2011; Salisbury and Ross 1992). It can, therefore, be inferred that low wind run conditions may reduce transpiration in winter.

These findings suggest that both VPD and wind run influenced the rate of transpiration. However, wind run and VPD could be partially separated when considering their influence on the rate of transpiration, in that, high levels of VPD (>1.5 kPa.24hr^{-1}) did not occur simultaneously with high levels of wind run (>250 m.24hr^{-1}) (Fig. 4). The present study indicated that the dominant driver of transpiration was VPD during low wind run conditions (Fig. 5a) and the dominant driver of transpiration was wind run during low VPD conditions (Fig. 5b). This suggests that decreased wind run may have the potential to reduced transpiration in winter when VPD is low. However, variable rates of transpiration corresponded with reduced wind run under low VPD conditions (Fig. 5b) and therefore transpiration is highly sensitive to minor fluctuations in VPD during low wind run conditions. Winter also includes short periods of increased PAR which may have increased transpiration resulting in some of the variability during low levels of wind run and VPD. Decreased wind run currently predicted for the future will therefore not have an effect on mass-flow mediated movement of nutrients in winter when water is available because VPD is the dominant driver of transpiration during low wind run conditions. However, the importance of evaluating the effect of both high VPD and wind run on transpiration should be investigated in the context of climate change because these conditions may occur in the summer drought when heat stress of the plant is at its threshold.

The present study indicated that VPD was the dominant driver of transpiration during the day and wind speed was the dominant driver of transpiration at night (Fig. 2, 3, 6 and Appendix 2). This was because air temperature increased during the day which had the potential to increase VPD. The relative importance of VPD decreased at night which increased the relative importance of wind speed at night. This suggests that reduced wind run under low VPD conditions at night has an effect on nocturnal transpiration (Fig 6d). A reduction in nocturnal transpiration may decrease mass-flow mediated movement of nutrients and allocate more moisture for plant growth, infiltration and runoff despite the widespread increase in temperature and reduction in rainfall (Hoffman et al. 2011; Yates et al. 2010), however the relative impact of nocturnal transpiration will be low. These results did not agree with the results of Zeppel et al. (2010) who suggested that VPD and not wind run was the dominant driver of nocturnal transpiration. Nevertheless, the results obtained by the present study highlight the importance of wind run in the CFR as a driver of nocturnal transpiration because the region is subject to exceptionally high levels of wind run.

Low levels of wind speed and VPD produced a highly variable range of leaf temperatures which did not reach lethal levels, at least during the course of the study (Fig. 7). Decreased wind run may have the potential to increase leaf temperatures, however leaf temperature is highly sensitive to both low wind run and low VPD conditions. Species with deep tap roots, such as *L. conocarpodendron*, have access to water all year round (Hoffman et al. 2011). This reduces the need for evaporative cooling through transpiration and therefore reduced wind run may not increase leaf temperatures (Hoffman et al. 2011). Large leaved species, such as *L. conocarpodendron*, will not become vulnerable in response to reduced wind run. These results did not agree with Salisbury and Ross (1992) who suggested that the leaf temperature of a plant should decline under low VPD and wind run conditions. However, decreased wind run together with increased air temperature and a reduction in rainfall could potentially exacerbate heat stress of plants during the summer drought (November – February), a time frame which was not captured by the present study (Hoffman et al. 2011).

In conclusion, the effect of low wind run conditions currently predicted for the future (Hoffman et al. 2011) does not pose a threat to the physiology (transpiration, nutrient acquisition, leaf temperature or photosynthesis), growth or survival of *L. conocarpodendron* plants on the Cape Peninsula. Even though low wind run inhibited nocturnal transpiration, the rate of transpiration is relatively low at night and therefore a reduction in wind run does not pose a threat to transpiration in plants. The present study identifies the drivers of transpiration during current wind run and VPD conditions, however their interaction is constantly changing and therefore it is important to anticipate the effects of both high wind run and high VPD conditions on transpiration.

Acknowledgements

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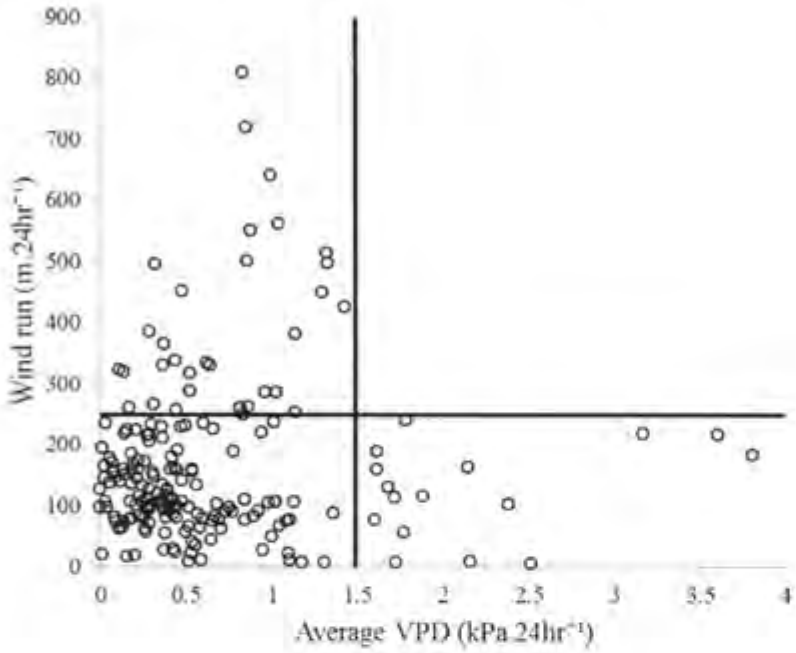
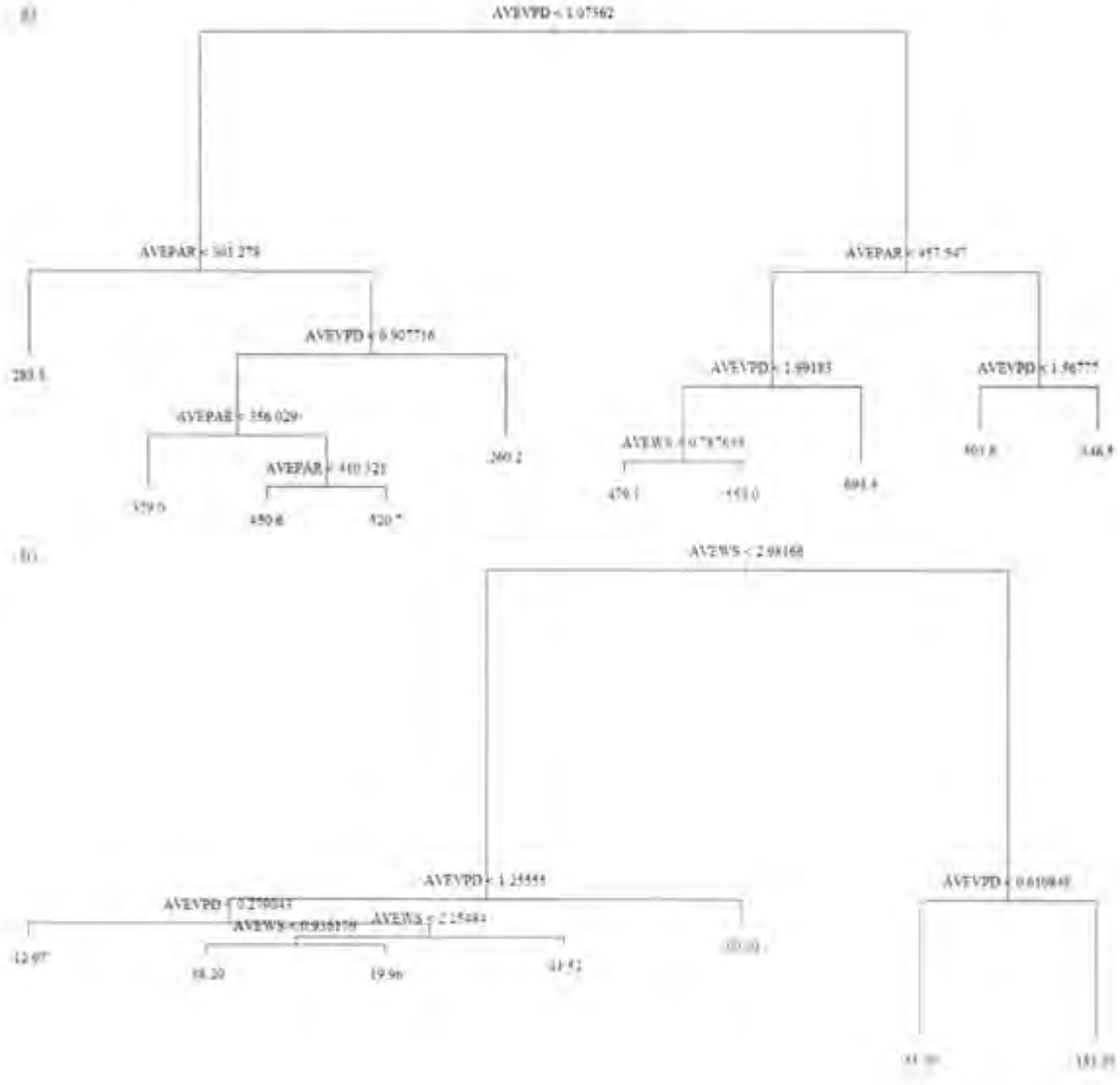
Appendix 1

The relationship between vapour pressure deficit (VPD) and wind run. The solid black lines indicate thresholds of high and low VPD and wind run located at 1.5 kPa.24hr^{-1} and 250 m.24hr^{-1}, respectively.



Appendix 2

Recursive portioning of sum sap flux density (SF; $g.m^{-2}.12hr^{-1}$) into subsets based on the relationship between sap flux density and average wind speed (AVEWS; $m.12hr^{-1}$), average VPD ($kPa.12hr^{-1}$) and average PAR ($W.12hr^{-1}$) diurnally (a) and nocturnally (b). N.B. the values and branch lengths in figures (a) and (b) are not comparable because sap flux density is less variable at night than during the day.



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