

Manuscript Number: JAE14-103R3

Title: Seasonal variations in tree water use and physiology correlate with soil salinity and soil water content in remnant woodlands on saline soils

Article Type: Research paper

Keywords: salinity, drought , tree water use, photosynthesis, sap flow, Eucalyptus macrorhyncha

Corresponding Author: Dr. Cate Macinnis-Ng, PhD

Corresponding Author's Institution: University of Auckland

First Author: Cate Macinnis-Ng

Order of Authors: Cate Macinnis-Ng; Melanie Zeppel; Anthony Palmer; Derek Eamus

Abstract: Ecophysiological studies of remnant woodlands in saline environments are scarce. We investigated seasonal fluctuations in soil water and salinity together with leaf and branch traits (area-based maximum assimilation (A_{max}), foliar nitrogen, specific leaf area (SLA) and Huber value (H_v)) and sap velocities of *Eucalyptus macrorhyncha* at four semi-arid sites in south-eastern Australia. Summer and winter soil salinities (10 cm depth) were 15-35 dS m⁻¹ and 8-10 dS m⁻¹ respectively. Gravimetric soil water content in the upper 20 cm was 2-5% in summer and 7-23% in winter, resulting in a significant inverse correlation between soil water and soil salinity. We found significant correlations between soil conditions and plant traits and function across seasons. Soil water content was significantly correlated with foliar N, SLA, H_v and maximum sap velocity while soil salinity was significantly correlated with A_{max} , H_v and maximum sap velocity. Correlations indicate co-variation of soil conditions and plant physiology in response to environmental conditions such as solar radiation and vapour pressure deficit (D). *E. macrorhyncha* tolerates the dual stresses of high salinity and low soil water during summer. While the plants appeared unhealthy, our data show that remnant vegetation can remain functional even in close proximity to saline scalds.

If you have simultaneous readings of RH and temperature, that is enough to calculate VPD-and could modify Fig.1 and text accordingly.
(If they are averages, should not calculate them, because it is a non-linear relationship)

The values of temperature and RH used to plot Fig. 1 were daily averages and these were then averaged to obtain monthly averages. As noted, using average values to calculate VPD will not provide accurate estimates of VPD so we have left Fig. 1 unchanged.

1 Seasonal variations in tree water use and physiology correlate with soil salinity and soil water
2 content in remnant woodlands on saline soils
3
4
5
6

7 Catriona M.O. Macinnis-Ng¹, Melanie J.B. Zeppel², Anthony R. Palmer^{3,4} and Derek Eamus⁵
8
9

10
11 ¹School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142,
12 New Zealand
13

14 ²Department of Biological Sciences, Macquarie University, Sydney NSW 2109, Australia
15

16 ³Centre for African Conservation Ecology, Nelson Mandela Metropolitan University, PO Box
17 7700, Port Elizabeth 6000, South Africa.
18

19 ⁴Agricultural Research Council – Animal Production Institute, PO Box 101, Grahamstown,
20 South Africa
21

22 ⁵School of Life Sciences, University of Technology Sydney, PO Box 123, Broadway 2007,
23 NSW, Australia and the National Centre for Groundwater Research and Training, UTS.
24
25
26
27
28
29
30

31 Corresponding author: C. Macinnis-Ng

32 e-mail: c.macinnis-ng@auckland.ac.nz,

33 Phone number +64 9 373 7599 ext 82343
34
35
36
37

38 Author contributions: CM and MZ conducted the fieldwork, analysed the data and prepared
39 the manuscript, AP contributed to data analysis and manuscript preparation, DE contributed to
40 experimental design, analysis and manuscript preparation.
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62

Highlights

- Dryland salinity is a significant problem in many semi-arid regions of the world.
- Woodlands combat salinity by lowering groundwater, reducing surface salt.
- We measured seasonal carbon assimilation, water use, soil salinity and water content.
- Some plant functional measurements were correlated with some soil measurements.
- Seasonal changes in meteorology drove unexpected plant-soil relationships.

Abstract

Ecophysiological studies of remnant woodlands in saline environments are scarce. We investigated seasonal fluctuations in soil water and salinity together with leaf and branch traits (area-based maximum assimilation (A_{\max}), foliar nitrogen, specific leaf area (SLA) and Huber value (H_v)) and sap velocities of *Eucalyptus macrorhyncha* at four semi-arid sites in south-eastern Australia. Summer and winter soil salinities (10 cm depth) were 15-35 dS m⁻¹ and 8-10 dS m⁻¹ respectively. Gravimetric soil water content in the upper 20 cm was 2-5% in summer and 7-23% in winter, resulting in a significant inverse correlation between soil water and soil salinity. We found significant correlations between soil conditions and plant traits and function across seasons. Soil water content was significantly correlated with foliar N, SLA, H_v and maximum sap velocity while soil salinity was significantly correlated with A_{\max} , H_v and maximum sap velocity. Correlations indicate co-variation of soil conditions and plant physiology in response to environmental conditions such as solar radiation and vapour pressure deficit (D). *E. macrorhyncha* tolerates the dual stresses of high salinity and low soil water during summer. While the plants appeared unhealthy, our data show that remnant vegetation can remain functional even in close proximity to saline scalds.

Keywords: salinity, drought, tree water use, photosynthesis, sap flow, *Eucalyptus macrorhyncha*

1. Introduction

Dryland salinity is widespread across Australia and other semi-arid regions of the globe (Lambers, 2003). Rising water tables bring salts to the surface of the soil (Eberbach, 2003) after clearing of deep-rooted perennial native vegetation has resulted in increased groundwater recharge (Lambers, 2003; Rengasmy, 2010). This serious land-degradation restricts agricultural productivity as increased salt concentrations and waterlogging of soils associated with dryland salinity can reduce plant growth and threaten plant survival (Sun and Dickinson, 1995). Studies testing methods for rehabilitation of saline soils have identified native salt-tolerant species which can be planted on salt-damaged soils and potentially improve soil quality (Bell, 1999). However, little is known about the ecophysiology of remnant vegetation remaining on saline soil (Pannell and Ewing, 2006). Consequently, the extent to which different native species respond to soil salinity *in situ* is not clear (Cramer and Hobbs, 2002).

Soil salinity affects plant function in a number of ways, for example, increased salinity reduces growth of stems, leaves and roots (Kayama et al., 2003; Myers et al., 1996; Rubinigg et al., 2004) in forest and greenhouse studies. The accumulation of salts in or below the root zone generally results in reduced tree growth and water use, and sometimes tree death (Macar et al., 1995; Sun and Dickinson, 1995; Feikema and Baker, 2011). High soil salinity can lead to changes in the soil-plant hydraulic conductance (Kayama et al., 2003; Rengasamy, 2006), leading to decreased tree water-use (Doody et al., 2009) which can end with death of non-halophytes (Akeroyd et al., 1998; Boland et al., 1996; Macar et al., 1995; Teobaldelli et al., 2004). This decreasing water-use may be a result of reductions in leaf area (Hatton et al., 1995; Hatton et al., 1998; Myers et al., 1998) or increased soil-to-leaf hydraulic resistance (Teobaldelli et al., 2004).

While the effects of high salinity on tree growth and tree water-use have been studied within many plantations (Benyon et al., 2001; Morris and Collopy, 1999; Hatton et al., 1998), few reports examine photosynthesis, growth and water-use of remnant vegetation on saline sites (Akeroyd et al., 1998; Barrett et al., 2005; Pannell and Ewing, 2006; Bann and Field, 2010; Bui, 2013). In one of the few studies of effects of salinity and waterlogging on native species *in situ*, Barrett et al. (2005) found very little measurable effect on pre-dawn leaf water potential, stomatal conductance and foliar ion concentrations, even when tree health was

1 visibly compromised. These results highlight the need to examine the ecophysiological
2 response of native trees *in situ* because visible symptoms and impaired ecophysiological
3 function may not always be correlated. Similarly, Marchesini et al. (2013) found predawn leaf
4 water potentials at disturbed and undisturbed sites were unchanged despite lower gravimetric
5 water content and lower electrical conductivity at disturbed semi-arid woodland sites.
6
7 However, Bui (2013) identifies salt as a major ecological driver over geological and more
8 recent time-scales in semi-arid areas. He suggests that salt has been largely ignored as an
9 ecological driver and soil salinity should be considered together with other factors such as soil
10 water and fire when exploring vegetation community composition (Bui, 2013). Pannell and
11 Ewing (2006) advocate for cost effective management options to prevent expansion of
12 salinised areas. Without adequate data on remnant vegetation, their value in the fight against
13 salinity is not clear.
14
15
16
17
18
19
20
21
22

23 Seasonal variations in soil salinity are associated with seasonal rainfall (Tomar and Gupta,
24 1985; Srivastava and Jefferies, 1995; Rengasamy, 2010) and changes in watertable depth
25 (Jackson et al., 1956; Peck, 1978). Heavy rains and rising watertables dilute salt in the soil
26 while drier periods are associated with higher salinities due to evaporation and transpiration of
27 soil water. Seasonal measurements are therefore required to capture the full range of
28 combinations of environmental conditions which occur naturally. Trees in semi-arid regions
29 affected by dryland salinity also have to tolerate winter frosts and high evaporative demands
30 in summer. Seasonal patterns in function often reflect changing environmental conditions. For
31 instance, the strong relationship between tree water-use and solar radiation (R_n), vapour
32 pressure deficit (D) and soil water content (θ) is often exploited in simple empirical models of
33 stand transpiration for well-coupled forest canopies (e.g. Whitley et al., 2008). In this study,
34 we explored the patterns of θ and soil salinity associated with coarse seasonal patterns of
35 water relations and productivity of remnant eucalyptus species in a region affected by dryland
36 salinity. Specifically, we measured transpiration rates, hydraulic architecture, photosynthesis
37 and leaf traits as well as θ and soil salinity across four sites in summer and winter and used
38 correlation analysis to explore co-variation of plant function and soil conditions.
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53

54 **2. Materials and methods**

55 *2.1. Study site and species*

56 The study sites were located near Crookwell, an agricultural and pastoral district in the
57 southern Tablelands of New South Wales (34.4572 S, 149.4690 E, elevation 887 m). All sites
58
59
60
61
62

1 had open forest with a grass understorey and very few shrubs and were within 3 km of each
2 other. Site 1 at Laggan Corner was dominated by *Eucalyptus dives* Schauer (peppermint)
3 directly adjacent to a saline scald, where salt crystals were forming on the soil surface and
4 vegetation was absent due to the high concentrations of salt. Site 2 (also at Laggan Corner)
5 was dominated by *Eucalyptus rossii* R. Baker & HG Smith (scribbly gum) and was 300 m
6 from the nearest visible saline scald. *Eucalyptus macrorhyncha* F. Muell. ex Benth (red
7 stringybark) occurred at both sites 1 and 2 as did *E. rossii*. Sites 3 and 4 at Laggan Dam were
8 equally dominated by *Eucalyptus goniacalyx* F. Muell. ex Miq. (box), *E. macrorhyncha* and
9 *E. dives*. Site 3 was directly adjacent to a saline scald while site 4 was over 200 m from the
10 saline scald. Trees closest to the saline scald appeared unhealthy with discoloured leaves.
11
12
13
14
15
16
17
18
19

20 Winter sampling took place in July 2003 and summer sampling occurred in January 2004. *E.*
21 *macrorhyncha* was studied at all four sites. *E. rossii* and *E. goniacalyx* were also studied at
22 Laggan corner and Laggan dam respectively but data are not shown because these data were
23 very similar to those for *E. macrorhyncha*. Red stringybark is wide-spread in south-eastern
24 NSW and locally dominant in dry sclerophyll forests and woodlands. It is hardy, tolerating
25 frosts and occasional snow (Boland et al., 2006). Six sample trees were identified within two
26 plots at each site (three trees per plot). All plant measurements were conducted on these trees.
27 Leaf and branch samples were selected haphazardly from within 5 m of the ground.
28
29
30
31
32
33
34
35

36 This research was conducted during a prolonged and extreme drought lasting three years, with
37 severe water deficiencies with rainfalls in the lowest 5% of historical totals (Bureau of
38 Meteorology 2003). The region is characterised by a long-term mean annual rainfall of 861
39 mm but is located in a rain shadow so the sites commonly experience drought conditions with
40 extended periods (months to years) with little rainfall. There is slightly more rain in winter
41 than summer and average temperatures are 10 – 27 °C in summer and 0 – 10 °C in winter (Fig.
42 1). Climate data were obtained from the nearest Bureau of Meteorology station at Crookwell
43 Post Office (approximately 8 km to the south of the experimental sites).
44
45
46
47
48
49
50
51
52
53

54 2.2. Soil salinity and water content

55 The soil is defined as coarsely cracking grey and brown clays (NSW Natural Resource Atlas,
56 <http://nratlas.nsw.gov.au>, accessed on 22nd July 2013). The soil type is a sodosol (Isbell,
57 2002) and is classed as sodic saline soil according to Rengasamy's (2010) categories. Particle
58 size analysis indicated the clay content was approximately 30%. Five soil samples were
59
60
61
62
63
64
65

1 collected from the base of each of the six sap flow sample trees to assess salt content of the
2 soil at each of the four sites. Approximately 1000 cm³ were excavated at a depth of 10 cm and
3 transported in a zip-lock bag to the laboratory. An aqueous saturated paste extract (of 50 mL
4 water to 10 g air-dried soil) was produced by shaking the sample for 5 min then allowing to
5 settle for an hour, following the methods of Rhoades (1982). The electrical conductivity (dS
6 cm⁻¹) of this solution was measured with a conductivity meter (YSI Incorporated, Ohio) and
7 divided by 100 to produce values of dS m⁻¹. The salinity of the saturated paste extract was
8 multiplied by 8.6 (for a sandy clay loam) to determine the salinity experienced by roots
9 (Taws, 2003). The remaining soil was dried to constant weight (110 °C) and weighed to
10 determine soil water content. As our sites were privately owned, we did not have permission
11 to dig deep holes so we were limited to non-invasive soil measurements in this project.
12
13
14
15
16
17
18
19
20
21

22 *2.3. Photosynthesis*

23 Photosynthesis was measured as maximum (light saturated) assimilation (A_{\max}) with a HCM-
24 1000 Portable Photosynthesis System (PPS) (Walz, Germany). Measurements were taken in
25 the morning (between 0930 and 1130) and in the afternoon (between 1400 and 1600), to avoid
26 any effects of midday down-regulation. The PPS is often used in the field to measure leaves
27 still attached to plants (McPherson et al., 2004) but due to the height of leaves on the
28 eucalypts in this study, small branches were cut off the trees with a long-armed pruner and
29 placed in water. These branches were re-cut underwater and placed under three 50 watt
30 halogen lamps delivering approximately 600 $\mu\text{mol photons m}^{-2} \text{sec}^{-1}$ at leaf height,
31 standardising light conditions. Preliminary investigations showed that removal of branches
32 from the tree did not cause a significant change in the rate of photosynthesis over a 45 min
33 period (data not shown).
34
35
36
37
38
39
40
41
42
43
44

45 Measurements were taken at ambient temperature, humidity and atmospheric CO₂
46 concentrations. The PPS was operated in differential mode with a 5 cm² closed cuvette, with a
47 2 mm fibre optic cable inserted through the cuvette lid for fluorescence measurements. Once
48 the CO₂ differential had stabilised, A_{\max} (defined as the rate of carbon fixation per unit of leaf
49 under saturating light conditions) was measured. Assimilation rate was measured on three
50 leaves on three plants in each plot, with two plots at each site (a total of 18 samples per site).
51
52
53
54
55
56
57
58
59
60
61
62

1
2 2.4. *Foliar nitrogen content and specific leaf area*
3

4 Leaves used in photosynthetic determination were collected for nitrogen analysis. Samples
5 were placed in moistened snap-lock bags and placed on ice for transportation to the
6 laboratory. Until analysis, samples were stored at -80°C. Leaf samples were prepared by
7 maceration in a ball grinder and nitrogen content was measured with a carbon and nitrogen
8 analyser (TruSpec CN 2000, Leco Corporation, Michigan).
9
10
11
12
13

14 Specific leaf area was calculated for three leaves from each sample tree (18 leaves at each
15 site). Samples were transported on ice in a cool box to the laboratory. Five 1 cm² leaf discs
16 were cut with a cork borer and dried at 70°C until constant weight (usually 5 days). Each disc
17 was weighed to four decimal places and the specific leaf area (SLA) was calculated as the
18 ratio of area to dry mass of the disc.
19
20
21
22
23
24

25
26 2.5. *Huber value*
27

28 Huber values (H_v) were calculated as the branch transverse area per leaf area distal to the cut
29 such that $H_v = SA/LA$ where SA is the cross-sectional area of the sapwood of the branch and
30 LA is the leaf area supported by that section of branch. The diameter of the basal end of each
31 branch was measured using a micrometer and the length of each branch was measured with a
32 ruler. Leaf area was determined using a WinDIAS (Type WDIGC-2 Delta-T Devices Ltd,
33 U.K) leaf area meter. Sapwood cross-sectional area was determined by soaking thin sections
34 of branch in 0.5% toluidine blue solution. The stained sapwood area was measured with a
35 calibrated eyepiece micrometer.
36
37
38
39
40
41
42
43

44 2.6. *Tree water-use*
45

46 Tree water-use was measured on *E. macrorhyncha* using sapflow sensors following Zeppel
47 et al. (2004). The sapwood depth of each tree was determined by inspecting samples collected
48 with an increment borer. There was a visible colour change between conducting and non-
49 conducting sapwood. The probe wound diameter was measured by taking wood samples back
50 to the laboratory and measured using a binocular microscope. Mean wound width was
51 estimated to be 2.67 mm. The radial profile of sap velocity through the sapwood depth was
52 measured by moving probes gradually further into the profile over a number of days to ensure
53 the probes were positioned in conducting sapwood. Heat-pulse method sapflow sensors
54 (Greenspan Technology Pty. Ltd., Warwick, Australia) were inserted into the sapwood of six
55
56
57
58
59
60
61
62

1 tree at varying depths (5-10 mm below the cambium) to obtain a range of sap velocities. Sap
2 velocities were recorded at hourly intervals and were used to estimate volumetric water use
3 (Q) following Edwards and Warrick (1984) but for clarity, we used peak flow rates (cm h^{-1}) in
4 our analysis. Peak (or maximum) flow was the highest flow rate measured across the day for
5 each tree. Sensors were positioned in sapwood according to Zeppel et al. (2004) so as to
6 capture the fastest sap flow rate.
7
8
9

10
11
12 At each site, tree water-use was measured for trees in two size classes, trees with a diameter at
13 breast height (DBH) < 20 cm (small) and trees with a DBH > 30 cm (large). Trees were
14 measured during a four week sampling period in July and August 2003, and in December to
15 January 2004. A roaming sampling strategy was used. During the first two weeks, three or
16 four trees were measured at each of the Laggan Dam sites, and one tree was measured at the
17 Laggan Corner sites. During the next two week period one tree was measured in both Laggan
18 Dam sites, while equipment was removed from the other two or three trees and set up in three
19 or four trees at Laggan Corner. By establishing the relationship between the fixed and
20 roaming sensors, sap flow rates could then be inferred for each tree for the whole period
21 (Zeppel et al., 2004).
22
23
24
25
26
27
28
29
30

31 32 33 *2.7. Statistical analysis*

34 We explored the seasonal relationship between soil water and soil salinity as well as the
35 correlation of these two factors with measured plant function and physiology. Correlation
36 analysis was conducted with Spearman-rank correlations (two-tailed) using SPSS v. 14.0,
37 2005.
38
39
40
41
42
43

44 45 **3. Results**

46 47 48 *3.1. Climate, soil salinity and water*

49 Sampling occurred after a prolonged drought (Bureau of Meteorology, 2003) of over three
50 years. Rainfall in the three months preceding and during the winter sampling period was
51 lower than average (Fig. 1). The three months between sampling periods had higher than
52 average rainfall, while the summer sampling period also had lower than average rainfall. The
53 mean maximum daily temperature was 27.5 ° C in summer and 11.3 ° C in winter (Fig. 1).
54 Minimum relative humidity was 57%, decreasing to 31% in summer, and there was a large
55 degree of variation in humidity between days, in summer, compared with winter (Fig. 1).
56
57
58
59
60
61
62

1
2 Soil salinity ranged from 6.9 dS m⁻¹ to 29.5 dS m⁻¹ while soil water content ranged from 3-
3 23% (Fig. 2). In both seasons, soil salinity and soil water contents (θ) were not significantly
4 different between sites directly adjacent to and 2-300 m away from the saline scalds
5 (statistical data not shown). These results indicated that elevated salinities within saline scalds
6 were localised to the scald and not detectable within the patches of woodland. However, there
7 was a significant negative correlation between soil water content (θ) and soil salinity across
8 sites and seasons (Fig. 2). Drier summer soils were associated with saltier conditions, while
9 wetter winter soils were less saline, consistent with more rainfall in winter (Fig. 1). On the
10 whole, seasonal differences in salinity were larger than differences between sites (Fig. 2).
11
12
13
14
15
16
17
18
19

20 *3.2. Soil properties and plant function*

21 Several measures of leaf gas exchange and leaf traits were significantly correlated with soil
22 salinity or water (Fig. 3). Leaf-area-based assimilation rate (A_{\max}) was negatively correlated
23 with soil salinity, and specific leaf area (SLA) was negatively correlated with soil water
24 content, while the concentration of foliar nitrogen was positively correlated with soil water
25 content (Fig. 3). Rates of assimilation ranged from 10-22 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3). A_{\max} was
26 higher in winter than summer. Specific leaf area ranged from 43-70 $\text{cm}^2 \text{g}^{-1}$ with higher values
27 in summer than in winter, while foliar N concentration ranged from 2-3 g m^{-2} with slightly
28 higher values in winter than in summer (Fig. 3).
29
30
31
32
33
34
35
36
37

38 Huber values ranged from 2 to 4 x 10⁴ across all sites, with larger values observed in winter
39 than in summer (Fig 4). Maximum daily sap velocities generally occurred close to midday
40 ranged between 8 and 37 cm h^{-1} across all sites and seasons (Fig. 4). Sap velocities were
41 higher in summer (18-37 cm h^{-1}) than winter (8-19 cm h^{-1}). Huber value and maximum sap
42 velocity were both significantly correlated with soil salinity and water (Fig. 4). Huber value
43 was negatively correlated with soil salinity and positively correlated soil water while
44 maximum sap velocity was positively correlated with soil salinity and negatively correlated
45 with soil water (Fig. 4).
46
47
48
49
50
51
52
53
54
55

56 **4. Discussion**

57 Our results indicate that at these semi-arid sites, plant function, soil salinity and soil moisture
58 (in the top 10 cm) are all seasonally variable. Assimilation rate (A_{\max}), SLA, sap velocity and
59 Huber value (H_v) were the most changeable between seasons, while foliar N was more stable
60
61
62
63
64
65

1 across the year but values recorded for all variables were indicative of healthy vegetation in
2 other parts of Australia. We present a valuable dataset describing the value of remnant trees in
3 an area suffering from dryland salinity. Despite the proximity of some of our sample trees to
4 severe saline scalds, the trees remain fully functional with strong rates of photosynthesis and
5 high sap flow rates. Visually assessing the health status of leaves (Seddon et al., 2007) may
6 not be the best way of defining the severity of saline impacts. While we have identified some
7 correlations between soil conditions and plant function across seasons, meteorological
8 conditions (especially evaporative demand) are the likely key drivers of these soil and plant
9 processes.
10

17 *4.1. Soil salinity*

19 Soil salinity concentrations are classified as ‘moderate’ for 2 to 6 dS m⁻¹, ‘high’ for 6 to 15 dS
20 m⁻¹ and over 15 dS m⁻¹ is ‘extreme’ (Richards, 1954; Taws, 2003). Winter soil salinity
21 concentrations were high at all sites at Crookwell, increasing to high and extreme levels in
22 summer. In both winter and summer, there was a large degree of variation in soil salinity
23 within sites due to variation in distance from the saline scald within each site (data not shown)
24 but high spatial variability of soil salinity is common (Feikema and Baker, 2011). The abrupt
25 change in soil salinities inside and outside of vegetated areas (data not shown) was also noted
26 by Taws (2003) and is consistent with the observations of Ban and Field (2010) that salinised
27 sites tend to be small and localised.
28
29
30
31
32
33
34
35
36

37
38 Soil salinity may be highly variable in space and time but salinity of saturated extracts of soils
39 at Crookwell (8-35 dS m⁻¹) were within the range of other saline sites in Australia (Thorburn
40 et al., 1993; Benyon et al., 1999; Morris and Collopy, 1999; Taws, 2003) so our results are
41 likely to be representative of other patches of remnant vegetation. Within each site, there was
42 some variation in soil salinity within a season as reported by Taws (2003). Similarly, an
43 increase in salinity from winter to summer has been reported in similar vegetation in NSW
44 (Benyon et al. 1999; Taws, 2003). Transient salinity is associated with patterns in rainfall,
45 surface evaporation, transpiration and leaching of the clay layer (Rengasamy, 2010). It is
46 common to find increased soil salinity during summer due to increased evapotranspiration
47 removing moisture from the soil and concentrating salts (Rengasamy, 2006). However, our
48 soil salinity method of drying samples before making the saturated soil extract reduced the
49 influence of seasonal variation in soil water content on salt concentrations. Therefore, the
50 significant inverse correlation in Fig. 2 does not merely show the effect of soil water content
51 changes on soil salinity, it indicates possible seasonal mobility of salts unrelated to soil water
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 content at the time of sampling. While most changes in salinity are likely to involve water as a
2 driver, it is difficult to tease apart the contributions of the different factors. We expect that soil
3 salinity would decline through the soil profile (Wong et al., 2009) so our values may
4 overestimate the salinity deeper roots are exposed to. What we can say for certain is that our
5 sample trees tolerated a large fluctuations of soil salinities within the moderate to extreme
6 ranges. These patches of vegetation are therefore very hardy and resistant to salt impacts.
7
8
9

10 11 12 4.2. Tree physiology

13 Rates of carbon assimilation, foliar N and SLA were similar to those of other Australian
14 native plants, including eucalypts (e.g. Eamus et al., 1999; Warren et al., 2000; Wright et al.,
15 2001; MacPherson et al., 2004; Lewis et al., 2011; Koerber et al., 2012) indicating that *E.*
16 *macrorhyncha* was healthy despite the recent prolonged drought and saline soils. In order to
17 understand the broader meaning of the correlations reported here, it is important to consider
18 the drivers of seasonal variation in soil salinity and water and plant traits and function.
19 Seasonal variation in assimilation rates is common across a variety of ecosystems. Changes in
20 temperature, solar radiation and water availability are common factors which influence
21 photosynthesis rates, often with higher rates in summer (King and Ball, 1998; MacPherson et
22 al., 2004). However, the A_{\max} measurements in this study were higher in winter than in
23 summer (Fig. 3). The inverse correlation between soil salinity and A_{\max} lead to higher
24 salinities being associated with lower A_{\max} values. While high salinity in the soil causes
25 impairment of the photosynthetic apparatus (Lawlor, 2002) or degradation of photosynthetic
26 pigments and the thylakoid membrane (Ashraf and Harris, 2013), it is more likely that the
27 reduction in A_{\max} during summer was caused by stomatal limitation rather than biochemical
28 limitation of photosynthesis because assimilation rates were within the range of healthy
29 eucalypts (Lewis et al., 2011) and Doody et al. (2009) found very little change in stress of
30 trees as watertables freshened and lowered. Higher concentrations of salt in the soil were
31 correlated with lower soil water content (Fig. 2) which would cause decreasing leaf water
32 potentials during summer. Dry conditions in air and soil result in declining stomatal
33 conductance which causes a decline in assimilation rate (Lawlor, 2002). We attribute the
34 inverse correlation between soil salinity and A_{\max} to reduction in stomatal conductance during
35 summer, when soil water content was reduced and soil salinity increased. The lack of a
36 significant correlation between soil water and A_{\max} is likely due to other complicating factors
37 such as the patchiness of soil water and water uptake from deeper soil. Unfortunately, we do
38 not have stomatal conductance measurements to confirm this but the mechanistic framework
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62

1 we describe is supported results from other systems (Lawlor, 2002; Flexas et al., 2004;
2 Koerber et al., 2012). Further data on depth of soil water uptake is also required to better
3 understand the salinity and importance of deep soil moisture.
4
5
6

7 Changes in foliar N and specific leaf area (SLA) may have also contributed to seasonal
8 variation in A_{\max} . There was a slight (but not significant) decline in foliar N during summer
9 which may have contributed to declining assimilation rates (Fig. 3; Reich et al., 1998),
10 seasonal patterns in SLA were associated with the onset of observed new leaf growth (leaf
11 flushing) in response to soil water. In the three months prior to summer sampling, rainfall was
12 above average (Fig. 1). This additional soil water prompted growth of new leaves, probably as
13 a response to rising water potentials of soil and consequently of leaves (Williams et al., 1997).
14 Our sample leaves were fully expanded but they were clearly younger than the leaves in
15 winter and this caused higher SLA values in summer (Fig. 4). Aging of eucalypt leaves is
16 associated with increased sclerophylly and therefore decreased SLA (Wright and Cannon,
17 2001). The SLA values measured at Crookwell were low on an international scale, across
18 multiple biomes (e.g. Reich et al., 1995) but consistent with other Australian studies (e.g.
19 Specht and Rundel, 1990; Eamus et al., 1999; Koerber et al., 2012). Foliar N concentrations
20 are also low but consistent with nutrient depleted soils of Australia (Specht and Rundel, 1990;
21 Warren et al., 2000).
22
23
24
25
26
27
28
29
30
31
32
33
34
35

36 Warmer and drier sites are associated with increased Huber values (Mencuccini, 2003) as the
37 water relations of these sites reduce photosynthetic revenue (Westoby et al., 2012). However,
38 seasonal variation in H_v at our saline sites showed declining H_v values as soil became drier
39 during summer because like SLA, H_v was also influenced by summer leaf flush (Fig. 4;
40 Macinnis-Ng et al., 2004). The significant correlations for H_v with salinity and soil water
41 content represent coordinated seasonal variation of these variables rather than a direct
42 response relationship. Coordination of H_v and tree water-use in response to changes in soil
43 water content and atmospheric aridity has been observed in eucalypts previously (Eamus et
44 al., 2001; Carter and White, 2009).
45
46
47
48
49
50
51
52
53

54 Maximum sap velocity was significantly correlated with both soil salinity and soil water
55 content (Fig. 4). Values were similar to those of Cook and O'Grady (2006) and the seasonal
56 pattern involved higher maximum flow rates in summer similar to that observed by Zeppel et
57 al. (2004). When the difference between soil salinity at different sites is large, other studies
58
59
60
61
62

1 report that increasing soil salinity decreases tree water-use (Akeroyd et al., 1998; Benyon et
2 al., 1999; Benyon et al., 2001; Boland et al., 1996; Kozlowski, 1997; Teobaldelli et al., 2004;
3 Doody et al., 2009). Reduction in sap velocity is attributed to increases in soil-to-leaf
4 hydraulic resistance (Teobaldelli et al., 2004) and the correlations reported here are likely to
5 have been driven by physiological responses to seasonal factors (described below) other than
6 soil conditions. Zeppel et al. (2004) identified three factors which led to increased sap flow
7 during summer: peak solar radiation, increased evaporative demand due to elevated air
8 temperatures and D and increased soil water. In the present study, the first two factors were
9 present but soil water content was lower in summer than winter. Therefore, we conclude that
10 solar radiation and evaporative demand were more important in controlling maximum rates of
11 sap flow than soil water content at our Crookwell sites. Despite indications that stomatal
12 conductance was limiting A_{\max} (discussed above), stomatal closure was insufficient to prevent
13 higher maximum sap flow in summer. Increased evaporative demand combined with leaf
14 flushing (which increased leaf area) were overriding any water-savings through stomatal
15 closure. The combined seasonal pattern of A_{\max} and maximum sap velocity implies water-use-
16 efficiency declined during summer, possibly due to new leaf growth. Seasonal variation in
17 tree water-use was a potential driver of decreasing soil water during summer (when tree
18 water-use was enhanced relative to the winter period), causing increased concentrations of salt
19 in the soil, particularly in the root zone (Feikema et al., 2010).

20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36 Overall, we found very little indication that physiology of *E. macrorhyncha* was
37 compromised by seasonal fluctuations of soil water and salinity because we did not find
38 significant differences between seasons for the measured variables (ANOVA data not shown).
39 A number of *Eucalyptus* species survive and even thrive in saline soils (Macar et al., 1995) so
40 it is not surprising that our study species remains productive and functioning at these sites. In
41 one of the few studies investigating physiological condition of native vegetation exposed the
42 saline groundwater, Barrett et al. (2005) found that predawn leaf water potential, stomatal
43 conductance and foliar salt concentrations were similar in trees exposed to varying depths and
44 salinities of ground water. Foliar concentrations of Na and K were high and varied seasonally
45 at all sites, independent of groundwater salinity and these authors suggested root hydraulic
46 redistribution of water between different soil layers may account for the lack of clear
47 physiological impacts of soil salinity. Similarly, lowering and freshening of watertables did
48 not have a detectable effect on tree stress (Doody et al., 2009). As woody thickening (the
49 increasing density of shrubs and trees) is enhanced by climate change in semi-arid regions due
50
51
52
53
54
55
56
57
58
59
60
61
62

1 to boosted water use efficiency of C3 plants (Macinnis-Ng et al., 2010), the water table will
2 lowered if sufficient vegetation establishes. Our results suggest *E. macrorhyncha* is a
3 promising candidate for phytoremediation under a changing climate (Jesus et al., 2015).
4
5
6

7 Further research is needed to disaggregate plant responses to seasonal fluctuations in soil
8 water and salinity and the role of the drought prior to our measurements. Identifying the depth
9 of soil water extraction by roots will improve our understanding of the impact of soil salinity
10 on tree physiology, particularly plant water use and the need for salinity adaptations. If the
11 trees are able to use deeper, cleaner water then surface fluctuations may not be an issue. Using
12 isotopic analysis and water balance calculations to identify sources of transpired water
13 (Feikema et al., 2010) along with more detailed physiological measurements will indicate
14 possible physiological adjustments these trees are using. *E. macrorhyncha* is commonly found
15 in saline and non-saline areas of NSW (Taws, 2003) but there is little information available on
16 the salinity tolerance of this species. Our data clearly indicate that *E. macrorhyncha* can be
17 resistant to high and extreme levels of soil salinity in the upper soil profile and is therefore an
18 excellent candidate for growth in saline areas. Furthermore, *E. macrorhyncha* is capable of
19 surviving fluctuations in soil salinity and water across seasons and is therefore suited to the
20 changing climate of south-eastern Australia.
21
22
23
24
25
26
27
28
29
30
31
32
33

34 *4.3. Conclusions*

35
36 On the whole, our sample species was very tolerant to field-based seasonal variations in
37 topsoil salinity. Remnant woodlands of *E. macrorhyncha* and associated species provide a
38 carbon store and pathway for transpiration. Such patches of native vegetation are also likely to
39 provide habitat and food for native fauna and are therefore a rich resource for conservation
40 and biodiversity. Visual inspection of our trees suggested those closest to saline scalds may be
41 physiologically compromised. However, our measurements showed no difference between
42 trees with or without leaf discolouration. We emphasise the importance of conserving existing
43 patches of remnant vegetation. Our data demonstrate the role of remnant woodlands in
44 ameliorating saline scalds as the trees adjacent to scalds were able to maintain performance
45 comparable to that of trees further from the scalds. Correlations between soil water content,
46 salinity and tree traits do not reflect causation but rather indicate that seasonal variation in
47 meteorological conditions is driving plant function, soil water and salinity in a coordinated
48 way. A complete suite of environmental variables (including meteorological conditions) must
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2 be collected when measuring plant performance on saline soils to properly understand drivers
3 of plant productivity and water use and seasonal variation in these values must be considered.
4

5 *Acknowledgements*

6
7 We thank the land owners for allowing access to their properties. CM, MZ and AP were
8 employed by the University of Technology Sydney while conducting this research.
9

10 11 12 *References*

13
14
15
16 Akeroyd MD, Tyerman SD, Walker GR, Jolly ID. 1998. Impact of flooding on the water use
17 of semi-arid riparian eucalypts. *Journal of Hydrology* **206**: 104-117. DOI: 10.1016/S0022-
18 1694(98)00092-4
19
20

21
22
23 Ashraf M, Harris PJC. 2013. Photosynthesis under stressful environments: an overview.
24 *Photosynthetica* **51**: 163-190. DOI: 10.1007/s11099-013-0021-6
25
26

27
28
29 Bann GR, Field JB, 2010. Dryland salinity, soil degradation and terrestrial biota in south
30 eastern Australia: problems and fallacies. *19th World Congress of Soil Science, Soil Solutions*
31 *for a Changing World*, Brisbane, Australia.
32
33
34

35
36 Barrett MS, Priess KA, Sinclair R. 2005. Influence of newly imposed salinity and
37 waterlogging on *Eucalyptus gracilis* in South Australia. *Tree Physiology* **25**: 1339-1346.
38 DOI:10.1093/treephys/25.10.1339
39
40

41
42
43 Bell DT. 1999. Australian trees for the rehabilitation of waterlogged and salinity-damaged
44 landscapes. *Australian Journal of Botany* **47**: 697-716.
45
46

47
48
49 Benyon RG, Marcar NE, Crawford DF, Nicholson AT. 1999. Growth, water use of
50 *Eucalyptus camaldulensis*, *E. occidentalis* on a saline discharge site near Wellington, NSW,
51 Australia. *Agricultural Water Management* **39**: 229-244.
52
53

54
55
56 Benyon RG, Marcar NE, Theiveyanathan S, Tunngley WM, Nicholson AT. 2001. Species
57 differences in transpiration on a saline discharge site. *Agricultural Water Management* **50**: 65-
58 81. DOI: 10.1016/S0378-3774(00)00121-9
59
60

1 Boland AM, Jerie PH, Mitchell PD, Irvine JL, Nardella N. 1996. The effect of a saline and
2 non-saline water table on peach tree water use, growth, productivity and ion uptake.
3 *Australian Journal of Agricultural Research* **47**: A121-A139.
4

5
6 Boland DJ, Brooker MIH, Chippendale GM, Hall N, Hyland BPM, Johnson RD, Kleinig DA,
7 McDonald MW, Turner JD. 2006. *Forest Trees of Australia*. CSIRO Publishing:
8 Collingwood.
9

10
11
12 Bui EN. 2013. Soil salinity: a neglected factor in plant ecology and biogeography. *Journal of*
13 *Arid Environments* **92**: 14-25. DOI: 10.1016/j.jaridenv.2012.12.014
14
15

16
17 Bureau of Meteorology (BOM) 2003. Statement on Drought for the 4 and 15-month periods
18 ending 30th June 2003. Issued 3rd JULY 2003 Australian Government, Canberra.
19
20
21
22
23 http://www.bom.gov.au/announcements/media_releases/climate/drought/20030703.shtml
24

25
26
27 Carter JL, White DA. 2009. Plasticity in Huber value contributes to homeostasis in leaf water
28 relations of a mallee Eucalypt with variation to groundwater. *Tree Physiology* **29**: 1407-
29 1418. DOI: 10.1093/treephys/tpp076
30
31

32
33
34 Cook PG, O'Grady AP. 2006. Determining soil and ground water use of vegetation from heat
35 pulse, water potential and stable isotope data *Oecologia* **148**: 97-107. DOI: 10.1007/s00442-
36 005-0353-4
37
38
39

40
41 Cramer VA, Hobbs RJ. 2002. Ecological consequences of altered hydrological regimes in
42 fragmented ecosystems in southern Australia: Impacts and/ possible management responses.
43 *Austral Ecology* **27**: 546-564.
44
45
46

47
48 Doody T, Holland K, Benyon R, Jolly I. 2009. Effect of groundwater freshening on riparian
49 vegetation water balance. *Hydrological Processes* **23**: 3485-3499. doi: 10.1002/hyp.7460.
50
51
52

53
54 Eamus D, Myers B, Duff G, Williams D. 1999. Seasonal changes in photosynthesis of eight
55 savanna tree species. *Tree Physiology* **19**: 665-672.
56
57
58
59
60
61
62

1 Eamus D, Hutley LB, O'Grady AP. 2001. Daily and seasonal patterns of carbon and water
2 fluxes above a north Australian savanna. *Tree Physiology* 21: 977-988. DOI:
3 10.1093/treephys/21.12-13.977
4
5

6
7 Eberbach PL. 2003. The eco-hydrology of partly cleared, native ecosystems in southern
8 Australia: a review. *Plant and Soil* 257: 357-369. DOI: 10.1023/A:1027392703312
9

10
11
12 Edwards WRN, Warrick NWM. 1984. Transpiration from a kiwifruit vine as estimated by the
13 heat-pulse technique and the Penman-Monteith equation. *New Zealand Journal of*
14 *Agricultural Research* 27: 537-543
15
16

17
18
19 Feikema PM, Morris JD, Connell LD. 2010. The water balance and water sources of a
20 *Eucalyptus* plantation over shallow saline groundwater. *Plant and Soil* 332: 429-449.
21
22

23
24
25 Feikema PM, Baker TG. 2011. Effect of soil salinity on growth of irrigated plantation
26 *Eucalyptus* in south-eastern Australia. *Agricultural Water Management* 98: 1180-1188. DOI:
27 10.1016/j.agwat.2011.03.005
28
29

30
31
32 Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD. 2004. Diffusive and metabolic limitations
33 to photosynthesis under drought and salinity in C3 plants. *Plant Biology* 6: 269-279. DOI:
34 10.1055/s-2004-820867
35
36

37
38
39 Hatton TJ, Moore SJ, Reece PH. 1995. Estimating transpiration in a *Eucalyptus populnea*
40 woodland, with the heat pulse method: measurement errors and sampling strategies. *Tree*
41 *Physiology* 15: 219-227.
42
43

44
45
46 Hatton TJ, Reece PH, Taylor P, Mc Ewan K. 1998. Does leaf water efficiency vary among
47 eucalypts in water-limited environments? *Tree Physiology* 18: 529-536.
48
49

50
51
52 Jackson EA, Blackburn G, Clarke ARP. 1956. Seasonal changes in soil salinity at Tintinara,
53 South Australia. *Australian Journal of Agricultural Research* 7: 20-44.
54
55

56
57
58 Jesus JM, Danko AS, Fiúza A, Borges MT. 2015. Phytoremediation of salt-affected soils: a
59 review of processes, applicability, and the impact of climate change. *Environmental Science*
60 *and Pollution Research* 22: 6511-6525.
61
62

1
2 Isbell RF. 2002. The Australian soil classification. Commonwealth Scientific and Industrial
3 Research Organization (Australia). Collingwood, VIC.
4
5

6
7 Kayama M, Quoreshi AM, Kitaoka S, Kitahashi Y, Sakamoto Y, Maruyama Y, Kitao M ,
8
9 Koike T. 2003. Effects of dessicating salt on the vitality and health of two spruce species,
10
11 *Picea abies* Karst. and *Picea glehnii* Masters planted along roadsides in northern Japan.
12
13 *Environmental Pollution* **124**: 127-137.
14
15

16 King DA, Ball MC. 1998. A model of frost impacts on seasonal photosynthesis of *Eucalyptus*
17
18 *pauciflora*. *Australian Journal of Plant Physiology* **25**: 27-37.
19
20

21 Koerber GR, Seekamp JV, Anderson PA, Whalen M.A, Tyerman SD. 2012. A putative hybrid
22
23 of *Eucalyptus largiflorens* growing on salt- and drought-affected floodplains has reduced
24
25 specific leaf area and leaf nitrogen. *Australian Journal of Botany* **60**: 358-367. DOI:
26
27 10.1071/BT12012
28
29

30
31 Kozlowski TT. 1997. Responses of woody plants to flooding and salinity. *Tree Physiology*
32
33 *Tree Physiology monograph No. 1*.
34
35

36 Lambers H. 2003. Introduction, dryland salinity: a key environmental issue in southern
37
38 Australia. *Plant and Soil* **257**: v-vii.
39
40

41 Lawlor DW. 2002. Limitation to photosynthesis in water-stressed leaves: stomata versus
42
43 metabolism and the role of ATP. *Annals of Botany* **89**: 871-885. DOI: 10.1093/aob/mcf110
44
45

46
47 Lewis JD, Phillips NG, Logan BA, Hricko CR, Tissue DT. 2011. Leaf photosynthesis,
48
49 respiration and stomatal conductance in six *Eucalyptus* species native to mesic and xeric
50
51 environments growing in a common garden. *Tree Physiology* **31**: 997-1006. DOI:
52
53 10.1093/treephys/tpr087
54
55

56 Macar NCD, Leppert P, Jovanovic T, Floyd R, Farrow R. 1995. *Trees for salt: a guide to*
57
58 *selecting native species for Australia*. CSIRO Division of Forestry: Canberra
59
60
61

1
2 Macinnis-Ng C, McClenahan K, Eamus D. 2004. Convergence in hydraulic architecture,
3 water relations and primary productivity amongst habitats and across seasons in Sydney.
4 *Functional Plant Biology* **31**: 429-439.
5

6
7 Macinnis-Ng C, Zeppel M, Williams M, Eamus D. 2011. Applying a SPA model to examine
8 the impact of climate change on GPP of open woodlands and the potential for woody
9 thickening. *Ecohydrology* **4**: 379-393.
10

11
12
13
14 Marchesini VA, Fernández RJ, Jobbágy EG. 2013. Salt leaching leads to drier soils in
15 disturbed semiarid woodlands of central Argentina. *Oecologia* **171**: 1003-1012.
16

17
18
19
20 McPherson S, Eamus D, Murray BR. 2004. Seasonal impacts on leaf attributes of several tree
21 species growing in three diverse ecosystems of south-eastern Australia. *Australian Journal of*
22 *Botany* **52**: 293-301. DOI: 10.1071/BT03104
23
24

25
26
27 Mencuccini M. 2003. Water relations of the plant xylem. In: *Encyclopaedia of Applied Plant*
28 *Sciences*, (B. Thomas, D.J. Murphy, B.G. Murray, eds.), Elsevier Academic Press, Vol.1:
29 1440-1449, St. Louis (MO, USA) & Sidcup, Kent (UK).
30
31

32
33
34 Morris JD, Collopy JJ. 1999. Water use and salt accumulation by *Eucalyptus camaldulensis*
35 and *Casuarina cunninghamiana* on a site with shallow saline groundwater. *Agricultural*
36 *Water Management* **39**: 205-227.
37
38

39
40
41 Myers BJ, Theiveyanathan S, O'Brien ND, Bond WJ. 1996. Growth and water use of
42 *Eucalyptus grandis* and *Pinus radiata* plantations irrigated with effluent. *Tree Physiology* **16**:
43 211-219.
44
45

46
47
48 Myers BA, Benyon RG, Theiveyanathan S, Criddle RS, Smith CJ, Falkiner RA. 1998.
49 Response of effluent-irrigated *Eucalyptus grandis* and *Pinus radiata* to salinity and vapour
50 pressure deficits. *Tree Physiology* **18**: 565-573.
51
52

53
54
55
56 Pannell DJ, Ewing MA. 2006. Managing secondary dryland salinity: options and challenges.
57 *Agricultural Water Management* **80**: 41-56.
58
59

1 Peck AJ. 1978. Note on the role of a shallow aquifer in dryland salinity. *Australian Journal of*
2 *Soil Research* **16**: 237-240.

3
4
5 Reich PB, Ellsworth DS, Walters MB. 1998. Leaf structure (specific leaf area) modulates
6 photosynthesis-nitrogen relations: evidence from within and across species and functional
7 groups. *Functional Ecology* **12**: 948-958. DOI: 10.1046/J.1365-2435.1998.00274.X
8
9

10
11
12 Rengasamy P. 2006. World salinization with emphasis on Australia. *Journal of Experimental*
13 *Botany* **57**: 1017-1023.
14
15

16
17
18 Rengasamy P. 2010. Soil processes affecting crop production in salt-affected soils. *Functional*
19 *Plant Biology*. **37**: 613-620.
20
21

22
23 Richards L. (Ed.) 1954. Saline and alkali soils. United States Department of Agriculture.
24 Agriculture Handbook No. 60. 166 pp.
25
26

27
28
29 Rhoades JD. 1982. Soluble salts. In 'Methods of soil analysis: Part 2: Chemical ,
30 microbiological properties'. Monograph Number 9 (Second Edition) (Ed. Page AL) pp. 167-
31 179. American Society of Agronomy : Soil Science Society of America: Madison Wisconsin.
32
33

34
35
36 Rubinigg M, Wenisch J, Elzenga JT, Stulen I. 2004. NaCl salinity affects lateral root
37 development in *Plantago maritima*. *Functional Plant Biology* **31**: 775-780.
38
39

40
41
42 Seddon JA, Zerger A, Doyle SJ, Briggs SV. 2007. The extent of dryland salinity in remnant
43 woodland and forest within an agricultural landscape. *Australian Journal of Botany*, **55**: 533-
44 540.
45
46

47
48
49 Specht RL, Rundel PW. 1990. Sclerophylly and foliar nutrient status of Mediterranean-
50 climate plant communities in southern Australia. *Australian Journal of Botany*. **38**: 459-74.
51
52

53
54
55 Srivastava DS, Jefferies RL. 1995. Mosaics of vegetation and soil salinity: a consequence of
56 goose foraging in an arctic salt marsh. *Canadian Journal of Botany* **73**: 75-83.
57
58

1 Sun D, Dickinson GR. 1995. Salinity effects on tree growth, root distribution and
2 transpiration of *Casuarina cunninghamiana* , *Eucalyptus camaldulensis* planted on a saline
3 site in tropical north Australia. *Forest Ecology and Management* **77**: 127-138.
4

5
6
7 Taws N. 2003. *Woodland remnants and dryland salinity*. Final report for NSW National Parks
8 and Wildlife Service. Greening Australia ACT & SE NSW, Canberra
9

10
11
12 Teobaldelli M, Mencuccini M, Piussi P. 2004. Water table salinity, rainfall and water use by
13 umbrella pine trees (*Pinus pinea* L.). *Plant Ecology* **171**: 23-33.
14

15
16
17 Thorburn P, Hatton TJ, Walker GR. 1993. Combining measurements of transpiration and
18 stable isotopes of water to determine groundwater discharge from forests. *Journal of*
19 *Hydrology* **150**: 563-587.
20
21

22
23
24 Tomar OS, Gupta RK. 1985. Performance of some forest tree species in saline soils under
25 shallow and saline water-table conditions. *Plant and Soil* **87**: 329-335.
26
27

28
29
30 Wang J, Ives NE, Lechowicz MJ. 1992. The relation of foliar phenology to xylem embolism
31 in trees. *Functional Ecology* **6**: 469-475.
32
33

34
35
36 Warren CR, Adams MA, Hen Z. 2000. Is photosynthesis related to concentrations of nitrogen
37 and Rubisco in leaves of Australian native plants? *Australian Journal of Plant Physiology* **27**:
38 407-416. DOI: 10.1071/PP98162
39
40

41
42
43 Westoby M, Cornwell WK, Falster DS 2012. An evolutionary attractor model for sapwood
44 cross section in relation to leaf area. *Journal of Theoretical Biology* **303**: 98-109. DOI:
45 10.1016/j.jtbi.2012.03.008
46
47

48
49
50 Wong NL, Dalal RC, Greene RSB. 2009. Carbon dynamics of sodic and saline soils following
51 gypsum and organic material additions: A laboratory incubation. *Applied Soil Ecology* **41**: 29-
52 40.
53
54

55
56
57 Whitley RJ, Zeppel MJ, Armstrong N, Macinnis-Ng CM, Yunusa IA, Eamus D. 2008. A
58 modified Jarvis-Stewart model for predicting stand-scale transpiration of an Australian native
59 forest. *Plant and Soil* **305**: 35–47. DOI: 10.1007/s11104-007-9399-x
60
61

1 Williams JE, Davis SD, Portwood K. 1997 Xylem embolism in seedlings and resprouts of
2 *Adenostoma fasciculatum* after fire. *Australian Journal of Botany* **45**: 291-300.
3
4

5
6
7 Wright IJ, Cannon K. 2001. Relationships between leaf lifespan and structural defences in a
8 low-nutrient, sclerophyll flora, *Functional Ecology* **15**: 351-359. DOI: 10.1046/J.1365-
9 2435.2001.00522.X
10
11

12
13
14 Wright IJ, Reich PB, Westoby M. 2001. Strategy shifts in leaf physiology, structure and
15 nutrient content between species of high- and low- rainfall and high- and low- nutrient
16 habitats. *Functional Ecology* **15**: 423-434. DOI: 10.1046/J.0269-8463.2001.00542.X
17
18
19

20
21
22 Zeppel MJB, Murray BR, Barton C, Eamus D. 2004. Seasonal responses of xylem sap
23 velocity to VPD and solar radiation during drought in a stands of native trees in temperate
24 Australia. *Functional Plant Biology* **31**: 461-470. DOI: 10.1071/FP03220
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62

Figure captions

1
2
3
4 Fig. 1. Mean annual temperatures, rainfall and relative humidity (shown as 100 year mean)
5 and actual rainfall for April 2003- March 2004 for Crookwell meteorological station. (Data
6 source: Australian Bureau of Meteorology).
7
8
9

10
11 Fig. 2. Relationship between soil water content and soil salinity of the saturated paste extract
12 across seasons for the four sites. Each point represents the site mean \pm standard error of the
13 mean in either summer or winter. Points joined with a line are summer and winter values for
14 one site.
15
16
17
18
19

20 Fig. 3. Relationships between saturated soil salinity and soil water content and area-based
21 assimilation under saturating irradiance (top panels), foliar N (middle panels) and specific leaf
22 area (lower panels). Each point represents the mean \pm standard error of the mean (n = 6 trees)
23 for each of the four sites in summer or winter. Summer values fall to the right of salinity plots
24 and to the left of soil water content plots. Correlation values are Spearman-rank coefficients.
25
26
27
28
29
30

31 Fig. 4. Relationships between saturated soil salinity and soil water content and Huber value
32 (top panels) and maximum sap velocity (lower panels). Each point represents the mean \pm
33 standard error of the mean (n = 6 trees) for each of the four sites in summer or winter.
34 Summer values fall to the right of salinity plots and to the left of soil water content plots.
35 Correlation values are Spearman-rank coefficients.
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Highlights

- Dryland salinity is a significant problem in semi-arid regions of the world.
- Woodlands combat salinity by lowering groundwater, reducing surface salt.
- We measured seasonal carbon assimilation, water use, soil salinity and water content.
- Some plant functional measurements were correlated with some soil measurements.
- Seasonal changes in meteorology drove unexpected plant-soil relationships.

Figures and Tables

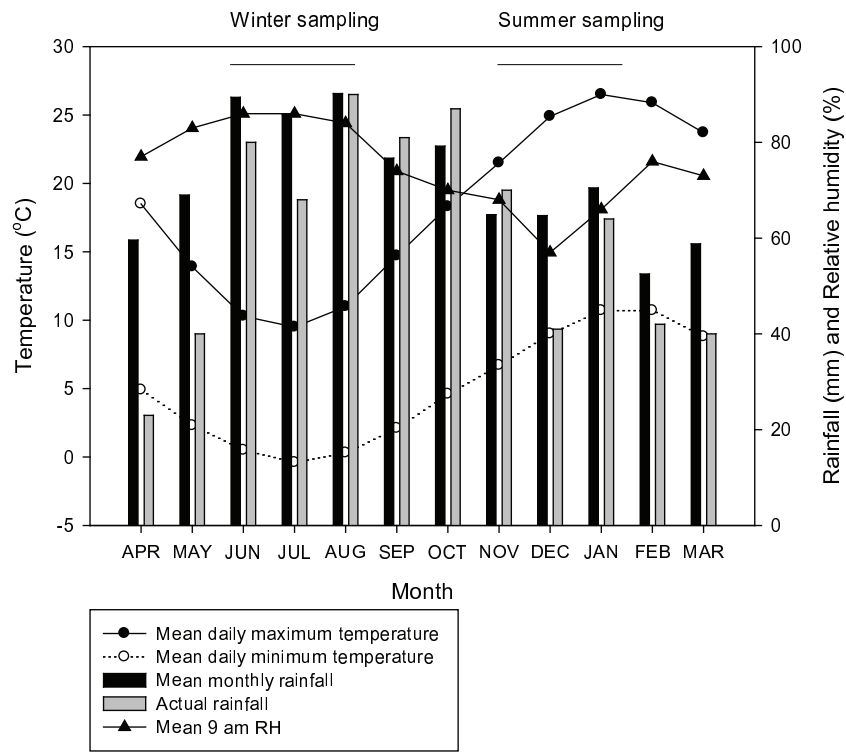


Fig. 1. Mean annual temperatures, rainfall and relative humidity for Crookwell meteorological station. Data represent the 100 year mean. In addition to actual rainfall for April 2003- March 2004. (data source: Australian Bureau of Meteorology).

Figure 2

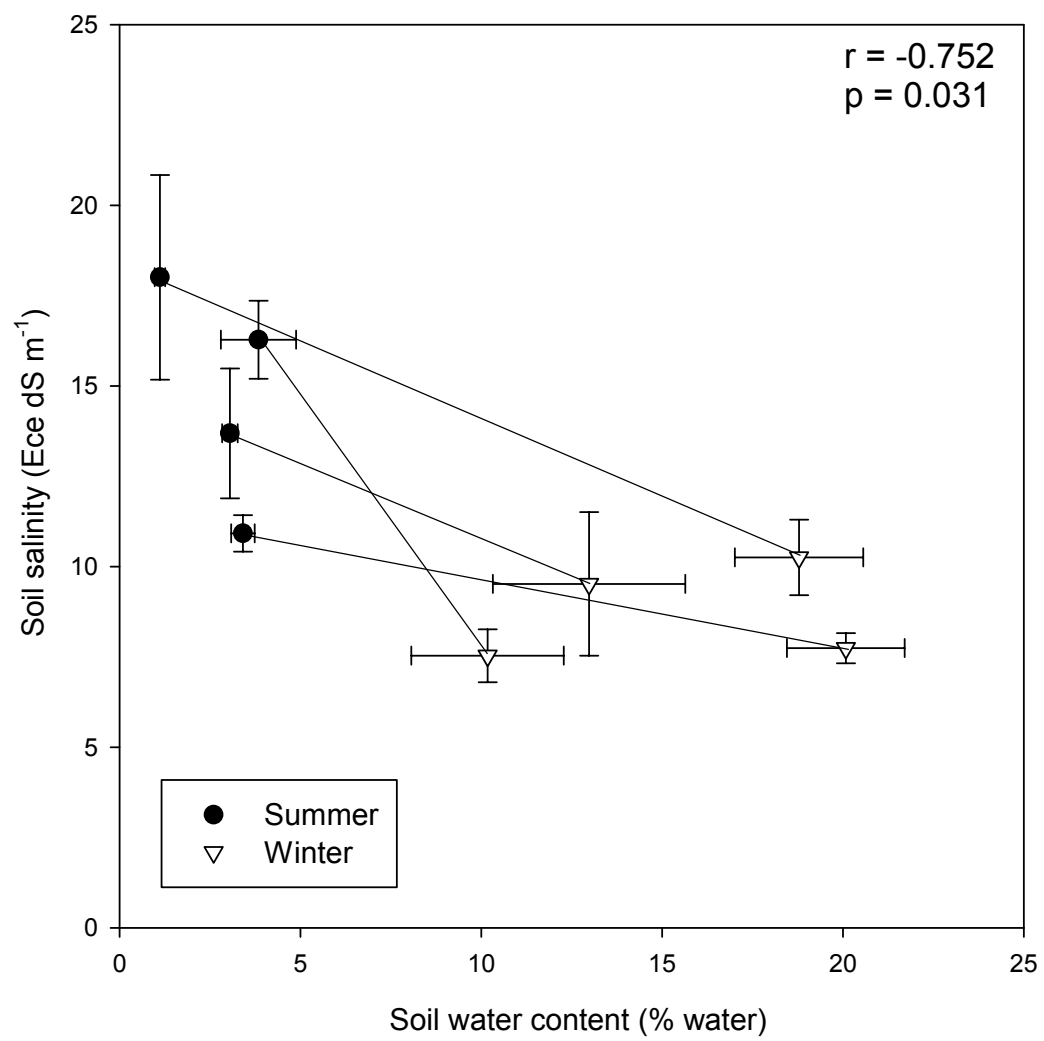


Figure 3

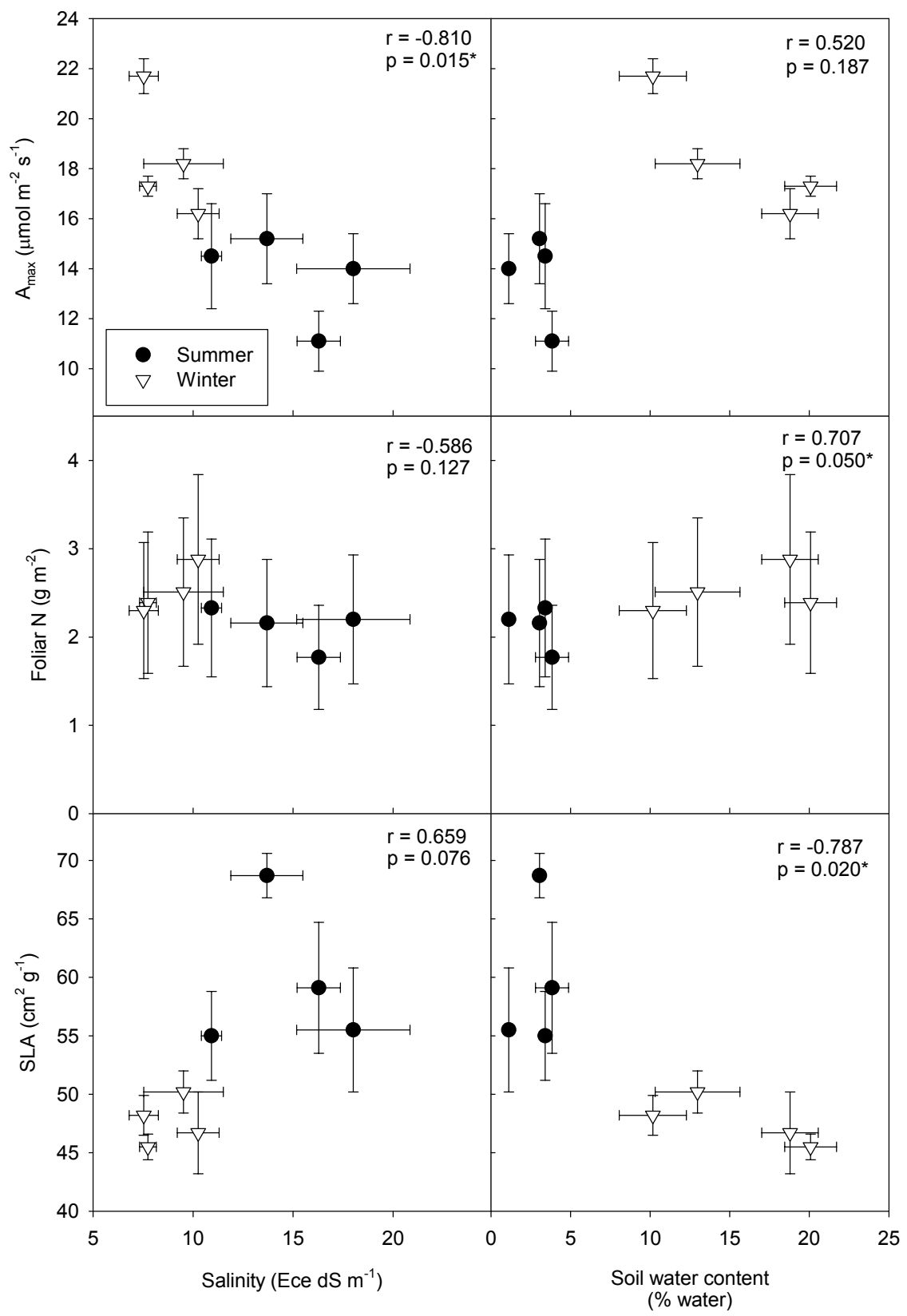


Figure 4

