

**SPATIOTEMPORAL DYNAMICS OF HIGH-TEMPERATURE
TOLERANCE IN AUSTRALIAN ARID-ZONE PLANTS**



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2017

BACHELOR OF SCIENCE IN ENVIRONMENTAL BIOLOGY (HONS)

A THESIS SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

DOCTOR OF PHILOSOPHY IN SCIENCE

CERTIFICATE OF ORIGINAL AUTHORSHIP

I certify that the work in this thesis has not previously been submitted for a degree, nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This research is supported by an Australian Government Research Training Program Scholarship.

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ACKNOWLEDGMENTS

This work would not have been possible if not for the kind support and interest of staff at the Port Augusta City Council (PACC) and Australian Arid Lands Botanic Gardens (AALBG), and members of the Friends of the AALBG. Special thanks must be extended to my amazing field volunteers: Ronda and Peter Hall of the Friends of the AALBG who, without hesitation, committed their support, and assisted me during every field campaign. Your company and support made all the difference! Also, many thanks to Alicia and Melinda Cook and Ben Ford who too volunteered their time and skills to assist me in the field; and to my fellow colleagues in the Leigh Research Lab: thank you for being outstanding people and sharing this experience with me.

During the formation of this thesis I have had the privilege of working with some wonderful people, whose roles were pivotal to the fruition of this thesis. In particular, I would like to extend special thanks to my supervisors. Firstly, my heartfelt thanks to the extraordinary Associate Professor Andy (Andrea) Leigh, who first introduced to me the wonderful world of arid plant ecology. Your positivity, passion and enthusiasm for teaching, research and life in general, are inspiring. Thank you for your kind, practical advice and guidance, for always challenging me, and for your never ending support. It has been an absolute pleasure to work with you these past years.

I would like also to extend my sincere thanks and gratitude to co-supervisors, Dr Brad Murray and Professor Charles Knight. Thank you both for your support and enthusiasm for my study, and for making time available when I was in need of your advice. I am further grateful to Charley for giving me the opportunity to visit with him in California to explore the amazing Death Valley; a truly wonderful experience. Brad and Charley, your efforts were always appreciated and never overlooked. Thank you.

Along the way, I have also had the pleasure of collaborating with numerous colleagues within the UTS School of Life Sciences including Dr James Cleverly, Dr John Gollan, Dr Ben Kefford, and Dr Katherina Petrou, who provided insightful discussions and showed interest in my study. I am grateful to have had the opportunity to consult with each of you on various aspects of my research; it allowed me to think outside the box and consider my data in new and interesting ways. I am further grateful to Dr Katherina Petrou and Professor Peter Ralph for their kind encouragement and gentle introduction to the intriguing world of chlorophyll *a* fluorescence.

Many thanks to Dr Norman Booth (ANSTO) and the UTS Workshop staff who assisted me during the early phase of my candidature, and to all Faculty of Science technical staff who have provided me with support throughout my time at UTS. I would like to thank especially Jane Easton, Rod Hungerford and Peter Jones who not only provided me with technical support the past years but in general have been encouraging and supportive. You are all magnificent individuals and have made my time at UTS all the more enjoyable. Thank you.

Special thanks to my husband, Wenfeng Ren, for his continued patience, encouragement and support; and to our son Max, whose budding curiosity inspires every day in me a new sense of wonder for the natural world. Thanks also to my parents and parents-in-law, Cheryl and Kevin and Li Li and Raymond, and my extended family and friends – you know who you are – that have encouraged and supported me in a myriad of ways in the years proceeding, and up to, now. My deepest thanks to Nana Joyce, who always asked me how I was progressing and each time listened with genuine interest as I explained my work; we miss you.

I am grateful to all organisations that have provided me with financial support during this study, including the University of Technology Sydney, Port Augusta City Council, the Friends of the Australian Arid Lands Botanic Garden and The Australian Wildlife Society. This study was further supported by an Australian Government Research Training Program Scholarship. Without these financial contributions, my research would not have been possible.

Lastly, I would like to thank the kind and insightful advice I received from two external examiners, whose comments contributed to improving the final version of my thesis.

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Figure 2.1 (For corresponding, published figure, see Fig. S2.1). **Step 1.** Leaves were sampled from branches collected from the north-facing outer canopy of a minimum of five plants per species. **Step 2.** For each species, six batches of ten leaves were randomly chosen from the sampling pool and treated to one of six temperature treatments. **Step 3.** Control measurements of maximum quantum yield of PSII (PS_{F_V/F_M})

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around species average T_{50} seasonally (winter, spring, summer), **c**). In this way, the interpretation of seasonal patterns of change in individual species' T_{50} could be kept consistent. In the example shown, the summer T_{50} (see **panel a**) for *Eucalyptus camaldulensis* ssp. *camaldulensis* was interpolated as $50.0\text{ }^{\circ}\text{C} \pm 0.83$, where 0.83 is the mean difference between T_{50} and temperatures corresponding to lower₅₀ ($49.3\text{ }^{\circ}\text{C}$) and upper₅₀ ($51.0\text{ }^{\circ}\text{C}$), respectively, equating to the CI around T_{50} for this species (see **panel b**). **Panel c** compares seasonal differences in T_{50} between paired species contrasted on typical water availability in their native microhabitats: *E. camaldulensis* (high-water) and *E. pimperiana* (low-water). In this panel, lines are for ease of reading patterns and do not represent continuous time. With estimated CI being applied, we can see that the error bars for T_{50} for each species do not overlap in spring, whereas clear separation of species T_{50} is not present in either winter or summer. Further, both species exhibit an Early Jump strategy (see Results and **Fig. 4.4**), defined for a given species as no overlap of their CI between winter and spring, but with overlap in spring and summer.

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species exhibiting minimal changes in their T_{50} between winter and spring but a substantial jump from spring to summer; **Steady Increase**, species exhibiting a steady increase in T_{50} values from winter to summer, with no marked step increase from winter to spring or spring to summer; **No Response**, species showing little change in T_{50} seasonally. Error bars are an estimation of within-species variation in T_{50} interpolated from 95% confidence intervals (see Methods and Results). For full species names see Methods and Table 4.1.

Figure 5.1 Seasonal projections of plant species grouped by preferred native microhabitat on the plane defined by principal component axes (PC) 1 and 2. Diamond symbol, W_{high} ; round symbols, W_{var} ; Square symbols, W_{low} (**a – c**). Solid lines indicate direction and weighing of vectors representing the seven traits considered: Leaf thickness, LT; leaf mass per area, LMA; near infrared reflectance, NIR; thermal damage threshold, T_{50} ; visible reflectance, VIS; effective leaf width, LW; water content, WC. Per cent variance explained by each axis indicated.

Figure 5.2 Mean seasonal (winter = 23 spp., spring = 22 spp., summer = 41 spp.) score distributions along the first (**a – c**) and second (**d – f**) principal components (PC1, PC2). Species grouped by preferred native microhabitat based on water availability W_{high} , W_{var} , W_{low} . Variables loading moderately to highly ($\geq \pm 0.4$) on each axis are presented to the left of each graph (see Table 5.1 for description of variables). Variables in bold consistently load across all seasons for a given PC axis. Variables in italics cross-load, having moderate loadings on both PC axes within a given season ($\geq \pm 0.4$). Data points with different letters above differed significantly at * $P < 0.05$. Component loadings between ± 0.4 and ± 0.6 are moderate in strength, with values above and below considered weak and strong, respectively (see Methods).

Figure 5.3 Mean seasonal score distributions along the first (**a – c**) and second (**d – f**) principal components (PC1, PC2) for phylogenetically independent species contrasts. Species contrasted on preferred native microhabitat based on water availability, being mesic-adapted or xeric-adapted species, respectively. Results of paired t -test provided inset ($\alpha = .05$). Refer to Fig. 5.1. for list of variables loading highly on each axis.

Figure 5.4 Thermal protection strategies among arid-zone plant species fell along two principal component (PC) axes. Microhabitat preference successfully predicted species'

placement along PC1. Xeric-adapted species had higher LMA and T_{50} and lower leaf water contents than their mesic counterparts. PC2 was consistently driven by variation in visible reflectance, and somewhat by leaf size (winter, spring) and T_{50} (spring, summer) but was independent of microhabitat. The strong association of LMA on PC1 suggests a strategy relating to protecting long lived leaves; whereas thermal protection described by PC2 is independent of LMA and the leaf economics spectrum. Solid black arrows indicate the direction and strength of leaf traits loading highly on each axis: 1) For a given principal component, variables with high positive loading indicate a strong correlation with the component and explain a large proportion of the variation among species for that axis. Traits with strong negative loadings also explain a large proportion of the variation among species for that axis, but in the opposite direction to positively loaded traits. 2) Greater arrow thickness indicates a comparatively higher loaded variable. 3) Variables depicted further away from the axis have loadings that become progressively weaker as indicated by the reduced arrow thickness. LMA, leaf mass per area; % WC, per cent water content; T_{50} , leaf thermal damage threshold; NIR, near infrared reflectance; VIS, visible reflectance; LW, effective leaf width. See Fig. 5.1 for seasonal results for these data.

Figure 6.1 Example of the placement of data loggers within the canopy of the study species, *Acacia papyrocarpa* Benth. Inset upper right: close-up of temperature/humidity data loggers and housing, shallow enough to allow adequate air flow around the sensor. Inset lower right: close-up of phyllodes.

Figure 6.2 Effect of within-canopy height and aspect on a range of microclimatic indicators and leaf physiological response in *Acacia papyrocarpa* plants ($n = 5$). PCA-determined climatic stress index (C_{STRESS}) **a**), predicted thermal time constant in seconds (τ) **b**), wind speed (m s^{-1}) **c**), frequency with which wind speeds drop ≤ 0.5 (m s^{-1}) **d**), frequency of days that maximum temperatures exceeded the critical threshold temperature of 49°C (AT_{49}) **e**), and thermal damage threshold (T_{50}) **f**) for outer canopy leaves at four positions: upper north-facing, UN; lower north-facing, LN; upper south-facing, US; lower south-facing canopy, LS. PCA variable loadings are presented left of C_{STRESS} , where AT_{MAX} , VPD_{MAX} , and RH_{MIN} are mean daily maximum ambient temperature ($^\circ\text{C}$) and vapour pressure deficit (kPa), and mean daily minimum relative

humidity (%), respectively (for loading interpretation see, Methods). See Tables 6.1 and 6.2, as well as text for statistical results.

Supporting information: figures

Figure S2.1 Photochemical quantum yield in response to heat stress treatments, as demonstrated in *Acacia papyrocarpa* during summer. Control measurements of maximum quantum yield of PSII ($PS_{FV/FM}$) and effective quantum yield ($PS_{\Delta F/FM'}$) were measured prior to heat stress. F_V/F_M was measured two hours after stress treatment and after a further recovery period of ca. 16 hours ($D2_{FV/FM}$, indicating day two of measurements) at 46, 48, 50, 52 to 54 °C and a control temperature of 28 °C **a**). $\Delta F/F_M'$ was measured immediately following stress treatment, 1.5 hours after and on day two following dark-adapted measurements and an additional 15 minutes under control conditions in order to light-adapt samples **b**). The difference between pre- stress and day two maximum quantum yield (F_V/F_M) was used as a simple measure of damage (D_{PSII}) to PSII where $D_{PSII} = 1 - (D2_{FV/FM} / PS_{FV/FM})$, solid symbols. Recovery ($R_{\Phi PSII}$) from heat stress was measured as the proportion of initial loss of photosynthetic efficiency ($\Delta F/F_M'$) that was recovered by day two of measurements, i.e., $R_{\Phi PSII} = (D2_{\Delta F/FM'} - 1.5 \text{ hr.}) / (PS_{\Delta F/FM'} - 1.5 \text{ hr.})$, open symbols **c**). For all data points $n = 10 \pm SE$. Dashed lines are for ease of reading patterns and not representative of continuous time.

Figure S2.2 Phylogenetic tree showing the relatedness among the 41 Australian southern desert plant species used in the study.

Figure S4.1 Species used in the current study were grown in a common environment at the Australian Arid Lands Botanic Garden (AALBG), located in Port Augusta, within the southern arid region of South Australia. Plants were sourced by the AALBG from locations throughout Australia's southern arid-zone, where the average annual rainfall is < 250 mm (information sourced: AALBG, 2016).

Figure S5.1 PCA biplot combining species data from all three seasons, winter (blue symbols), spring (green symbols), summer (orange symbols). Species grouped by preferred native microhabitat: diamond symbol, W_{high} ; round symbols, W_{var} ; Square symbols, W_{low} . Lines indicate direction and weighing of vectors per season for the seven traits considered: Leaf thickness, LT; leaf mass per area, LMA; near infrared

reflectance, NIR; thermal damage threshold, T_{50} ; visible reflectance, VIS; effective leaf width, LW; water content, WC. The approximate positions of some example species are shown.

Figure S5.2 Mean (\pm SE) effective leaf width **a**), percentage of visible reflectance **b**), and percentage of near infrared reflectance **c**) for Australian arid-zone plant species from three seasons: winter ($n = 23$), spring ($n = 21$), summer ($n = 41$). Results show a general tendency for effective leaf width to decrease and spectral parameters to increase over the course of the year, from winter to summer. Results shown inset are for Welch's ANOVA with post-hoc comparisons based on the Games-Howel test. Data points with different letters above differed significantly at * $P < 0.05$.

Figure S6.1 Half-hourly measurements of light levels (PAR $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) adjacent to the canopy for a representative *Acacia papyrocarpa* tree. Measurements shown are for a single day between 900 to 1600 hrs for the north- and south-facing canopy.

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Figure S6.3 Mean daily maximum ambient temperature (AT_{MAX} , $^{\circ}\text{C}$) (**a – c**), daily minimum per cent relative humidity (RH_{MIN} , %) (**d – f**), and mean daily maximum vapour pressure deficit (VPD_{MAX} , kPa) (**g – i**) measured at four positions of height (upper, lower) and aspect (north, south) and jointly: upper north canopy, UN; lower north canopy, LN; upper south canopy, US; lower south canopy, LS. The significance of main effects for factorial ANOVA is indicated: $\alpha = 0.05$, *** $P < .001$, ** $P < .01$, * $P < .05$. Interaction effects were nonsignificant.

Figure S7.1 Damage (being the difference between pre- and post-stress levels of photosystem health, D_{PSII} , \pm SE) of *Acacia papyrocarpa* leaves exposed to 28 (control), 48, 50, 52 $^{\circ}\text{C}$ treatment temperatures for three **a**) or fifteen minutes **b**) duration. Note,

higher D_{PSII} values indicate greater long-term damage. Treatments varied in the number of stress events and duration of recovery phases. For instance, comparisons in panels **a** – **b** are for a single stress event followed by a single 90 min recovery phase under sub-saturating conditions and an extended overnight recovery phase (R_{ON}), or three consecutive heat stress events interspersed with recovery phases varying in duration: 90 minutes (R_{90}), 30 minutes (R_{30}) and 10 minutes (R_{10}). In all instances, final recovery phases under sub-saturating light were followed by an extended overnight recovery phase. Comparison of D_{PSII} after single 3 (grey symbols) and 15 minute (black symbols) heat stress at control and treatment temperatures **c**). Comparison of D_{PSII} after a single heat stress event at 50 °C followed by an overnight recovery phase (R_{ON}) and three consecutive heat stress events of 3 and 15 minutes, also at 50 °C **d**). Recovery phases for consecutive stress treatments are as described above. All treatment combinations were replicated three times randomly over the course of the 2-week measurement period.

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Main text tables

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Table 2.2 Pearsons correlation (r) relationships between damage and recovery after five heat stress treatment temperatures for 41 Australian arid-zone species measured during summer. Damage to PS II following heat stress (D_{PSII}) was calculated as the difference between pre- and post-stress levels of maximum quantum yield of PSII (F_V/F_M). Recovery of photosynthetic efficiency ($R_{\Phi\text{PSII}}$) was calculated as the proportion of the initial loss of photosynthetic functional efficiency ($\Delta F/F_M'$) that was recovered the day after heat stress. Heat stress was applied for 15 minutes at five treatment temperatures (46, 48, 50, 52 and 54 °C). Levels of significance are indicated as: * = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$. $n = 41$. Values in bold-type are complimentary to correlative relationships depicted in Fig. 2.2.

Table 2.3 Relationships between damage and recovery after stress with thermal tolerance thresholds during summer, measured at five stress treatment temperatures, for 41 Australian arid zone species using Pearson correlations (r). Details of how damage and recovery were derived are as for Table 1. Species' thermal tolerance thresholds (T_{50}) were defined as the temperature at which F_V/F_M declined to 50% of the maximum prestress levels. Levels of significance are indicated as: * = $p < 0.05$. ** = $p < 0.01$. *** = $p < 0.001$. $n = 41$.

Table 3.1 List of the 42 Australian desert plant species used in this study, arranged from lowest to highest thermal damage thresholds (T_{50} , °C). Growth form is given in parentheses: g, grass; h, herb; p, hemi-parasite; s, shrub; t, tree. T_{50} was calculated as the temperature at which maximum quantum yield (F_V/F_M) declines to 50% of the maximum prestress F_V/F_M measurement. Native microhabitats were defined as the environments that species naturally tend to occupy and that differ broadly on the availability of water: W_{low} , relatively low water availability, W_{var} , availability of water is variable; W_{high} , relatively high water availability. Warming tolerance (WT) was defined as the difference between a species' physiological limit to temperature (T_{50}) and

a thermal index of its habitat (T_{hab}). The measure of T_{hab} was based on maximum values across each species' Australia-wide distribution using four different thermal indices: annual maximum mean temperature (amm); annual mean temperature (am); warmest maximum period (wmp); warmest quarter (wq).

Table 3.2 Pearson correlations ($n = 42$) between warming tolerance (WT) and i) species' thermal damage thresholds (T_{50}) and ii) their mean maximum latitudinal Australia-wide distributions. WT is calculated as the difference between the maximum recorded values of any relevant long-term mean climatic temperature variable across a given species' distribution minus its thermal damage threshold (see Table 3.1 legend). Here, WT was calculated using four different thermal indices: annual maximum mean temperature (amm); annual mean temperature (am); warmest maximum period (wmp); warmest quarter (wq). The strongest relationship for each bivariate combination is shown in bold (***) ($P < .001$).

Table 4.1 Comparison of models predicting the influence of season, microhabitat and priming temperature (PT) on the thermal damage threshold (T_{50}). Each model incorporates a different priming temperature metric as a covariate: PT_{min} (model 1) and PT_{max} (model 2), respectively based on the daily minimum and maximum temperature recorded three days preceding collection of species' T_{50} . Results are for the most parsimonious models, assuming Gaussian distributions with identity link functions. Omnibus tests confirmed that each fitted model was significantly different from its null model Significant differences appear in bold ($\alpha = 0.05$).

Table 4.2 Pairwise comparisons of the estimated marginal means for significant model main effects (see Table 4.1). Model compares the effects of season and microhabitat on species' thermal damage thresholds (T_{50}), while accounting for effects of minimum (PT_{min} , model 1) or maximum (PT_{max} , model 2) priming temperatures. Dashes indicate where the main effect was nonsignificant in the overall model. Significant differences appear in bold ($\alpha = 0.05$).

Table 4.3 Analysis of covariance investigating the influence of priming temperature on species' thermal damage threshold (T_{50}) within season (winter, spring, summer) (results complement Table 4.2). For each season, separate models incorporating the two

different priming temperature metrics as a covariate were conducted: PT_{\min} (model 1) and PT_{\max} (model 2). Significant differences appear in bold ($\alpha = 0.05$).

Table 4.4 Paired t -tests used to assess differences in seasonal thermal damage thresholds (T_{50}) between phylogenetically independent contrasts ($n = 11$ pairs). Species are contrasted on low- versus high-water availability in their native microhabitat. As priming temperature was found to influence variation in T_{50} (see Tables 4.1, 4.3), t -tests also were performed on PT_{\min} and PT_{\max} . Significant differences appear in bold ($\alpha = 0.05$).

Table 4.5 List of species belonging to each of five acclimatisation groups reflecting different trajectories of seasonal changes in T_{50} . Details in text Methods. Shading for ease of reading.

Table 5.1 Variable component loadings along PC1 and PC2 for winter, spring, and summer PCA. Moderate to high loadings in bold, complex variables appear in italics if 1) they cross-load at or near the cut-off criterion of ± 0.4 and 2) their primary-secondary difference is small (< 0.3), making clear placement to either component difficult. Initial eigenvalues, variation explained by each principal component, and communalities listed. See Methods for detailed descriptions of selection criteria and leaf traits.

Table 5.2. Seasonal ANOVA for differences among three microhabitats based on species' native water availabilities: W_{high} , W_{var} , W_{low} (see Methods). Results are for traditional F-tests with the exception of summer PC1, which was based on Welch's F-test ($\alpha = 0.05$). Results correspond with Fig. 5.2.

Table 6.1 Summary of two-way ANOVA tests for the effect of canopy position on the climatic stress index (C_{STRESS}), wind speed (m s^{-1}), frequency with which wind speeds drop $\leq 0.5 \text{ m s}^{-1}$, and predicted leaf time constant (τ) in five replicate *Acacia papyrocarpa* plants. The canopy positions were: upper north-facing, UN; lower north-facing, LN; upper south-facing, US; lower south-facing outer canopy, LS. Significant differences in bold ($\alpha = 0.05$) and the directions of significant effects for height and aspect are indicated with arrows.

Table 6.2 Generalised liner models predicting the influence of four canopy positions and one of two covariates on the thermal damage threshold (T_{50}) of *Acacia papyrocarpa*

leaves. Height and aspect were factors and the climatic stress index, C_{STRESS} (Model 1) and predicted thermal time constant of a leaf, predicted τ (Model 2) were covariates. Results are for the most parsimonious models, assuming Gaussian distributions with identity link functions. Significant differences in bold ($\alpha = 0.05$). Omnibus tests confirmed that each fitted model was significantly different from its null model.

Supporting information: tables

Table S3.1 Pearson correlations (r values) of T_{50} with the minimum, maximum, range and mean of three climate-based parameters: mean annual rainfall, mm; solar radiation, $\text{MJ}\cdot\text{m}^{-2}\cdot\text{day}$; mean annual aridity index. Results shown are for all 42 species and individually for W_{high} ($n = 10$), W_{var} ($n = 14$), and W_{low} ($n = 18$) species. $P > 0.05$ in all cases except where indicated in bold ($P < 0.05$).

Table S3.2 Species rank according to their warming tolerance (WT), calculated as the difference between a species' physiological limit to temperature (T_{50}) and a thermal index of its habitat (T_{hab}). The measure of T_{hab} was based on the highest value across each species' Australia-wide distribution using four different thermal indices. Here, T_{hab} values were based on the highest annual maximum mean temperature (WT_{amm}).

Table S3.3 Species rank according to their warming tolerance (WT), calculated as the difference between a species' physiological limit to temperature (T_{50}) and a thermal index of its habitat (T_{hab}). The measure of T_{hab} was based on the highest value across each species' Australia-wide distribution using four different thermal indices. Here, T_{hab} values were based the highest annual mean temperature.

Table S3.4 Species rank according to their warming tolerance (WT), calculated as the difference between a species' physiological limit to temperature (T_{50}) and a thermal index of its habitat (T_{hab}). The measure of T_{hab} was based on the highest value across each species' Australia-wide distribution using four different thermal indices. Here, T_{hab} values were based on the highest warmest maximum period (WT_{wmp}).

Table S3.5 Species rank according to their warming tolerance (WT), calculated as the difference between a species' physiological limit to temperature (T_{50}) and a thermal index of its habitat (T_{hab}). The measure of T_{hab} was based on the highest value across

each species' Australia-wide distribution using four different thermal indices. Here, T_{hab} values were based on the highest warmest quarter (WT_{wq}).

Table S4.1. Pearson correlations between species' thermal damage thresholds and the daily minimum, daily maximum, daily cumulative minimum, daily cumulative maximum and daily range temperatures obtained one to ten days prior to physiological measurements; here termed 'priming temperature'. Analyses revealed few significant relationships between T_{50} and priming temperature for the days preceding our experiment in winter and spring. For summer measurements, statistically significant correlations were consistent across priming temperature metrics by the third day prior to T_{50} measurements (indicated by dashed line); with the exception of daily temperature range, which remained nonsignificant irrespective of day or season. Results suggest ambient temperature has a stronger influence on T_{50} during summer than typically cooler seasons. From these analyses, we chose to incorporate daily ambient temperature recordings from day three as a proxy for priming temperature in all generalised linear models. Statistically significant relationships appear in bold. $\alpha = 0.05$.

Table S5.1 Seasonal minimum, maximum and mean (\pm SE) values for six leaf morphological and structural traits: leaf thickness, leaf mass per area, leaf water content, effective leaf width, and visible and near infrared reflectance. Values are for all species within each season (total) and for species grouped by microhabitat: high water, W_{high} ; low water, W_{low} ; variable water availability, W_{var} .

ABSTRACT

Many aspects of the Earth's climate are predicted with high certainty to undergo substantial and rapid changes in the near future, potentially resulting in a plethora of new high stress conditions to which plants must respond to survive. Living in extreme environments, desert plants are expected to be among the most vulnerable. Due to the thermal dependence of photosynthesis, changes in temperature are particularly important for plants. Extreme high-temperature events are becoming more frequent and intense and projected to increase in many regions. General expectations are that species' vulnerability to increased temperatures varies with latitude, but less is known about how local-scale habitat variation influences thermal tolerance. Variation in the ability to plastically adjust thermal tolerance will undoubtedly influence the distribution of different species and affect community composition. Yet, the extent of variation in thermal acclimatisation in plant species is poorly understood. The overall objective of my PhD research was to provide insight into leaf-level thermal responses of plants under extreme high temperatures in light of a warming climate. Through a series of linked experiments, my research demonstrates how dynamic and varied the heat stress response can be, including cross-species variation of critical thermal limits, heat stress recovery, acclimatisation patterns within and among species over time, and spatial differences relating to native microhabitat. I developed a novel protocol for measuring biologically relevant, species-specific thermal damage thresholds (Chapter 2), which I subsequently used to demonstrate seasonal and spatial effects on species' thermal responses (Chapters 3 and 4). The latter findings emphasise that a deeper understanding of plant thermal responses requires insight into their capacity to shift their thermal response over time and space. I then showed that species' innate physiological thermal tolerance aligns in multi-trait space with two alternative leaf-level morphological pathways of thermal protection (Chapter 5). This raises the possibility that other thermal protective processes, e.g., heat shock protein production and increased membrane stability, may also sit along these axes. Lastly, I demonstrated intracanalopy variation in leaf-level physiological response, which expands our mechanistic understanding of plant-environment interactions and could benefit models predicting the cost to species of a warming climate (Chapter 6). By revealing these and other key thermal response

patterns, this thesis offers a meaningful contribution to the field of plant ecophysiology, and provides information that is crucial for our understanding and management of desert– and potentially many other – ecosystems.

DECLARATION OF CONTRIBUTION TO EACH PUBLICATION

The following publications have resulted directly from the research presented within this thesis:

- 1) Curtis EM, Knight CA, Petrou K, Leigh A. 2014. A comparative analysis of photosynthetic recovery from thermal stress: a desert plant case study. *Oecologia*, 175: 1051-1061.
Associate Professor Andy Leigh and I designed the thermal tolerance work; I also collected and analysed the data and led the writing, with all authors contributing to the text. Dr Katherina Petrou provided valuable insight into chlorophyll a fluorescence protocols. Professor Charles Knight advised on the initial experimental setup.
- 2) Curtis EM, Gollan JR, Murray BR, Leigh A. 2016. Native microhabitats better predict tolerance to warming than latitudinal macro-climatic variables in arid-zone plants. *Journal of biogeography*, 43.6 (2016): 1156-1165.
Associate Professor Andy Leigh and I designed the thermal tolerance work; I also collected and analysed the data and led the writing, with all authors contributing to the text. Dr Brad Murray contributed to analyses and interpretations, and Dr John Gollan contributed the ideas on warming tolerance.

The following chapters are in review or prepared for imminent submission for publication:

- 1) Chapter 4: Curtis EM, Murray BR, Leigh A. (In review) Temporal dynamics of upper thermal damage thresholds: variation among desert plant species with contrasting microhabitat associations. Submitted to *Global Change Biology*.
Associate Professor Andy Leigh and I planned and designed the thermal tolerance work; I also performed experiments, conducted fieldwork, collected and analysed the data; Dr. Brad Murray provided analytical advice; I led the writing, with all authors contributing to the text.
- 2) Chapter 5: Curtis EM, Knight CA, Leigh A. Extending the global leaf economics spectrum to include metrics of plant thermal tolerance: Two new axes identified from a suite of desert plant species. Ready for submission to the *Journal of Vegetation Science*.

Associate Professor Andy Leigh and I generated hypotheses and designed the thermal tolerance work; I also collected and analysed the data; Professor Charles Knight provided advice on the initial experimental setup and contributed intellectual input; I led the writing, with all authors contributing to the text.

- 3) Chapter 6: Curtis EM, Knight CA, Leigh A. Intracanalopy adjustment of leaf-level thermal tolerance is associated with microclimatic variation across the canopy of *Acacia papyrocarpa* Benth. Ready for submission to *Oecologia*.

Associate Professor Andy Leigh and I generated hypotheses and designed the thermal tolerance work; I also collected and analysed the data; Professor Charles Knight provided advice and contributed intellectual input; I led the writing, with all authors contributing to the text.

Signature of Student:

Ms. Ellen Curtis

Date: 26 September 2017