

Climate change impacts on genetically differentiated *Telopea speciosissima* (NSW Waratah) coastal and upland populations

Guomin Huang, Paul Rymer and David Tissue

Hawkesbury Institute for the Environment, University of Western Sydney, Richmond, NSW 2753, Australia

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Summary

Changes in key climatic variables (e.g., atmospheric CO₂, air temperature and water availability) are occurring at unprecedented rates and having substantial impacts on functionality, biodiversity and productivity of terrestrial ecosystems. Because forests dominate terrestrial net primary production and play a prominent role in the global carbon cycle, understanding the capacity of woody species to cope with simultaneously changing climatic variables is critical for the management of natural resources and the conservation of biodiversity. One fundamental way that plants may respond to rapid climate change in the short-term is to adjust their growth and physiology via phenotypic plasticity – the ability of a genotype to express multiple phenotypes in response to environmental change, which is thought to be particularly important for woody species with long generation times. For any given species, plant populations originating from different environments usually differ in their responses to the same environmental change, as evidence of intraspecific variation in phenotypic plasticity. Although some progress has been made on intraspecific variation in woody plant response to climate change, no studies have looked into the interactive effects of concurrently changing climatic variables on their intraspecific variation in phenotypic plasticity. Therefore, this project was designed to assess the impacts of key climatic variables (i.e., [CO₂], temperature, and water availability) on growth and physiology of woody plant populations originating from contrasting environments, with a focus on the intraspecific variation in their capacity to cope with climate change. *Telopea speciosissima* (Proteaceae; Shrub; open woodland), consisted of two populations originating from climatically differentiated regions. Treatment levels (i.e., changes in [CO₂], temperature, and water availability) in this research were chosen based on predicted climatic conditions within this century. The goal was to use this woody species to generate improve understanding of woody plant growth and physiological responses under future climatic scenarios.

In the first experiment, the main and interactive effects of elevated [CO₂] (CE) and elevated temperature (TE) on growth and physiology of the Coastal (warmer, less variable temperature environment) and the Upland (cooler, more variable temperature environment) genotypes of *T. speciosissima* were assessed. Seedlings were grown under two [CO₂] (400 µl l⁻¹ and 640 µl l⁻¹) and two temperature (26/16 °C and 30/20 °C for day/night) treatments. Both genotypes were positively responsive to CE (35% and 29% increase in whole-plant dry mass and leaf area, respectively), but only the Coastal genotype exhibited positive growth responses to TE. It was observed that the Coastal genotype exhibited greater growth response to TE (47% and 85% increase in whole-plant dry mass and leaf area, respectively) when compared with the Upland genotype (no change in dry mass or leaf area). No intraspecific variation in physiological plasticity was detected under CE or TE, and the interactive effects of CE and TE on intraspecific variation in phenotypic plasticity were also largely absent. Overall, TE

was a more effective climate factor than CE in exposing genotypic variation in this woody species. Results from the chapter contradict the paradigm that genotypes from more variable climates will exhibit greater phenotypic plasticity in future climate regimes.

In the second experiment, the main and interactive effects of elevated [CO₂] (CE) and elevated temperature (TE) on growth and physiological responses to drought of the Coastal (warmer and relatively wetter environment) and the Upland (cooler and relatively drier environment) genotypes of *T. speciosissima* were investigated. Seedlings were grown under two [CO₂] (400 μl l⁻¹ and 640 μl l⁻¹) and two temperatures (26/16 °C and 30/20 °C for day/night). During the period of experiment, half of the seedlings were supplied with full watering (i.e., the well-watered treatment), while the other was subjected to controlled drought/recovery cycles (i.e., the drought treatment). The two genotypes showed similar declines in growth and photosynthesis under drought conditions across [CO₂] and temperature treatments, and did not exhibit differences in response to drought stress. Regardless of genotype, TE negatively affected plant drought resistance by accelerating the process of drought seedlings becoming physiologically stressed, while CE did not influence the capacity of plant drought resistance or alter the sensitivity of photosynthesis to declines in soil water content. Furthermore, CE did not ameliorate the negative effects of TE on drought response. Overall, these results suggest that woody plant populations originating from different environments may not necessarily show intraspecific variation in response to drought under current or predicted future climates. These findings also indicate that temperature is likely to be a stronger determinant than [CO₂] in affecting woody plant response to drought in the context of climate change.

In conclusion, the research addressed the main and interactive effects of changes in multiple climatic variables (i.e., [CO₂], temperature, and water availability) on growth and physiology of *Telopea speciosissima*, with a focus on the intraspecific variation in their responses between populations originating from different environments. Results of this research were reported based on the treatment levels chosen for the experiments. Significant intraspecific variation in growth plasticity when responding to a constant mild warming (TE; ambient + 3.5–4.0 °C) was found. In contrast, populations did not differ in their growth or photosynthetic responses to elevated [CO₂] (CE) or to sustained drought. These results together suggest that temperature would be more effective than [CO₂] or water availability in exposing intraspecific variation in phenotypic plasticity for woody plant populations under future climates. The predicted relationships between phenotypic plasticity and source environment variability of plant populations was not supported by the findings from *T. speciosissima*, indicating that woody plant populations originating from more variable environments may not necessarily show greater phenotypic plasticity in response to climate change. This work expands current knowledge regarding the interactive effects of simultaneously changing climatic variables on woody plant growth and physiology.

More importantly, this research contributes valuable information on intraspecific variation in phenotypic plasticity of woody plant populations in response to changing climatic variables, as well as the association between phenotypic plasticity and source environment variability, which will assist in making robust predictions of the distribution and abundance of woody species under future climates.

Introduction

Increasing emissions of greenhouse gases from anthropogenic activities including rapid fossil fuel consumption and land use changes are contributing to the ongoing global climate change. Atmospheric carbon dioxide concentrations ($[\text{CO}_2]$) have been increasing from about $280 \mu\text{l l}^{-1}$ before the industrial revolution to over $400 \mu\text{l l}^{-1}$ nowadays and are projected to exceed $550\text{--}900 \mu\text{l l}^{-1}$ by the end of this century (Collins *et al.*, 2013). Rising $[\text{CO}_2]$ is expected to cause a $0.3\text{--}4.8 \text{ }^\circ\text{C}$ increase in the global mean air temperature during same time period (Solomon *et al.*, 2009; Collins *et al.*, 2013). Embedded with this climatic warming trend, increases in the frequency and intensity of extreme climatic events such as drought and heat waves are also anticipated through this century according to current climate change models (Meehl & Tebaldi, 2004; Della-Marta *et al.*, 2007; Kharin *et al.*, 2007; Ballester *et al.*, 2010; Yao *et al.*, 2013). Similar predictions have been made for Australia in terms of climate change. By 2070, annual mean air temperatures in Australia are projected to increase by $1\text{--}6 \text{ }^\circ\text{C}$, with summer temperatures exceeding $35 \text{ }^\circ\text{C}$ expected to occur over 10 times more frequently in the meantime (Pearce *et al.*, 2007). Annual precipitation is also predicted to decline in many parts of Australia in the coming decades (Pittock, 2003; Pearce *et al.*, 2007; Moise & Hudson, 2008).

Changes in these climatic variables are likely to substantially regulate plant growth, function and development, thereby affecting functionality, biodiversity and productivity of terrestrial ecosystems (Nemani *et al.*, 2003; Ciais *et al.*, 2005; Williams *et al.*, 2008; Allen *et al.*, 2010; Matesanz *et al.*, 2010; Barnosky *et al.*, 2012). On the global scale, forests cover about 30% of land surface and dominate terrestrial net primary production (up to *c.* 70%), playing a prominent role in the global carbon cycle (Schimel *et al.*, 2001; Karnosky, 2003; Norby *et al.*, 2005; FAO, 2006; Bonan, 2008; Beer *et al.*, 2010; Pan *et al.*, 2011). Therefore, quantifying and understanding the capacity of woody species to cope with simultaneously changing climatic variables is of particular importance for the management of natural resources and the conservation of biodiversity (Sala *et al.*, 2000; Mawdsley *et al.*, 2009).

To cope with the ongoing rapid anthropogenic climate change, species will have to rely on different approaches such as distinct ecological (e.g., habitat shifts and phenotypic plasticity) and evolutionary strategies (e.g., adaptation and gene flow), as well as in combination (Kawecki, 2008; Anderson *et al.*, 2012). One fundamental way that plant species may respond to changing climatic variables in the short-term is to adjust their growth and physiology via phenotypic plasticity – the ability of a genotype to express multiple phenotypes in response to environmental change (Bradshaw, 1965; Sultan, 2000; Nicotra *et al.*, 2010; Anderson *et al.*, 2012). For woody plant species with long generation times, phenotypic plasticity is thought to be particularly important for acting as a buffer against rapid climate change and providing growth advantages (Valladares *et al.*, 2007; Chevin *et al.*, 2010; Nicotra *et al.*, 2010), because their evolutionary responses by natural selection might be too slow to mitigate the effects of rapid environmental change.

For any given plant species, when genotypes show differentiated responses to the same environmental change, intraspecific variation in phenotypic plasticity exists, known as significant genotype (G) by environment (E) interactions (Nicotra *et al.*, 2010; Aspinwall *et al.*, 2015). Intraspecific variation in phenotypic plasticity would not only influence the habitat range occupied by plant species, but also affect the ecological and evolutionary responses of plant species to changing environments (Sultan, 2000; Van Kleunen & Fischer, 2005; Valladares *et al.*, 2007; Williams *et al.*, 2008; Nicotra *et al.*, 2010; Aspinwall *et al.*, 2015). For instance, genotypes with low phenotypic plasticity may tolerate and persist under extreme conditions to survive and maintain growth (Schlichting, 1986; Thompson, 1991), while genotypes with high phenotypic plasticity may be capable of rapid resource uptake and show increased growth when conditions are optimal (Grime & Mackey, 2002). Therefore, studies on intraspecific variation in phenotypic plasticity of woody plants in response to changing climates are essential for making robust predictions of woody species responses under global climate change, as well as identifying genotypes that exhibit the capacity to increase or maintain productivity under more extreme climatic conditions in the future (Nicotra *et al.*, 2010; Aspinwall *et al.*, 2015; Moran *et al.*, 2016).

Although previous studies have demonstrated intraspecific variation in growth or physiological plasticity of woody plant species in response to elevated [CO₂] (e.g., Dickson *et al.*, 1998; Mohan *et al.*, 2004; Cseke *et al.*, 2009), or elevated temperature (e.g., Weston & Bauerle, 2007; Weston *et al.*, 2007; Drake *et al.*, 2015), or water deficit (e.g., Cregg & Zhang, 2001; Monclus *et al.*, 2006; Ramirez-Valiente *et al.*, 2010; Bansal *et al.*, 2015), the nature and basis of intraspecific variation in phenotypic plasticity within woody species under climate change remains largely unknown. To date, no study has looked into the interactive effects of concurrently changing climatic variables on intraspecific variation in phenotypic plasticity of woody plant species. To better understand and predict how woody plants would respond to future climatic scenarios, manipulations of combinatorial experiments assessing the main and interactive effects of [CO₂], temperature and water availability on intraspecific variation of woody plant responses are necessary.

The overall objective of this research was to assess the impacts of key climatic variables (i.e., [CO₂], temperature, and water availability) on growth and physiology of woody plant populations originating from contrasting environments, with a focus on the intraspecific variation in their capacity to cope with climate change. The ecologically and economically important Australian native woody species, *Telopea speciosissima* (Proteaceae; Shrub; open woodland), consisting of two populations originating from climatically differentiated regions. The research was conducted in a state-of-the-art glasshouse facility located at the University of Western Sydney with pot-grown woody plant seedlings. The glasshouse was set to control [CO₂] (ambient and ambient + 240 µl l⁻¹) and temperature (ambient and ambient + 4.0 °C) conditions for simulating current and future climatic scenarios within this century based on model predictions. These combinatorial studies on woody species representing varying taxa and functional attributes were aimed to improve understanding on intraspecific variation of woody plant growth and physiological responses to simultaneously changing climatic variables (i.e., [CO₂], temperature, and water availability). Specifically, addressing the following questions:

- (1) Do changes in climatic variables independently or interactively expose intraspecific variation in phenotypic plasticity of woody plant populations originating from different environments?
- (2) If differentiated responses between woody plant populations exist, what are the relationships between phenotypic plasticity and their source environmental variability?
- (3) How will climatic variables interactively affect growth and physiology of woody plants under future climates?

Methodology

Telopea speciosissima R.Br. (Proteaceae), commonly known as the Waratah (Weston & Crisp, 1994), is an endemic woody species (and New South Wales floral emblem) in the Sydney Bioregion of Australia. This species occurs sporadically in small populations across a range of climatic and altitudinal zones, and generally flowers over a six-week period in spring (September – October in warmer areas, but later in cooler areas), followed by a vegetative flush of growth (Nixon, 1997). A previous study on morphology and population genetics of *T. speciosissima* has revealed three distinct gene pools (coastal, upland and southern) among natural populations; the coastal and upland gene pools mix at mid-elevations along an altitudinal gradient (Rossetto *et al.*, 2011). Distinction in climate between habitats of coastal and upland gene pools is mainly characterized by differences in air temperature and precipitation. The coastal region is warmer and wetter than the upland region, but the latter experiences greater levels of temperature variability (Table 2-1). Thus, *T. speciosissima* is well suited for studying the association between phenotypic plasticity and source environment variability of genetically differentiated woody plant populations.

Results from such studies will provide useful information on the importance of intraspecific variation in phenotypic plasticity in determining woody species growth and physiology under climate change.

Plant material and growing conditions

Seeds were collected in May-June 2012 from two *T. speciosissima* populations along the elevational gradient, which are from coast to upland gene pools. At least 10 waratah mother plants from each population were selected for the glasshouse experiment. Seeds were directly sown into pots and cultivated in four adjacent, naturally lit glasshouse compartments (3.0 m × 5.0 m × 3.5 m, width × length × height each) which are [CO₂] and temperature controlled (more details are provided in Ghannoum et al. 2010). Of the four glasshouse compartments, two are set to simulate the ambient temperature (26/18 °C for day/night; ambient temperature treatment) and the other two are programmed to simulate a constant 4 °C increase in temperature (30/22 °C for day/night; high temperature treatment). Within each temperature treatment, plants were grown at ambient [CO₂] (target 400 μL L⁻¹) and elevated [CO₂] (target 640 μL L⁻¹).

Table Error! No text of specified style in document.-1 The 40-year (1971–2010) summary of precipitation and air temperature in the coastal (180 m altitude) and upland (1150 m altitude) regions, from which the *Telopea speciosissima* Coastal and Upland genotypes were sampled for this study

Coastal region			Upland region		
Mean	Range	CV	Mean	Range	CV
<i>Precipitation (mm)</i>					

Annual	1243	792–2044	0.266	856	393–1265	0.255
Summer	372	146–946	0.458	276	53–539	0.381
<i>T_{max}</i> (°C)						
Annual	22.8	21.9–23.8	0.159	18.5	17.0–20.0	0.296
Summer	26.9	24.1–29.8	0.043	24.9	20.8–29.1	0.069
<i>T_{min}</i> (°C)						
Annual	13.2	12.2–14.0	0.319	7.4	6.2–8.4	0.585
Summer	18.1	15.9–20.4	0.054	12.6	9.4–15.3	0.095

Range refers to the minimal and maximal values of annual/summer Means. CV, coefficient of variation, defined as the ratio of the standard deviation to the mean; T_{max} , maximum air temperature; T_{min} , minimum air temperature. CVs for precipitation were calculated based on the annual/summer means ($n = 40$); while CVs for temperature were first calculated based on the monthly means within each year ($n = 12$) or summer ($n = 3$), and then averaged across 40 years. Air temperatures selected as the reference for T_A in the experiment are shown in bold.

Drought treatment

After seed germination and seedling growth, successfully established seedlings from each population were randomly selected for conducting a sustained drought experiment. Half of the selected seedlings were watered daily to field capacity (well watered treatment), while the other half of seedlings underwent two sustained periods of water stress (3 – 4 weeks for each period; sustained drought treatment). In addition, we re-watered the drought-treatment plants

following extensive drought to field capacity (i.e. recovery phase). Drought was achieved by initial cessation of daily watering and followed by controlled additions of small amounts of water on a daily basis to maintain low stomatal conductance.

Growth measurements

Seedling germination rates, seedling growth and survivorship were recorded for several months prior to the drought treatment. Seedling height, leaf number, area and weight, and stem and root weights for each treatment were measured throughout the project to calculate the following growth indices: specific leaf weight (SLW), leaf weight ratio (LWR), leaf area ratio (LAR) and shoot/root weight ratio (SRR). Additional leaves will be used to analyse leaf N and P concentrations, and total nonstructural carbohydrates (TNCs; sugars and starch).

Plant physiological traits

Gas exchange measurements were conducted on attached, recently fully expanded leaves using the Li-Cor 6400 portable photosynthesis system (Li-Cor Inc. USA). Measurements of net photosynthesis at saturating light (A_{sat}), stomatal conductance (g_s), the ratio of intercellular to ambient CO₂ concentration (C_i/C_a) and leaf water use efficiency (WUE_L) were conducted before measuring the responses of photosynthetic assimilation rates to intercellular CO₂ concentrations (A/C_i curves) and the responses of assimilation rates to leaf temperature (A/T_L curves). Photosynthetic responses of each treatment will be monitored on a weekly basis during the whole experimental period. A/C_i curves within different water availability phase (i.e. pre-drought, drought, and recovery phases) were also determined.

All data were analysed using a general linear model, factorial analysis of variance (ANOVA) with three main factors – genotype, growth [CO₂] and growth temperature, with two levels within each factor. The effect of ontology was also tested with the addition of plant dry mass as a covariate in the analyses, but overall there was no change from the original analyses. Tukey's HSD tests were used to compare means for both genotypes among the [CO₂] and temperature treatments (see Tables 2-3 and 2-4). Relationships between whole-plant dry mass and other parameters were analysed using linear regression analysis. Data were log-transformed when necessary to meet assumptions of homoscedasticity and normality. Results were considered significant in all cases if $P < 0.05$. All analyses were performed in R (version 3.1.0; R Foundation for Statistical Computing, Vienna, Austria).

Results

PART 1: Plant growth and physiology

Plant growth and dry mass allocation

Whole-plant dry mass and leaf area varied significantly between genotypes and were both affected by growth [CO₂] and temperature (Fig. 2-1a and 1b; Table 2-2 and 2-3). Overall, the Coastal genotype was more productive and possessed higher leaf area, compared to the Upland genotype. Across genotypes, C_E increased whole-plant dry mass and leaf area by 35% and 29%, respectively. T_E also increased whole-plant dry mass and leaf area in the Coastal genotype by 47% and 85%, respectively, but did not significantly affect either trait in the Upland genotype, indicating genotypic variation in growth responses to

temperature. LMA was higher under C_E and in the Upland genotype, but did not vary with temperature (Fig. 2-1c; Table 2-2 and 2-3). LAR did not show differences between genotypes or vary with $[CO_2]$, but increased 24% under T_E (Fig. 2-1d; Table 2-2 and 2-3).

Dry mass allocation to different plant organs differed between genotypes, with allocation varying strongly with temperature (Fig. 2-2; Table 2-2 and 2-3). Across genotypes and $[CO_2]$ treatments, T_E increased leaf and stem mass fractions, but decreased tuber and root mass fractions, thereby generating a 50% reduction in the mean Root/Shoot ratio. Compared to the Upland genotype, the Coastal genotype allocated more dry mass to below-ground organs (higher fraction of tuber and root mass; Fig. 2-2c and 2d), but less dry mass to above-ground organs (a lower fraction of leaf mass; Fig. 2-2a), resulting in significantly higher ratios of Root/Shoot (Fig. 2-2e). The fraction of stem mass did not vary between genotypes; the Coastal genotype showed a 43% increase in stem mass fraction under T_E , but no change occurred in the Upland genotype, suggesting a significant genotype \times temperature interaction (Fig. 2-2b and Table 2-2). C_E did not affect dry mass allocation.

Leaf gas exchange

In general, genotypes did not differ in leaf gas exchange parameters. However, C_E and T_E significantly affected all photosynthetic parameters, except g_s and A/T_L parameters (Table 2-2 and 2-3). Photosynthesis (A_{sat}) was 30% higher in $C_E T_A$ and 19% higher in $C_E T_E$ compared with the C_A treatments (Fig. 2-3a). Stomatal conductance (g_s) was not affected by C_E or T_E , although there was a significant interaction between genotype and temperature (Fig. 2-3b). Across temperature treatments, photosynthetic capacity traits (A_{max} , V_{cmax} and J_{max}) decreased by *c.* 20% under C_E (Fig. 2-3c, 3d and 3e). Growth temperature had little effect on A_{max} or V_{cmax} , but J_{max} was significantly reduced by *c.* 16% under T_E ; consequently, there was an 8% decline (on average) in J_{max}/V_{cmax} under T_E (Fig.

2-3f). C_E alone had no significant effect on $J_{\max}/V_{c\max}$, but a 15% decrease in $J_{\max}/V_{c\max}$ was observed under $C_E T_E$, suggesting a significant interaction between $[CO_2]$ and temperature (Table 2-2 and 2-3). Photosynthetic thermal optimum (T_{opt}) and light-saturated photosynthesis at thermal optimum (A_{opt}) did not differ between genotypes or vary between growth temperatures, but increased under C_E by an average of 8% and 26%, respectively (Fig. 2-4; Table 2-2 and 2-3). The average increase of T_{opt} was 2.4 °C for the Coastal genotype and 1.9 °C for the Upland genotype, respectively. The main and interactive effects of genotype, $[CO_2]$, and temperature had little effect on A/T_L parameters, except for a marginally significant interaction between genotype and temperature on parameter C (Table 2-2).

Table Error! No text of specified style in document.-2 Main and interactive effects of genotype, $[CO_2]$ and temperature on growth, photosynthetic and carbohydrate parameters of two *Telopea speciosissima* genotypes grown at two $[CO_2]$ and two temperatures

Parameter	Main effects			Interactions			
	Genotype	$[CO_2]$	Temperature	Genotype $\times [CO_2]$	Genotype \times Temperature	$[CO_2] \times$ Temperature	Genotype $\times [CO_2] \times$ Temperature
<i>Growth</i>							
Whole-plant DM (g)	0.000	0.004	0.033	0.452	0.024	0.406	0.511
Leaf Area (cm ²)	0.000	0.013	0.000	0.52	0.008	0.720	0.338
LMA (g m ⁻²)	0.024	0.025	0.346	0.90	0.467	0.391	0.128

Table 2-2 (continued)

Parameter	Main effects			Interactions			
	Genotype	[CO ₂]	Temperature	Genotype × [CO ₂]	Genotype × Temperature	[CO ₂] × Temperature	Genotype × [CO ₂] × Temperature
—LAR (m ² kg ⁻¹)	0.129	0.658	0.000	0.330	0.364	0.353	0.622
Leaf mass fraction	0.000	0.268	0.000	0.638	0.693	0.650	0.780
Stem mass fraction	0.095	0.270	0.000	0.221	0.014	0.649	0.375
Tuber mass fraction	0.000	0.071	0.000	0.781	0.063	0.379	0.607
Root mass fraction	0.012	0.615	0.000	0.239	0.271	0.860	0.748
Root/Shoot ratio	0.000	0.507	0.000	0.408	0.401	0.580	0.985
<i>Leaf gas exchange</i>							
<i>A</i> _{sat} (μmol m ⁻² s ⁻¹)	0.961	0.000	0.021	0.344	0.647	0.325	0.605
<i>g</i> _s (mol m ⁻² s ⁻¹)	0.247	0.836	0.304	0.941	0.020	0.367	0.081
<i>A</i> _{max} (μmol m ⁻² s ⁻¹)	0.374	0.000	0.106	0.363	0.394	0.101	0.628
<i>V</i> _{cmax} (μmol m ⁻² s ⁻¹)	0.175	0.000	0.080	0.897	0.446	0.319	0.740
— <i>J</i> _{max} (μmol m ⁻² s ⁻¹)	0.177	0.000	—————	0.440	0.301	0.884	0.688
0.000				0.583	0.808	0.029	0.099
<i>J</i> _{max} / <i>V</i> _{cmax}	0.614	0.059	0.002				
<i>A</i> / <i>T</i> _L	0.702	0.384	0.387	0.477	0.277	0.785	0.902
Parameter A				0.393	0.164	0.590	0.914
Parameter B	0.732	0.067	0.302				

Table 2-2 (continued)

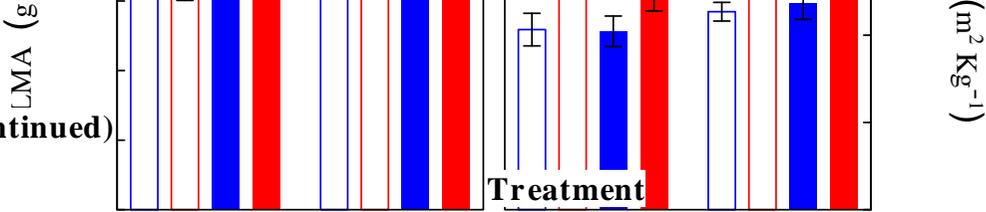
Parameter	Main effects		Interactions				
	Genotype	[CO ₂]	Temperature	Genotype ×			
				Genotype	Genotype × Temperature	[CO ₂] × Temperature	[CO ₂] × Temperature
Parameter C	0.486	0.104	0.141	0.214	0.043	0.584	0.778
<i>T</i> _{opt} (°C)	0.837	0.000	0.380	0.666	0.252	0.194	0.677
<i>A</i> _{opt} (μmol m ⁻² s ⁻¹)	0.578	0.000	0.932	0.929	0.774	0.318	0.455
<i>Carbohydrates</i>							
Whole-plant St (mg g ⁻¹)	0.031	0.020	0.000	0.891	0.507	0.542	0.385
Whole-plant Ss (mg g ⁻¹)	0.004	0.149	0.086	0.605	0.105	0.879	0.830
Whole-plant NSC (mg g ⁻¹)	0.015	0.049	0.033	0.570	0.399	0.504	0.584
Leaf St (mg g ⁻¹)	0.338	0.002	0.000	0.763	0.810	0.871	0.133
Stem St (mg g ⁻¹)	0.002	0.723	0.000	0.317	0.549	0.787	0.772
Tuber St (mg g ⁻¹)	0.000	0.234	0.004	0.052	0.597	0.675	0.677
Root St (mg g ⁻¹)	0.014	0.665	0.136	0.637	0.262	0.288	0.165
Leaf Ss (mg g ⁻¹)	0.000	0.702	0.540	0.406	0.164	0.115	0.293
Stem Ss (mg g ⁻¹)	0.273	0.043	0.173	0.640	0.743	0.074	0.420
Tuber Ss (mg g ⁻¹)	0.278	0.002	0.143	0.709	0.013	0.135	0.248
Root Ss (mg g ⁻¹)	0.019	0.000	0.000	0.373	0.290	0.014	0.005

DM, dry mass; LMA, leaf area per mass; LAR, leaf area ration; St, starch; Ss, soluble sugars; NSC, non-structural carbohydrates. *P*-values from the three-way ANOVA are presented, based on ten replicates ($n = 10$) for growth parameters and five replicates ($n = 5$) for the others. Significant values ($P < 0.05$) are shown in bold.

Table Error! No text of specified style in document.-3 Summary of means for growth, photosynthetic and carbohydrate parameters of *Telopea speciosissima* Coastal and Upland genotypes grown under the four [CO₂] and temperature treatments, as described in the Materials and methods

Parameter	Genotype	Treatment			
		C _A T _A	C _A T _E	C _E T _A	C _E T _E
<i>Growth</i>					
Whole-plant DM (g)	Coastal	6.3 ± 0.9 ^{bcd}	9.2 ± 1.0 ^{ab}	8.0 ± 1.1 ^{abc}	11.7 ± 1.5 ^a
	Upland	4.5 ± 0.2 ^{cd}	4.3 ± 0.8 ^d	6.1 ± 0.8 ^{bcd}	6.5 ± 0.6 ^{abcd}
Leaf Area (cm ²)	Coastal	267 ± 46 ^c	524 ± 64 ^{ab}	322 ± 57 ^{bc}	559 ± 64 ^a
	Upland	205 ± 14 ^c	231 ± 44 ^c	283 ± 43 ^c	350 ± 31 ^{abc}
LMA (g m ⁻²)	Coastal	98.5 ± 3.8 ^a	92.3 ± 2.1 ^a	102.0 ± 4.9 ^a	109.0 ± 5.0 ^a
	Upland	102.5 ± 2.7 ^a	109.0 ± 4.6 ^a	106.9 ± 4.2 ^a	109.6 ± 1.8 ^a
LAR (m ² kg ⁻¹)	Coastal	4.13 ± 0.37 ^b	5.64 ± 0.11 ^a	4.09 ± 0.35 ^b	4.98 ± 0.42 ^{ab}
	Upland	4.54 ± 0.21 ^{ab}	5.43 ± 0.28 ^{ab}	4.73 ± 0.37 ^{ab}	5.42 ± 0.18 ^{ab}
Leaf mass fraction (%)	Coastal	39.6 ± 2.7 ^e	52.1 ± 1.8 ^{abc}	40.6 ± 2.5 ^{de}	52.5 ± 2.2 ^{abc}
	Upland	46.2 ± 1.8 ^{cde}	58.3 ± 1.7 ^{ab}	49.4 ± 2.6 ^{bcd}	59.3 ± 1.6 ^a
Stem mass fraction (%)	Coastal	11.6 ± 0.9 ^{cd}	17.2 ± 0.9 ^a	10.9 ± 0.8 ^d	15.0 ± 0.7 ^{abc}
	Upland	13.7 ± 0.6 ^{abcd}	15.4 ± 0.9 ^{ab}	13.5 ± 0.6 ^{bcd}	15.7 ± 0.9 ^{ab}
Tuber mass fraction (%)	Coastal	17.2 ± 2.5 ^a	3.7 ± 0.5 ^{cd}	13.8 ± 2.3 ^{ab}	3.8 ± 0.6 ^{cd}

Table 2-3 (continued)



Parameter	Genotype	$C_A T_A$	$C_A T_E$	$C_E T_A$	$C_E T_E$
Root mass fraction (%)	Upland	8.6 ± 1.2^{ab}	3.3 ± 0.5^{cd}		
	Coastal	31.5 ± 2.4^{ab}	27.0 ± 1.6^{abc}		
	Upland	31.5 ± 2.1^{ab}	23.0 ± 1.8^{bc}		
Root/Shoot ratio	Coastal	1.06 ± 0.18^a	0.45 ± 0.03^{bc}		
	Upland	0.69 ± 0.06^{ab}	0.36 ± 0.03^c		
<i>Leaf gas exchange</i>					
A_{sat} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Coastal	9.6 ± 1.1^{ab}	8.8 ± 0.6^b		
	Upland	10.1 ± 0.7^{ab}	9.4 ± 0.9^{ab}		
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	Coastal	0.17 ± 0.02^a	0.17 ± 0.02^a		
	Upland	0.19 ± 0.01^a	0.18 ± 0.02^a		
A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Coastal	19.6 ± 1.0^a	18.8 ± 0.9^{ab}		
	Upland	18.7 ± 1.2^{abc}	19.8 ± 1.2^a		
V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Coastal	60.6 ± 5.9^a	52.5 ± 4.2^{ab}		
	Upland	56.8 ± 3.5^{ab}	50.7 ± 3.4^{ab}		
J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Coastal	81.5 ± 4.3^a	$66.7 \pm$		
	Upland	76.7 ± 4.4^{ab}	69.4 ± 4.0^{abcd}		
J_{max}/V_{cmax}	Coastal	1.37 ± 0.07^{ab}	1.28 ± 0.04^b		
	Upland	1.35 ± 0.02^{ab}	1.38 ± 0.06^{ab}		

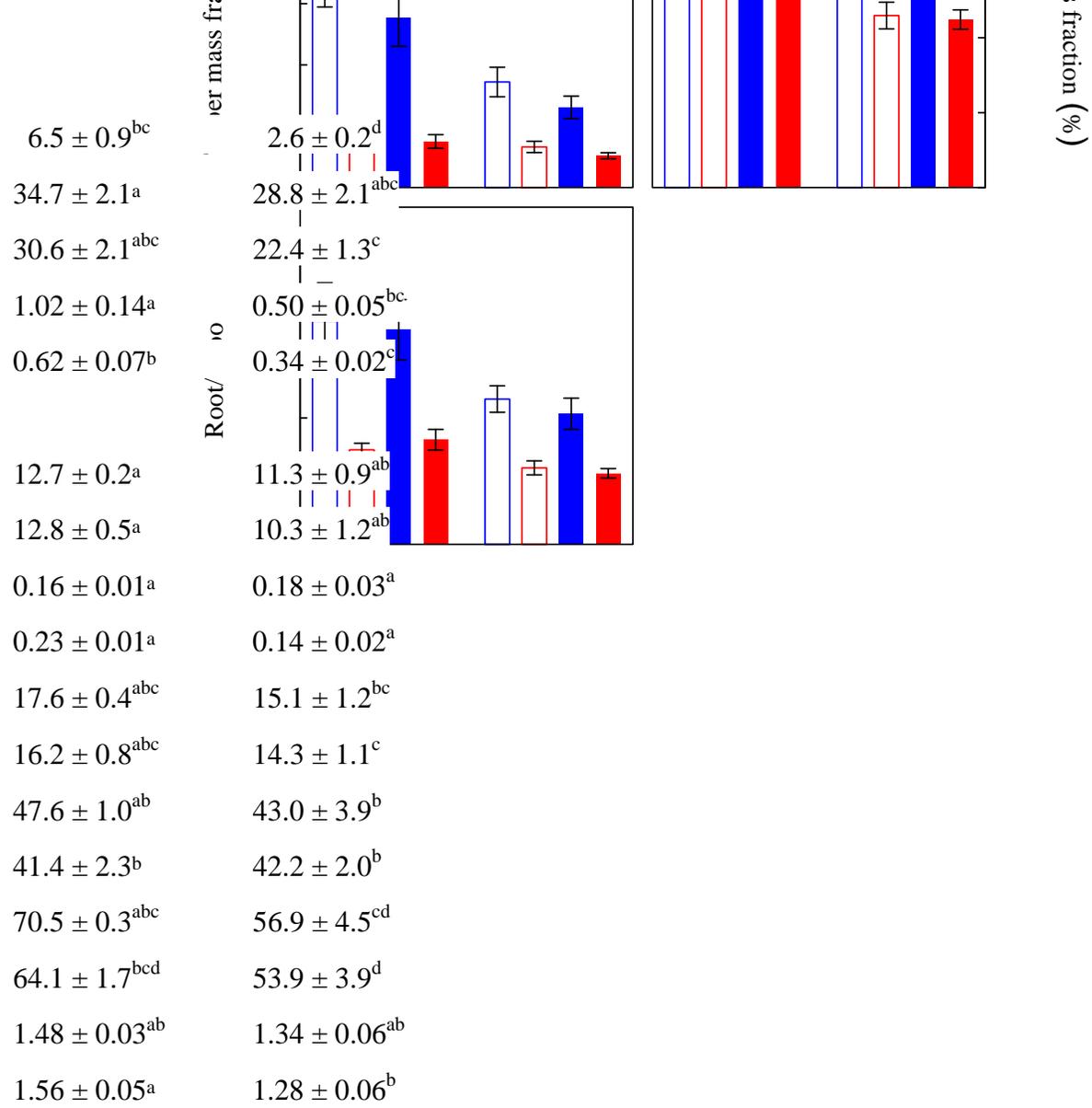
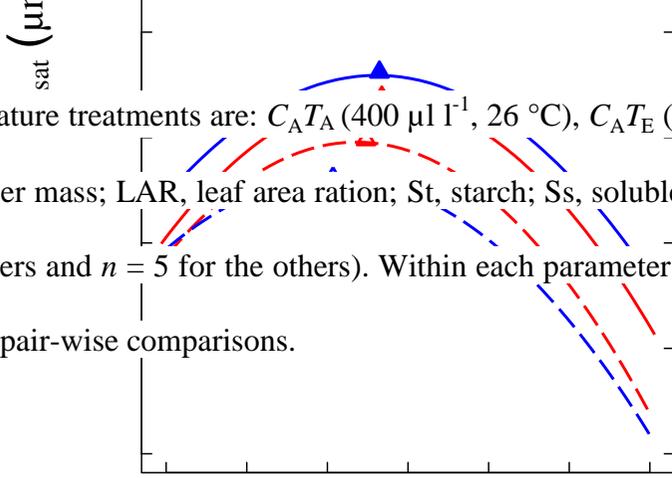


Table 2-3 (continued)

Parameter	Genotype	$C_A T_A$	$C_A T_E$	$C_E T_A$	$C_E T_E$
Parameter A	Coastal	-0.019 ± 0.002^a	-0.019 ± 0.001^a	-0.022 ± 0.002^a	-0.021 ± 0.001^a
Parameter B	Coastal	0.98 ± 0.09^a	0.98 ± 0.07^a	1.29 ± 0.12^a	1.21 ± 0.07^a
Parameter C	Coastal	-4.04 ± 0.91^a	-4.20 ± 0.75^a	-7.71 ± 1.62^a	-6.27 ± 0.40^a
	Upland	-4.32 ± 0.15^a	-7.91 ± 1.90^a	-4.97 ± 1.31^a	-8.03 ± 1.94^a
T_{opt} ($^{\circ}C$)	Coastal	25.8 ± 0.5^a	26.1 ± 0.6^a	28.7 ± 0.5^a	28.0 ± 0.8^a
	Upland	25.3 ± 0.1^a	27.4 ± 1.1^a	28.2 ± 1.2^a	28.4 ± 0.6^a
A_{opt} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Coastal	8.6 ± 0.6^a	8.6 ± 0.6^a	10.9 ± 0.7^a	10.7 ± 0.8^a
	Upland	7.9 ± 0.7^a	8.9 ± 0.6^a	10.9 ± 0.4^a	10.1 ± 1.0^a
<i>Carbohydrates</i>					
Whole-plant St (mg g^{-1})	Coastal	16.2 ± 4.0^{ab}	10.1 ± 1.4^{bc}	25.7 ± 3.7^a	11.5 ± 1.1^{abc}
	Upland	15.8 ± 4.3^{abc}	6.4 ± 0.9^c	20.5 ± 5.0^{ab}	8.9 ± 1.0^{bc}
Whole-plant Ss (mg g^{-1})	Coastal	37.2 ± 2.3^a	43.1 ± 2.5^a	40.4 ± 3.5^a	46.2 ± 1.5^a
	Upland	35.8 ± 0.4^a	35.4 ± 1.8^a	36.7 ± 3.3^a	37.6 ± 2.2^a
Whole-plant NSC (mg g^{-1})	Coastal	53.4 ± 4.7^{ab}	53.3 ± 3.1^{ab}	66.1 ± 6.9^a	57.7 ± 1.9^{ab}
	Upland	51.6 ± 4.1^{ab}	41.8 ± 2.6^b	57.2 ± 7.4^{ab}	46.5 ± 3.0^{ab}

The four [CO₂] and temperature treatments are: $C_A T_A$ (400 $\mu\text{l l}^{-1}$, 26 °C), $C_A T_E$ (400 $\mu\text{l l}^{-1}$, 30 °C), $C_E T_A$ (640 $\mu\text{l l}^{-1}$, 26 °C) and $C_E T_E$ (640 $\mu\text{l l}^{-1}$, 30 °C). DM, dry mass; LMA, leaf area per mass; LAR, leaf area ration; St, starch; Ss, soluble sugars; NSC, non-structural carbohydrates. Values represent means \pm 1 SE ($n = 10$ for growth parameters and $n = 5$ for the others). Within each parameter, different superscript letters indicate means that are significantly different at $P < 0.05$ based on Tukey's pair-wise comparisons.



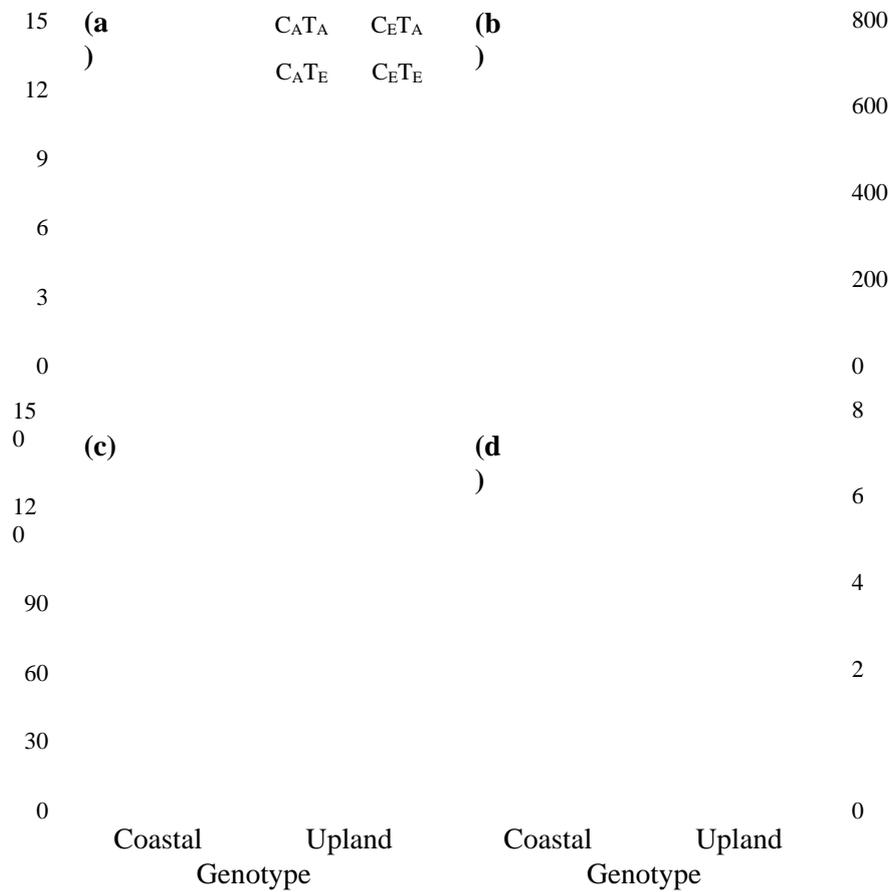
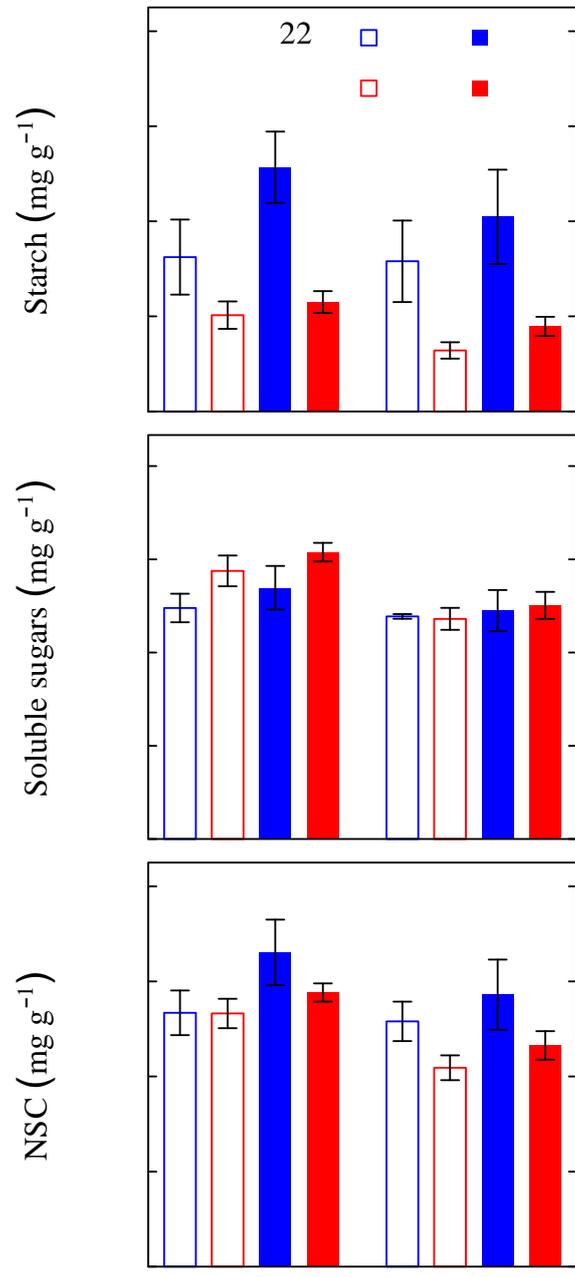


Figure Error! No text of specified style in document.-1 Whole-plant dry mass (a), leaf area (b), leaf mass per area (LMA) (c), and leaf area ratio (LAR) (d) of *Telopea speciosissima* Coastal and Upland genotypes grown under the four [CO₂] and temperature treatments: $C_A T_A$ (400 $\mu\text{l l}^{-1}$, 26 °C; open blue), $C_A T_E$ (400 $\mu\text{l l}^{-1}$, 30 °C; open red), $C_E T_A$ (640 $\mu\text{l l}^{-1}$, 26 °C; closed blue), and $C_E T_E$ (640 $\mu\text{l l}^{-1}$, 30 °C; closed red). Values represent means ± 1 SE ($n = 10$).



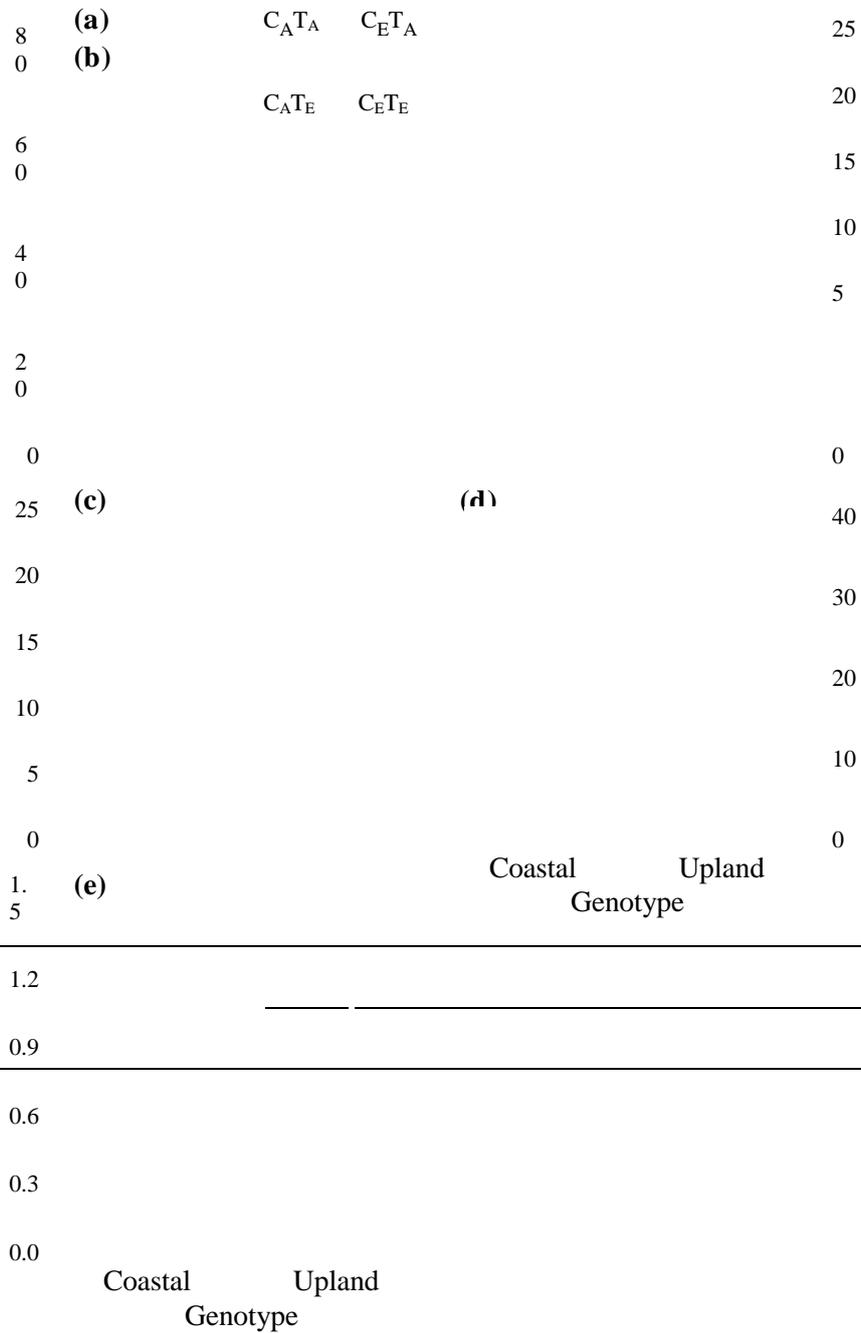


Figure Error! No text of specified style in document.-2 Plant dry mass allocation of *Telopea speciosissima* Coastal and Upland genotypes grown under the four [CO₂] and temperature treatments, including leaf mass fraction (a), stem mass fraction (b), tuber mass fraction (c), root mass fraction (d), and the Root/Shoot ratio (e). Values represent means ± 1 SE ($n = 10$).

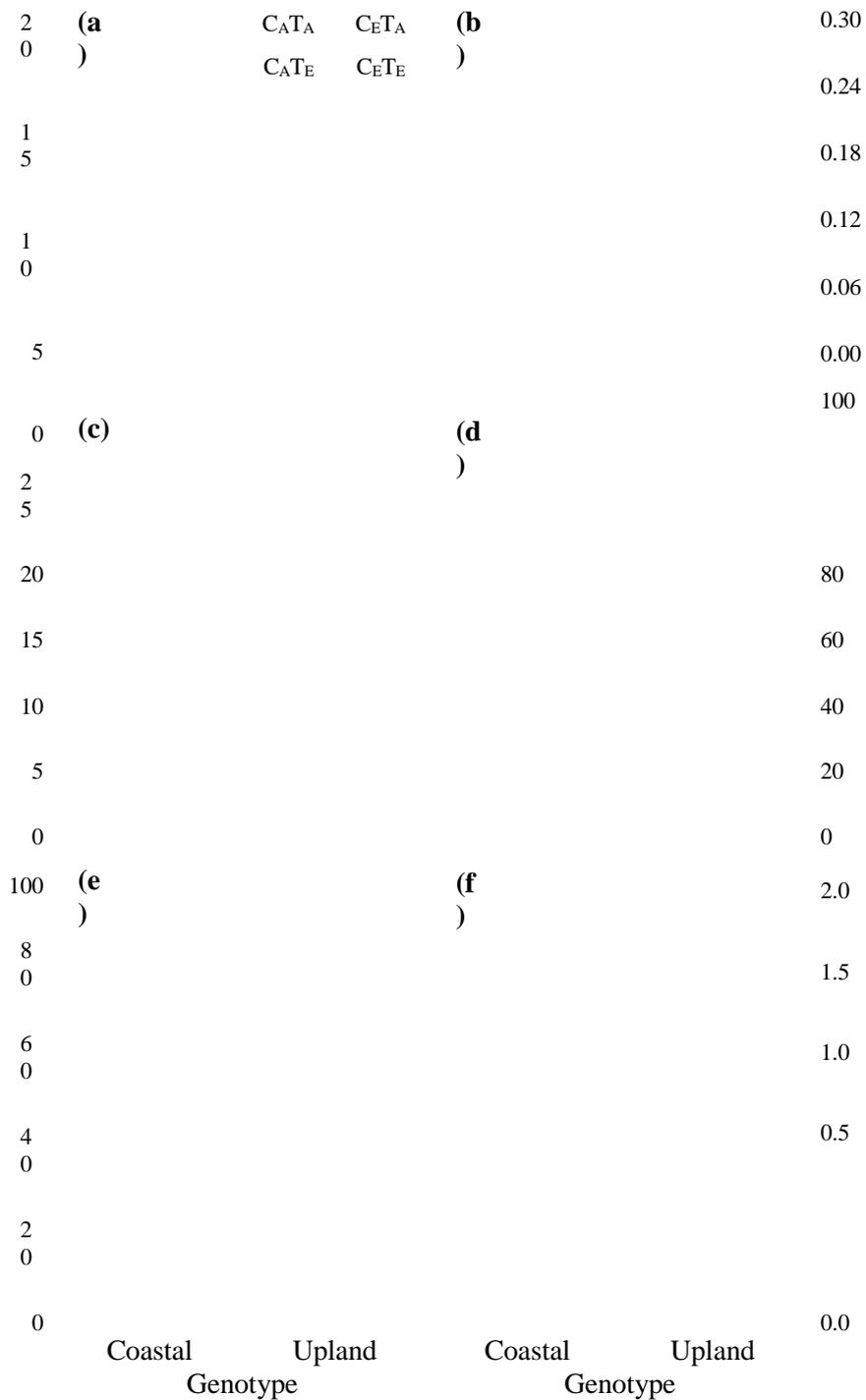
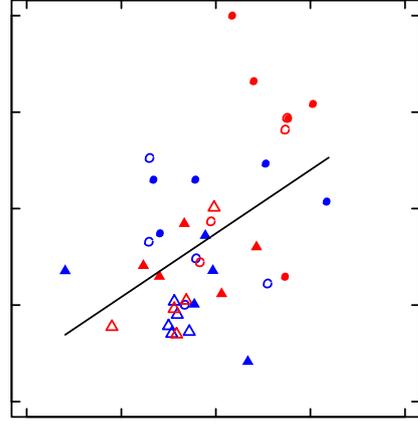
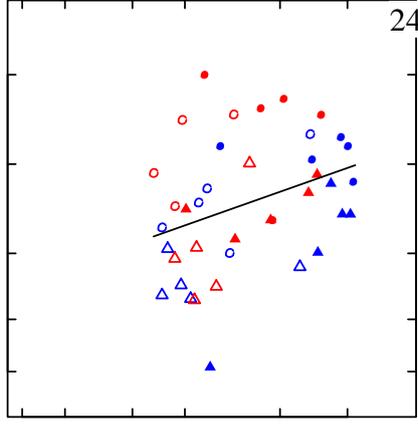
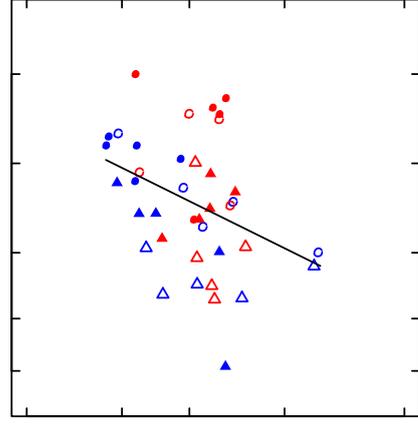
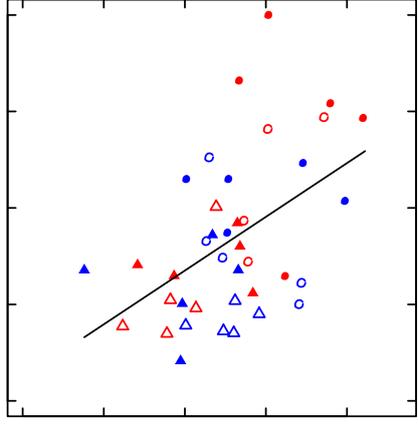


Figure Error! No text of specified style in document.-3 Light-saturated photosynthesis (A_{sat}) (a), stomatal conductance (g_s) (b), CO_2 - and light-saturated assimilation rates (A_{max}) (c), maximum rate of photosynthetic carboxylation (V_{cmax}) (d), maximum rate of photosynthetic electron transport (J_{max}) (e), and the J_{max}/V_{cmax} ratio (f) of *Telopea speciosissima* Coastal and Upland genotypes grown under the four $[CO_2]$ and temperature treatments. Values represent means \pm 1 SE ($n = 5$).

Whole-plant dry mass (g)



Whole-plant dry mass (g)



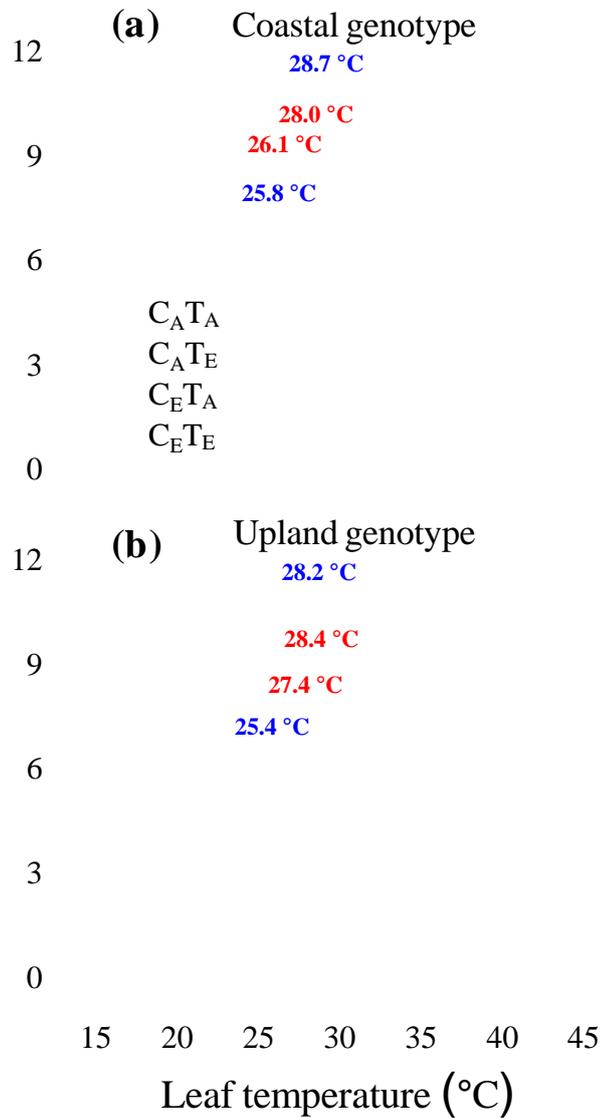


Figure Error! No text of specified style in document.-4 The simulated responses of CO_2 assimilation rates to leaf temperature (A/T_L) in *Telopea speciosissima* Coastal genotype (a) and Upland genotype (b) grown under the four $[\text{CO}_2]$ and temperature treatments: $C_A T_A$ (dashed blue), $C_A T_E$ (dashed red), $C_E T_A$ (solid blue), and $C_E T_E$ (solid red). Curves represent the output of the averaged polynomial fits ($A_{\text{sat}} = A \cdot T_L^2 + B \cdot T_L + C$, where T_L is leaf temperature and A, B and C are the fitted parameters shown in Table 2-3) from 4 seedlings for each genotype per treatment. Coloured triangles and texts around the top of simulated curves indicate the photosynthetic thermal optimums (T_{opt}) under different treatments.

Non-structural carbohydrates (NSC)

Concentrations of whole-plant starch (St), soluble sugars (Ss), and non-structural carbohydrates (NSC) all varied between genotypes, but only St and NSC were significantly influenced by growth [CO₂] and temperature (Fig. 2-5; Table 2-2 and 2-3). Across treatments, the Coastal genotype had *c.* 25% and 15% higher whole-plant St and Ss, respectively, resulting in 18% higher (on average) NSC compared with the Upland genotype. C_E stimulated whole-plant St by 35%, while T_E reduced whole-plant St by 52%. No significant [CO₂] or temperature effect was found on whole-plant Ss. Consequently, C_E increased whole-plant NSC by 14%, but T_E decreased whole-plant NSC by 13% (Fig. 2-5c).

Across [CO₂] and temperature treatments, the Coastal genotype had higher stem, tuber and root St, but similar leaf St when compared with the Upland genotype (Tables 2-2 and 2-4). Regardless of genotype, C_E stimulated leaf St by *c.* 65% but did not change St in other organs. T_E decreased leaf, stem and tuber St by 65%, 54% and 52%, respectively, without affecting root St. Averaged across treatments, the Coastal genotype had 25% higher leaf Ss and 10% higher root Ss, compared with the Upland genotype (Tables 2-2 and 2-4). C_E reduced stem Ss by 13%, but increased tuber and root Ss by 24% and 35%, respectively. T_E decreased root Ss for both genotypes, but reduced tuber Ss for the Upland genotype only (significant genotype × temperature interaction). For the Upland genotype, the positive effect of C_E on root Ss was offset by T_E (significant [CO₂] × temperature interaction), resulting in a significant genotype × [CO₂] × temperature interaction (Tables 2-2 and 2-4).

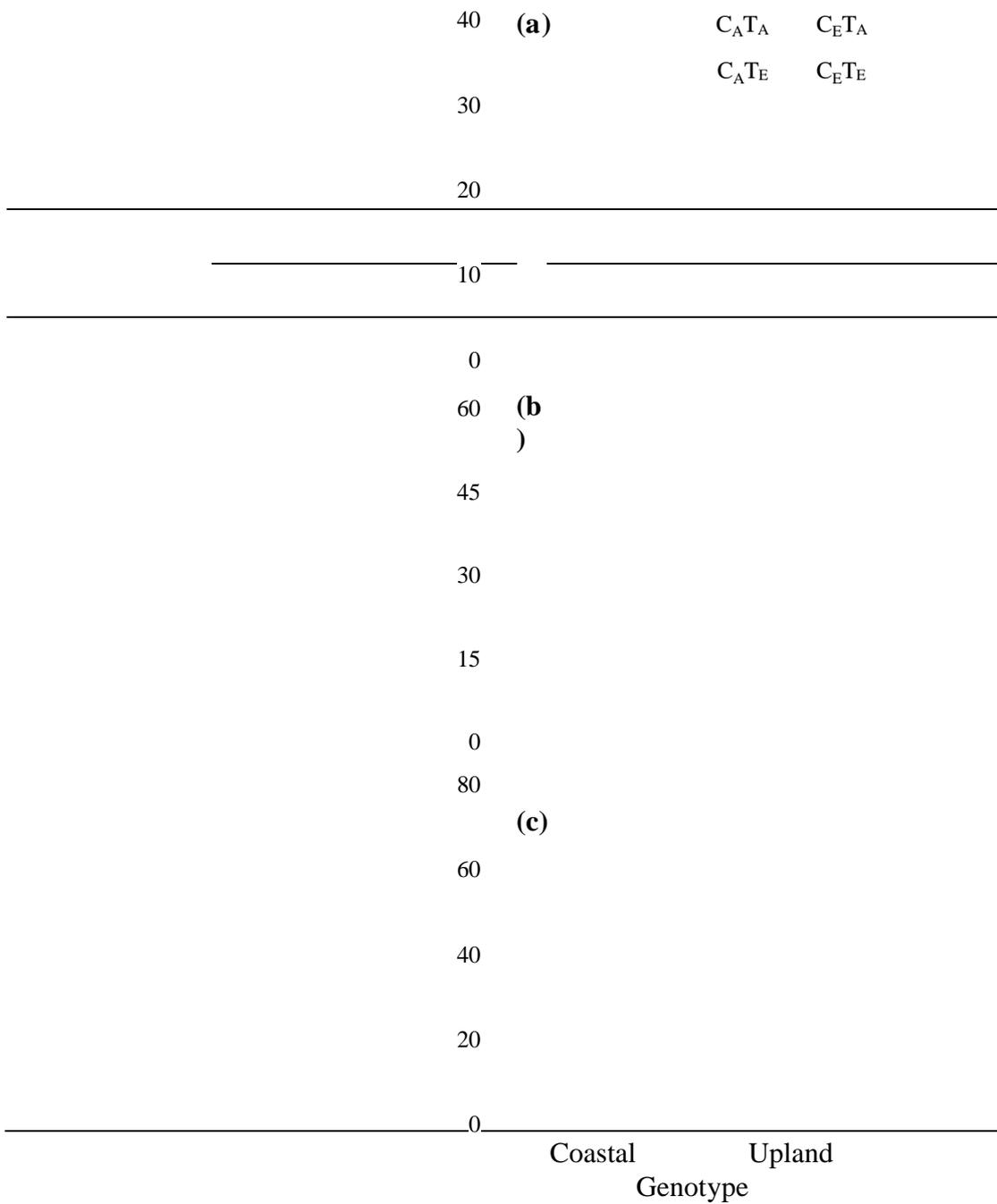
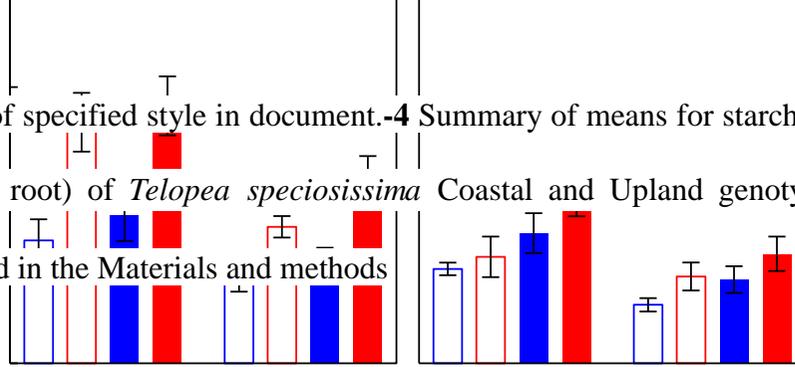


Figure Error! No text of specified style in document.-5 Whole-plant starch (a), soluble sugars (b), and non-structural carbohydrates (NSC) (c) of *Telopea speciosissima* Coastal and Upland genotypes grown under the four [CO₂] and temperature treatments. Values represent means \pm 1 SE ($n = 5$).

Table Error! No text of specified style in document.-4 Summary of means for starch and soluble sugar concentrations in different organs (leaf, stem, tuber and root) of *Telopea speciosissima* Coastal and Upland genotypes grown under the four [CO₂] and temperature treatments, as described in the Materials and methods



Parameter	Genotype	Treatment			
		$C_A T_A$	$C_A T_E$	$C_E T_A$	$C_E T_E$
<i>Starch</i>					
Leaf (mg g ⁻¹)	Coastal	19.4 ± 4.4 ^{abc}	9.2 ± 2.4 ^{cd}	41.0 ± 7.4 ^a	11.3 ± 0.6 ^{bcd}
	Upland	25.3 ± 7.6 ^{abc}	6.3 ± 0.8 ^d	30.8 ± 6.9 ^{ab}	12.4 ± 2.1 ^{bcd}
Stem (mg g ⁻¹)	Coastal	6.2 ± 1.2 ^a	2.6 ± 0.6 ^{abc}	6.5 ± 1.2 ^a	4.1 ± 1.5 ^{abc}
	Upland	4.3 ± 0.5 ^{ab}	2.0 ± 0.6 ^{bc}	3.7 ± 0.7 ^{abc}	1.3 ± 0.1 ^c
Tuber (mg g ⁻¹)	Coastal	16.8 ± 4.8 ^a	7.2 ± 2.6 ^{ab}	16.9 ± 5.7 ^a	5.3 ± 1.5 ^{ab}
	Upland	2.8 ± 0.5 ^{ab}	1.9 ± 0.7 ^b	6.3 ± 1.1 ^{ab}	3.1 ± 0.1 ^{ab}
Root (mg g ⁻¹)	Coastal	15.6 ± 6.4 ^a	17.1 ± 1.7 ^a	10.9 ± 3.3 ^a	15.9 ± 2.2 ^a
	Upland	7.3 ± 1.7 ^a	11.5 ± 2.2 ^a	10.8 ± 2.4 ^a	7.4 ± 1.1 ^a
<i>Soluble sugar</i>					
Leaf (mg g ⁻¹)	Coastal	61.6 ± 4.0 ^{ab}	65.9 ± 3.4 ^{ab}	63.5 ± 5.3 ^{ab}	70.7 ± 4.1 ^a
	Upland	57.9 ± 2.2 ^{ab}	48.1 ± 2.9 ^b	49.0 ± 4.8 ^b	54.4 ± 4.1 ^{ab}
Stem (mg g ⁻¹)	Coastal	22.8 ± 3.3 ^a	20.6 ± 1.7 ^a	15.8 ± 0.9 ^a	20.9 ± 1.3 ^a

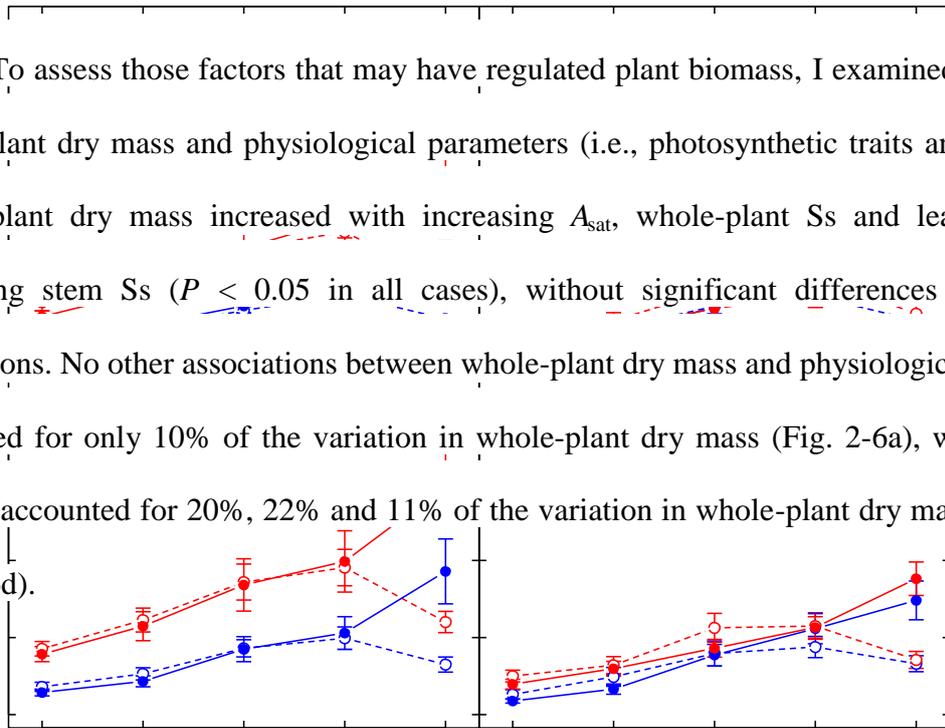
Table 2-4 (continued)

Parameter	Genotype	Treatment			
		$C_A T_A$	$C_A T_E$	$C_E T_A$	$C_E T_E$
Tuber (mg g ⁻¹)	Upland	22.8 ± 3.1 ^a	22.2 ± 0.9 ^a	18.8 ± 1.8 ^a	21.3 ± 1.1 ^a
	Coastal	24.0 ± 1.0 ^b	26.7 ± 1.2 ^{ab}	31.1 ± 1.6 ^{ab}	32.7 ± 2.1 ^{ab}
Root (mg g ⁻¹)	Upland	25.3 ± 1.8 ^{ab}	22.8 ± 1.8 ^b	35.5 ± 4.7 ^a	23.6 ± 3.0 ^b
	Coastal	16.8 ± 0.9 ^{abc}	13.6 ± 0.3 ^{bc}	20.0 ± 1.6 ^{ab}	17.3 ± 1.7 ^{abc}
	Upland	12.4 ± 0.8 ^c	12.7 ± 0.7 ^c	24.2 ± 3.8 ^a	12.5 ± 1.1 ^c

The four [CO₂] and temperature treatments are: $C_A T_A$ (400 μl l⁻¹, 26 °C), $C_A T_E$ (400 μl l⁻¹, 30 °C), $C_E T_A$ (640 μl l⁻¹, 26 °C) and $C_E T_E$ (640 μl l⁻¹, 30 °C). Values represent means ± 1 SE ($n = 5$). Within each parameter, different superscript letters indicate means that are significantly different at $P < 0.05$ based on Tukey's pair-wise comparisons.

Relationships between biomass and physiological parameters

To assess those factors that may have regulated plant biomass, I examined the relationships between whole-plant dry mass and physiological parameters (i.e., photosynthetic traits and carbohydrate variables). Whole-plant dry mass increased with increasing A_{sat} , whole-plant S_s and leaf S_s , but decreased with increasing stem S_s ($P < 0.05$ in all cases), without significant differences between within-treatment correlations. No other associations between whole-plant dry mass and physiological traits were observed. A_{sat} accounted for only 10% of the variation in whole-plant dry mass (Fig. 2-6a), while whole-plant, leaf and stem S_s accounted for 20%, 22% and 11% of the variation in whole-plant dry mass, respectively (Fig. 2-6b, 6c and 6d).



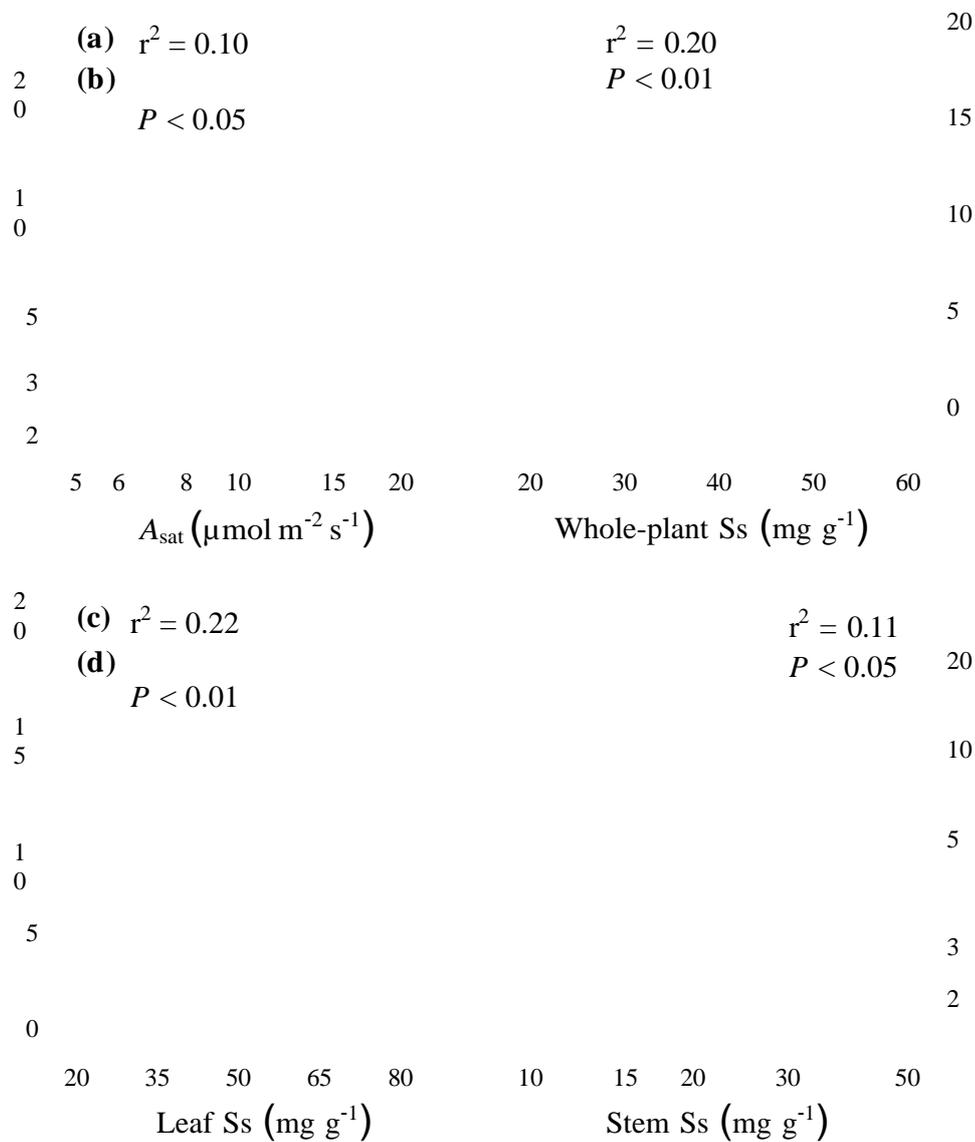
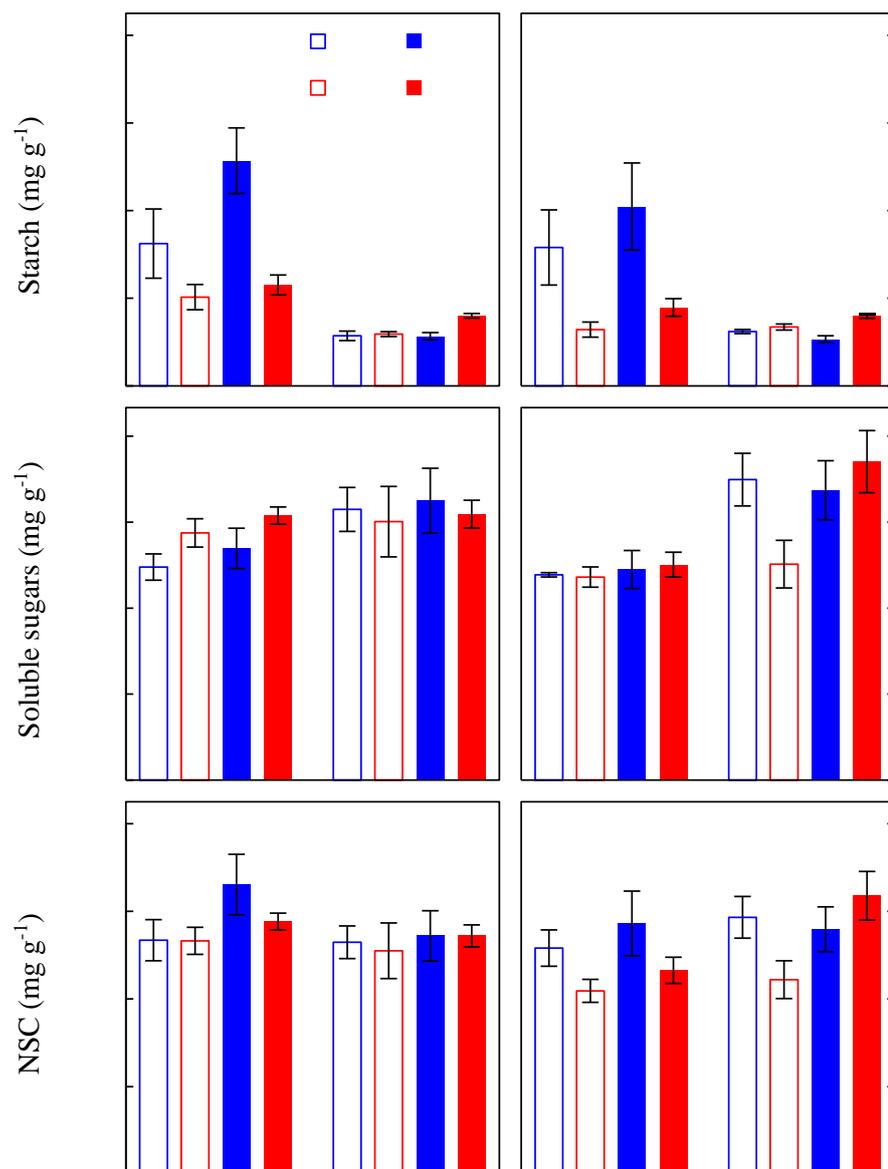


Figure **Error! No text of specified style in document.**-6 The relationships between whole-plant dry mass and A_{sat} (a), whole-plant soluble sugars (whole-plant Ss) (b), leaf soluble sugars (leaf Ss) (c) and stem soluble sugars (stem Ss) (d) of *Telopea speciosissima* Coastal (circles) and Upland (triangles) genotypes grown under the four [CO₂] and temperature treatments: C_AT_A (open blue), C_AT_E (open red), C_ET_A (closed blue) and C_ET_E (closed red). There were five replicates per treatment, and each data point represents a single observation. Data were fitted using a linear regression (solid line). Data points for A_{sat} and stem Ss were log-log transformed before fitting. The adjusted r² value and its significance for each fitting are shown



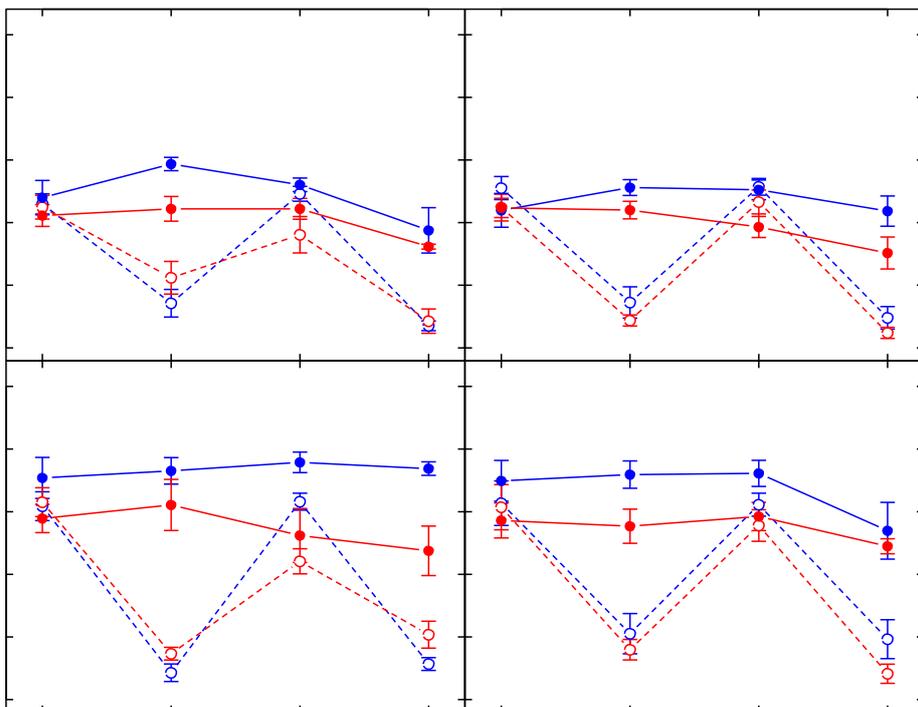
PART 2: Drought experiment

At the onset of the *first drought*, growth parameters (i.e., stem length, basal diameter, and stem volume) and physiological traits (i.e., A_{sat} and g_s) were all similar between seedlings assigned to the *well-watered* and *drought* treatments within each $[\text{CO}_2]$ and temperature treatment combination of each genotype ($P \geq 0.15$ in all cases), suggesting no bias in the initial allocation of seedlings to different watering treatments.

Plant growth

Across $[\text{CO}_2]$, temperature and watering treatments, the Coastal genotype had higher whole-plant dry mass and leaf area than the Upland genotype (Fig. 3-1; Table 3-1). Regardless of watering treatment, C_E had positive effects on growth performance for both genotypes, while the positive growth response to T_E was only found in the Coastal genotype (significant genotype \times temperature interaction; Table 3-1). The *drought* treatment, on the other hand, negatively affected dry mass accumulation and leaf growth in both genotypes, causing a reduction of 15–39% in whole-plant dry mass and an 18–43% decline in leaf area, respectively. However, declines induced by *drought* did not vary between genotypes or show significant difference among $[\text{CO}_2]$ and temperature treatment combinations, indicating no interaction between *drought* and other treatments (Fig. 3-1; Table 3-1).

Stem volume in both genotypes had a similar pattern with plant dry mass in the response to experimental treatments, showing substantial increase under C_E but significant decline in the *drought*, as well as differentiated responses to T_E (Fig. 3-2; Table 3-2). Although a significant decrease in stem volume was found in *drought* seedlings (averaged across the five stages; $P = 0.015$) in relative to their *well-watered* counterparts, the effect of *drought* on stem volume was not significant until the *final harvest* (Fig. 3-2). For the other four stages (i.e., the *pre drought*, *first drought*, *recovery*, and *second drought*), there was no significant difference in stem volume between the two watering treatments. Changes in stem volume

$A_{\text{sat}} (\mu\text{mol m}^{-2} \text{s}^{-1})$ 

induced by *drought* at the *final harvest* were mainly attributed to declines in the main stem basal diameter,

but not due to changes in the main stem length (Fig. A-1 and A-2; Table 3-2).

g_s ($\text{mol m}^{-2} \text{s}^{-1}$)

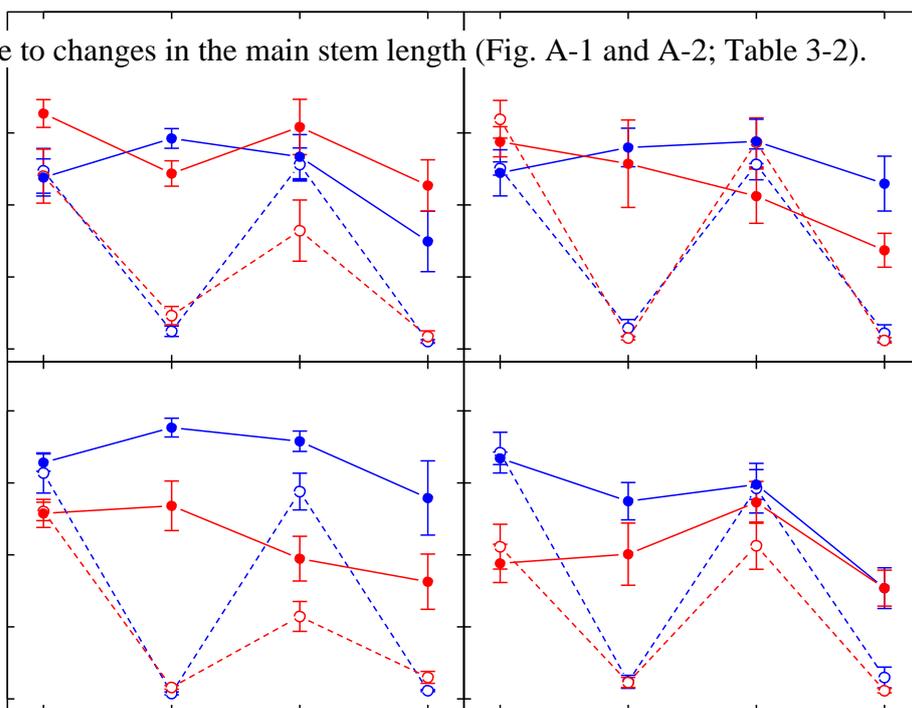


Table Error! No text of specified style in document.-5 Summary (*P* values) of four-way ANOVAs testing for the main and interactive effects of [CO₂] (C), temperature (T) and watering (W) treatments on growth and carbohydrate parameters of two *Telopea speciosissima* genotypes (G)

Effect	Growth		Carbohydrates		
	Dry mass	Leaf area	St	Ss	NSC
G	< 0.001	< 0.001	0.068	0.404	0.196
C	< 0.001	< 0.001	0.005	0.059	0.013
T	0.012	< 0.001	0.001	0.850	0.048
W	< 0.001	< 0.001	< 0.001	< 0.001	0.667
G × C	0.662	0.383	0.535	0.527	0.837
G × T	0.009	0.005	0.608	0.276	0.400
C × T	0.558	0.975	0.557	0.163	0.422
G × W	0.503	0.785	0.018	0.049	0.026
C × W	0.561	0.984	0.087	0.549	0.761
T × W	0.497	0.970	< 0.001	0.081	0.280
G × C × T	0.554	0.694	0.380	0.160	0.158
G × C × W	0.493	0.457	0.719	0.274	0.318
G × T × W	0.442	0.344	0.450	0.694	0.731
C × T × W	0.513	0.636	0.083	0.208	0.085
G × C × T × W	0.696	0.340	0.435	0.223	0.513

St, starch; Ss, soluble sugars; NSC, non-structural carbohydrates. Significant values ($P < 0.05$) are shown in bold. Analyses were run on data obtained from harvest samples, with ten replicates ($n = 10$) for growth and five replicates ($n = 5$) for carbohydrates.

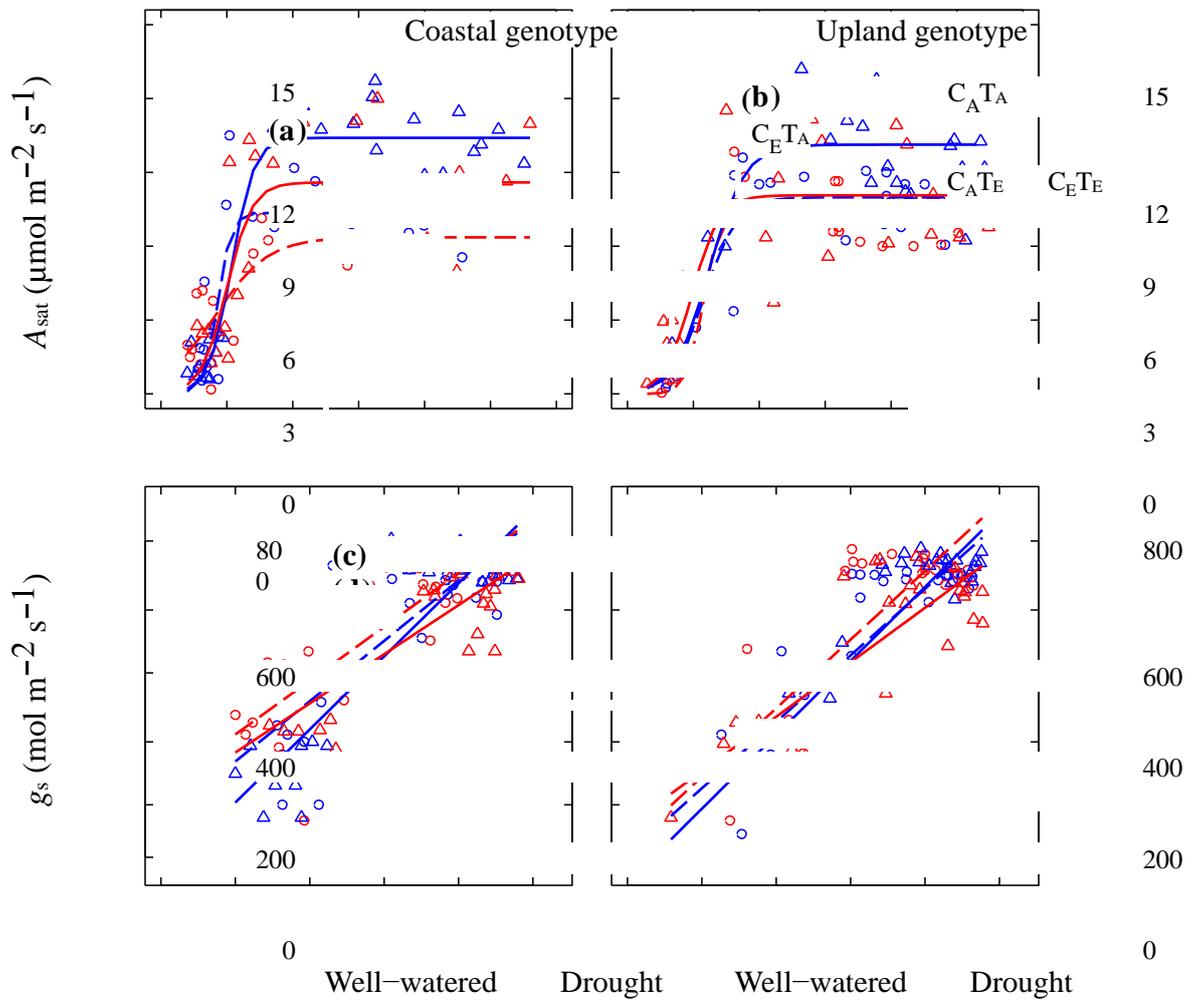


Figure Error! No text of specified style in document.-7 Whole-plant dry mass (a and b) and leaf area (c and d) of *Telopea speciosissima* Coastal (the left panel) and Upland (the right panel) genotypes in *well-watered* and *drought* conditions exposed to four $[\text{CO}_2]$ and temperature treatment combinations: $C_A T_A$ ($400 \mu\text{l l}^{-1}$, 26°C ; open blue), $C_A T_E$ ($400 \mu\text{l l}^{-1}$, 30°C ; open red), $C_E T_A$ ($640 \mu\text{l l}^{-1}$, 26°C ; closed blue), and $C_E T_E$ ($640 \mu\text{l l}^{-1}$, 30°C ; closed red). Values represent means ± 1 SE ($n = 10$).

Table Error! No text of specified style in document.-6 Summary (*P* values) of four-way repeated measures ANOVAs testing for the main and interactive effects of [CO₂] (C), temperature (T) and watering (W) treatments on growth and gas exchange parameters of two *Telopea speciosissima* genotypes (G)

Effect	Growth			Gas exchange	
	Length	Diameter	Volume	<i>A</i> _{sat}	<i>g</i> _s
G	< 0.001	0.179	< 0.001	0.765	0.558
C	0.002	0.002	< 0.001	< 0.001	0.732
T	< 0.001	0.045	< 0.001	< 0.001	< 0.001
W	0.821	0.030	0.015	< 0.001	< 0.001
G × C	0.419	0.756	0.804	0.950	0.300
G × T	< 0.001	0.021	< 0.001	0.823	0.938
C × T	0.599	0.472	0.369	0.292	< 0.001
G × W	0.959	0.348	0.268	0.264	0.013
C × W	0.876	0.845	0.663	0.003	0.687
T × W	0.484	0.475	0.884	0.014	0.376
G × C × T	0.091	0.844	0.938	0.714	0.251
G × C × W	0.724	0.665	0.855	0.597	0.612
G × T × W	0.769	0.976	0.519	0.224	0.486
C × T × W	0.771	0.139	0.680	0.300	0.353
G × C × T × W	0.458	0.780	0.894	0.592	0.056

*A*_{sat}, light-saturated photosynthesis; *g*_s, stomatal conductance. Significant values (*P* < 0.05) are shown in bold. Analyses were run on data obtained during the experiment (multiple measurements), with ten replicates (*n* = 10) for growth parameters and five replicates (*n* = 5) for gas exchange traits.

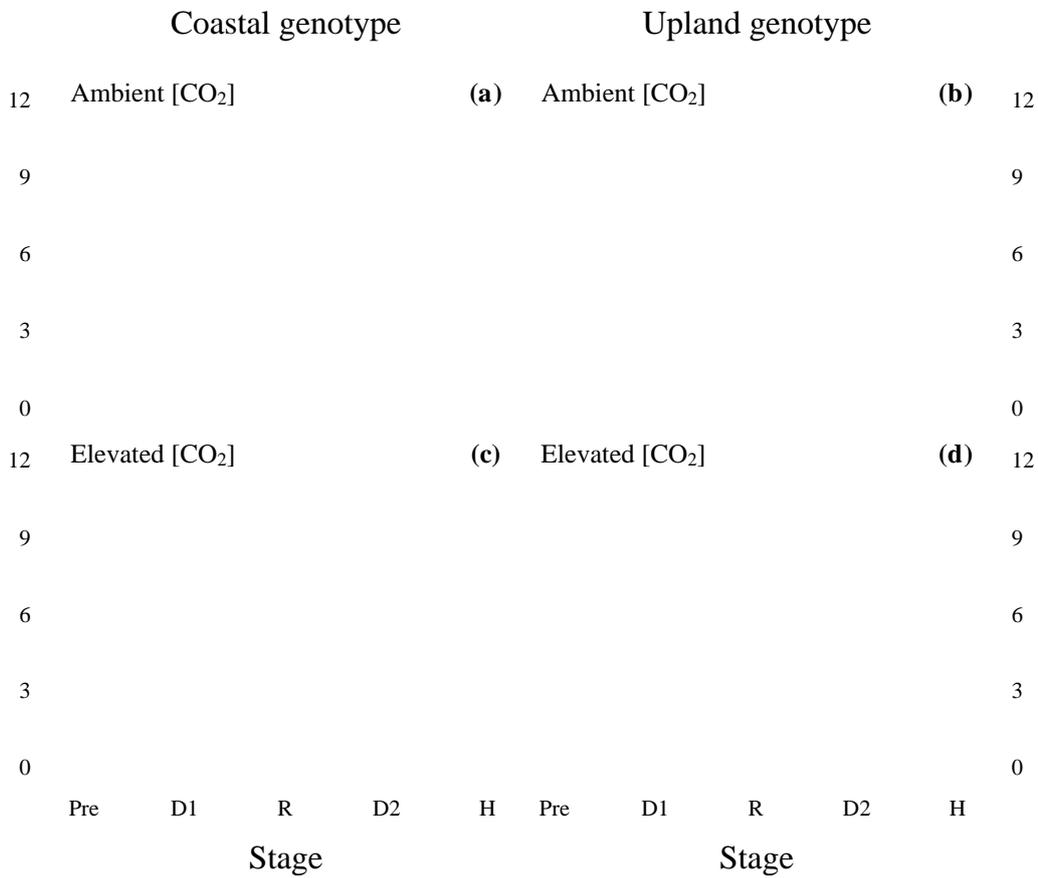
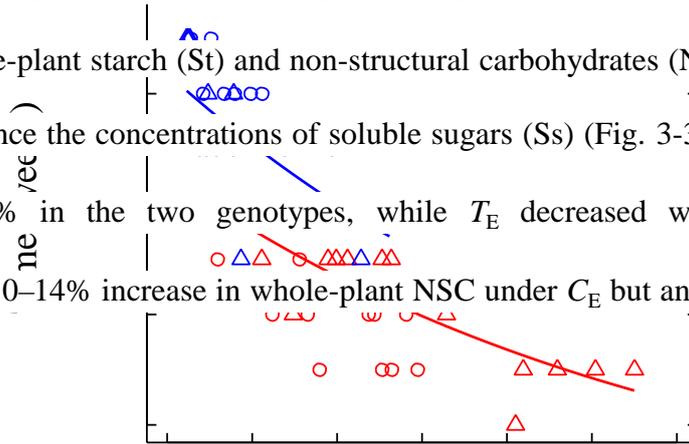


Figure Error! No text of specified style in document.-8 Progression of stem volume in *Telopea speciosissima* Coastal (the left panel) and Upland (the right panel) genotypes in *well-watered* (closed symbols) and *drought* (open symbols) conditions subjected to *ambient* (T_A ; blue) and *elevated* (T_E ; red) temperatures and *ambient* (C_A ; the top panel) and *elevated* (C_E ; the bottom panel) [CO₂] during the experimental stages: *pre drought* (Stage Pre), *first drought* (Stage D1), *recovery* (Stage R), *second drought* (Stage D2), and *final harvest* (Stage H). Values represent means \pm 1 SE ($n = 10$).

Non-structural carbohydrates

Regardless of watering treatment, both $[\text{CO}_2]$ and temperature treatments had significant effects on the concentrations of whole-plant starch (St) and non-structural carbohydrates (NSC) in both genotypes, but did not significantly influence the concentrations of soluble sugars (Ss) (Fig. 3-3; Table 3-1). C_E stimulated whole-plant St by 22–32% in the two genotypes, while T_E decreased whole-plant St by 33–37%, consequently leading to a 10–14% increase in whole-plant NSC under C_E but an 8% (on average) decline in whole-plant NSC under T_E .



The *drought* treatment had contrasting effects on whole-plant St and Ss, and the effect size on each parameter varied between genotypes (significant genotype \times watering interactions) (Fig. 3-3; Table 3-1). Averaged across genotypes, $[\text{CO}_2]$ and temperature treatments, *drought* seedlings decreased whole-plant St by 56% but increased whole-plant Ss by 23%, when compared with *well-watered* seedlings. The negative effect of *drought* on whole-plant St was larger in the Coastal genotype (-61%) than in the Upland genotype (-49%). In contrast, the Coastal genotype showed a smaller increase (+12%) in whole-plant Ss under *drought* conditions, when compared with the increase in the Upland genotype (+35%). As a consequence of the opposite effects and the different effect sizes of *drought* on St and Ss, the *drought* treatment diminished the difference in whole-plant NSC between genotypes (significant genotype \times watering interaction; Table 3-1). In addition, for both genotypes, the negative effect of *drought* on whole-plant St differed between temperature treatments (significant temperature \times watering interaction; Fig. 3-3; Table 3-1). Averaged across genotypes and $[\text{CO}_2]$ treatments, a larger decline in whole-plant St induced by *drought* was observed in T_A (-71%), when compared with the decrease in T_E (-22%).

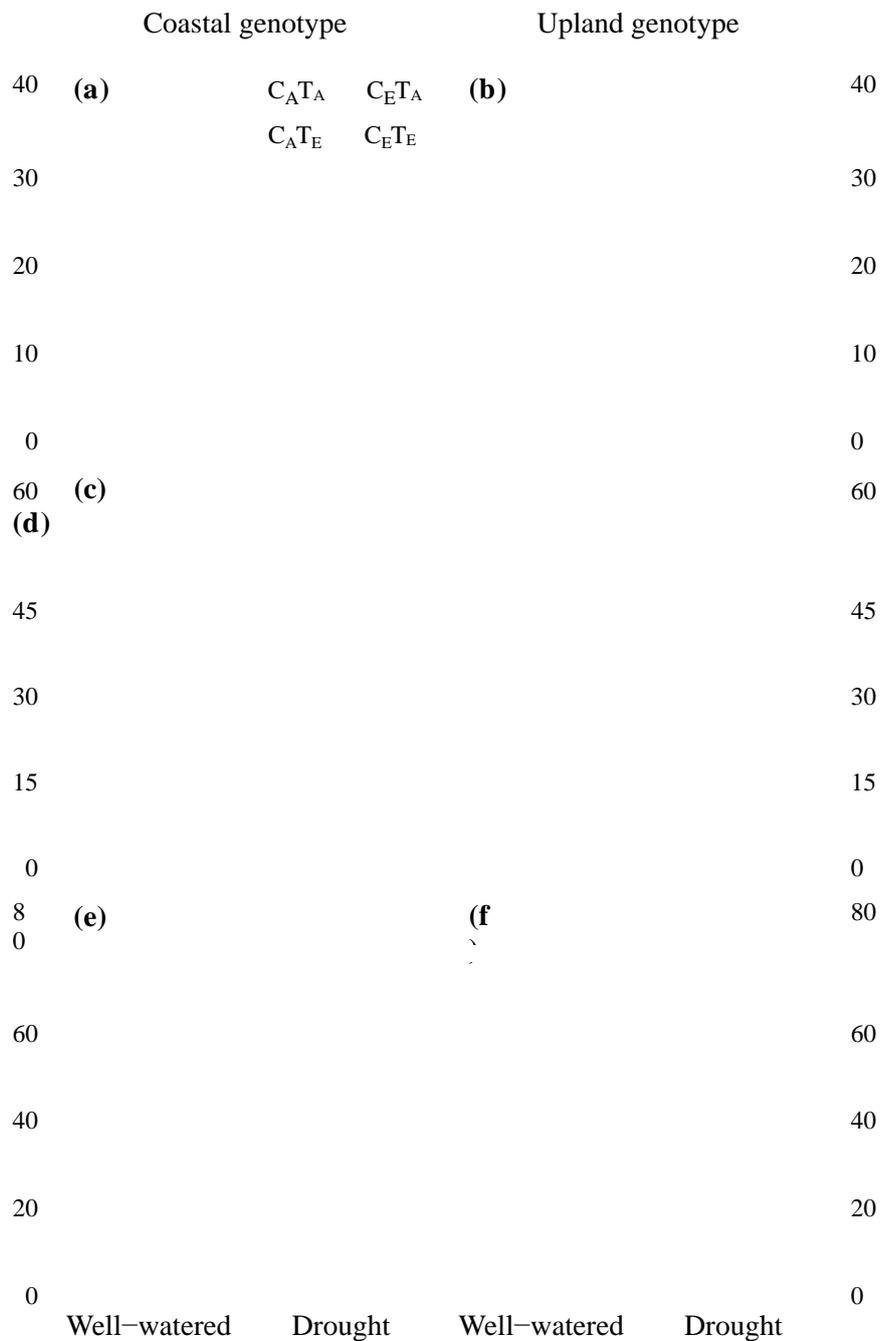


Figure Error! No text of specified style in document.-9 Whole-plant starch (a and b), soluble sugars (c and d), and non-structural carbohydrates (NSC) (e and f) of *Telopea speciosissima* Coastal and Upland genotypes in *well-watered* and *drought* conditions exposed to four [CO₂] and temperature treatment combinations. Values represent means ± 1 SE (*n* = 5). Other details are as described for Fig. 3-1.

Leaf gas exchange

During the experimental period, both photosynthetic rates (A_{sat}) and stomatal conductance (g_s) did not differ between the two genotypes, but were significantly affected by temperature or watering treatments (Fig. 3-4 and 3-5; Table 3-2). C_E stimulated A_{sat} of both genotypes, but the magnitudes of stimulation varied between watering treatments. Averaged across stages, genotypes and temperature treatments, a larger increase of A_{sat} under C_E was found in *well-watered* seedlings (+40%) when compared with *drought* seedlings (+28%), suggesting a significant genotype \times watering interaction. In contrast, T_E overall tended to decrease A_{sat} of both genotypes at both $[\text{CO}_2]$ treatments, but the negative effect was only significant for the *well-watered* treatment (significant temperature \times watering interaction), leading to an average 17% decline in A_{sat} of *well-watered* seedlings (Fig. 3-4). The *drought* treatment substantially decreased A_{sat} and g_s for both genotypes (Fig. 3-4 and 3-5; Table 3-2). The decline of g_s under *drought* was larger in the Coastal genotype (-52%; averaged across stages, $[\text{CO}_2]$ and temperature treatments) than in the Upland genotype (-39%), indicating a significant genotype \times watering interaction. In addition, the decline in g_s induced by T_E was only significant under C_E (-31% on average across stages, genotypes and watering treatments; Fig. 3-5; Table 3-2).

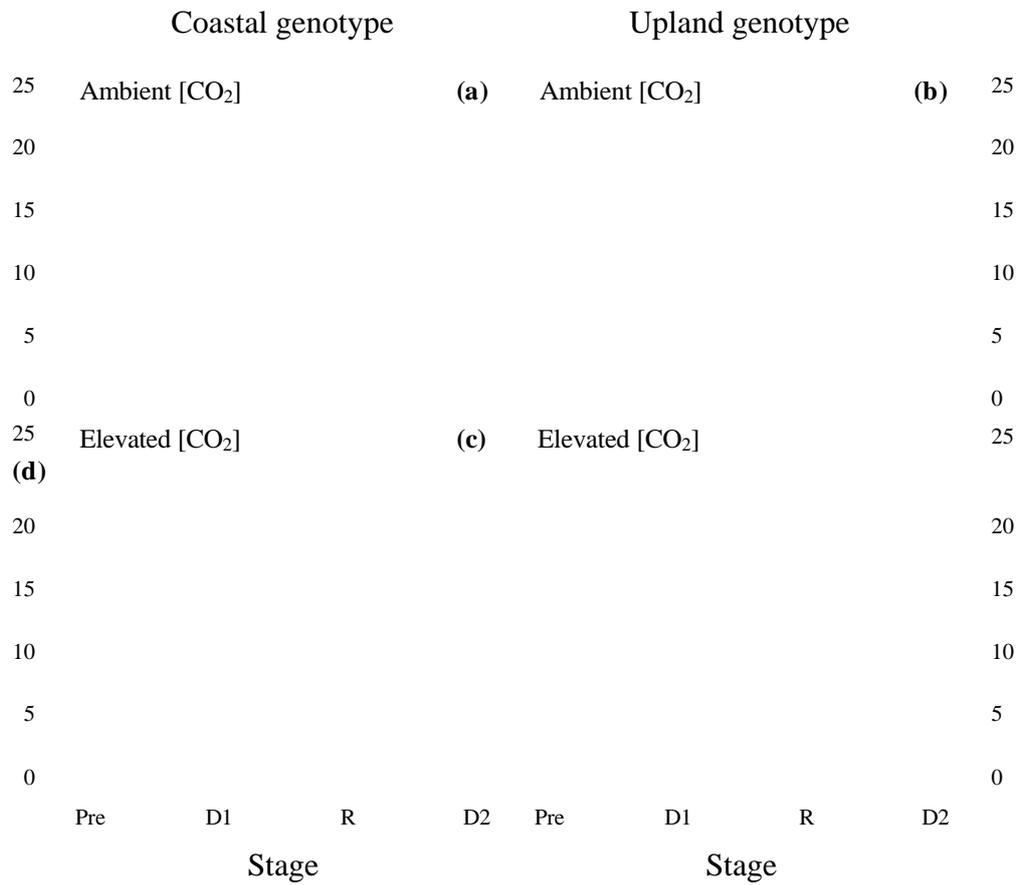


Figure Error! No text of specified style in document.-10 Progression of light-saturated photosynthesis (A_{sat}) in *Telopea speciosissima* Coastal (the left panel) and Upland (the right panel) genotypes in *well-watered* (closed symbols) and *drought* (open symbols) conditions subjected to *ambient* (T_A ; blue) and *elevated* (T_E ; red) temperatures and *ambient* (C_A ; the top panel) and *elevated* (C_E ; the bottom panel) [CO₂] during the four experimental stages: *pre drought* (Stage Pre), *first drought* (Stage D1), *recovery* (Stage R). Values represent means \pm 1 SE ($n = 5$).

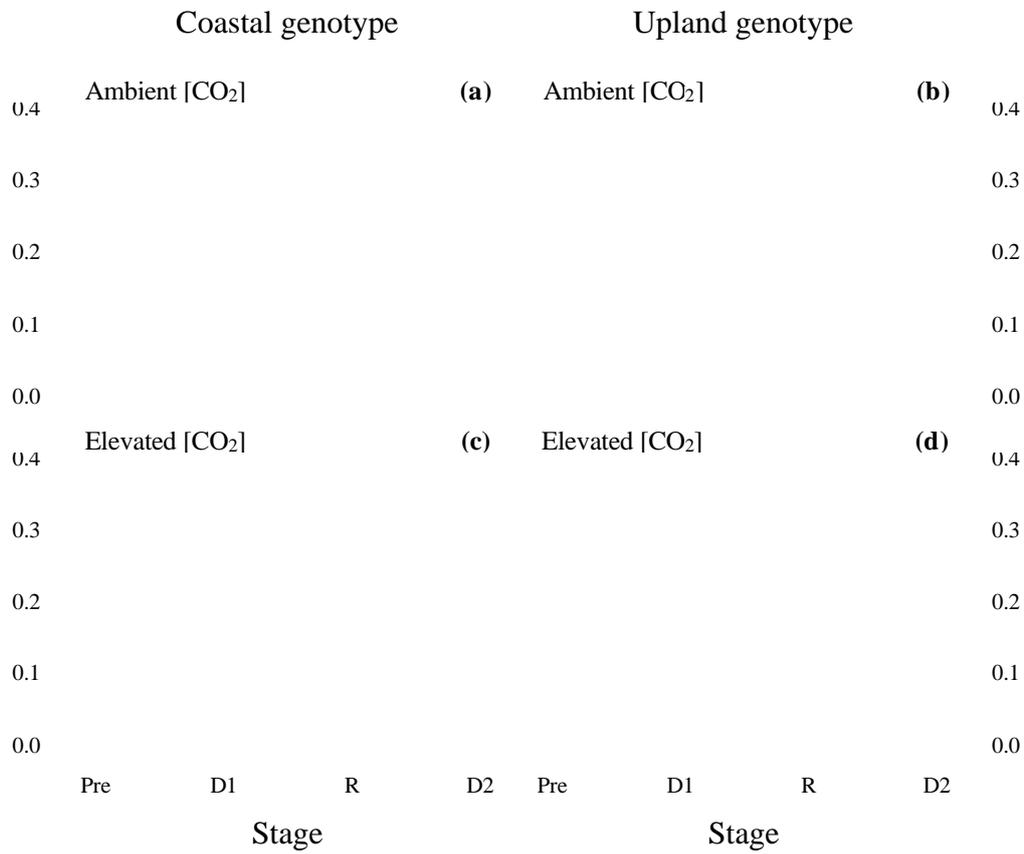


Figure Error! No text of specified style in document.-11 Progression of stomatal conductance (g_s) in *Telopea speciosissima* Coastal and Upland genotypes in *well-watered* and *drought* conditions subjected to four [CO₂] and temperature treatment combinations during the four experimental stages. Values represent means \pm 1 SE ($n = 5$). Other details are as described for Fig. 3-4.

The relationships between A_{sat} and soil VWC were fitted with three-parameter sigmoid functions. Overall, no significant difference between the two genotypes was found in any of the three fitted parameters at any $[\text{CO}_2]$ and temperature treatment combination, suggesting no intraspecific variation in the sensitivity of A_{sat} to declines in soil water content (Fig. 3-6; Table 3-3). Regardless of temperature treatment, when soil water was not limiting, the estimated asymptote for A_{sat} was higher under C_E than C_A by 36% in the Coastal genotype and by 20% in the Upland genotype, respectively. However, the estimated asymptote for A_{sat} did not differ between temperature treatments for both genotypes (Fig. 3-6a and 6b; Table 3-3). As drought stress intensified (i.e., soil water content decreased), A_{sat} of both genotypes converged among the four $[\text{CO}_2]$ and temperature treatment combinations, thereby promoting 50% loss of A_{sat} at similar soil water content across $[\text{CO}_2]$ and temperature treatments. In other words, the inflection point (VWC_{mid}) of each sigmoid regression did not differ among $[\text{CO}_2]$ and temperature treatments for both genotypes (Fig. 3-6a and 6b; Table 3-3). The relationships between g_s and soil VWC were assessed by linear regressions (on log-log scales). The linear fitting parameters did not differ between genotypes or among $[\text{CO}_2]$ and temperature treatments, suggesting that there was no intraspecific variation in the sensitivity of g_s to declines in soil water content, and that the sensitivity was not affected by either $[\text{CO}_2]$ or temperature (Fig. 3-6c and 6d; Table 3-4).

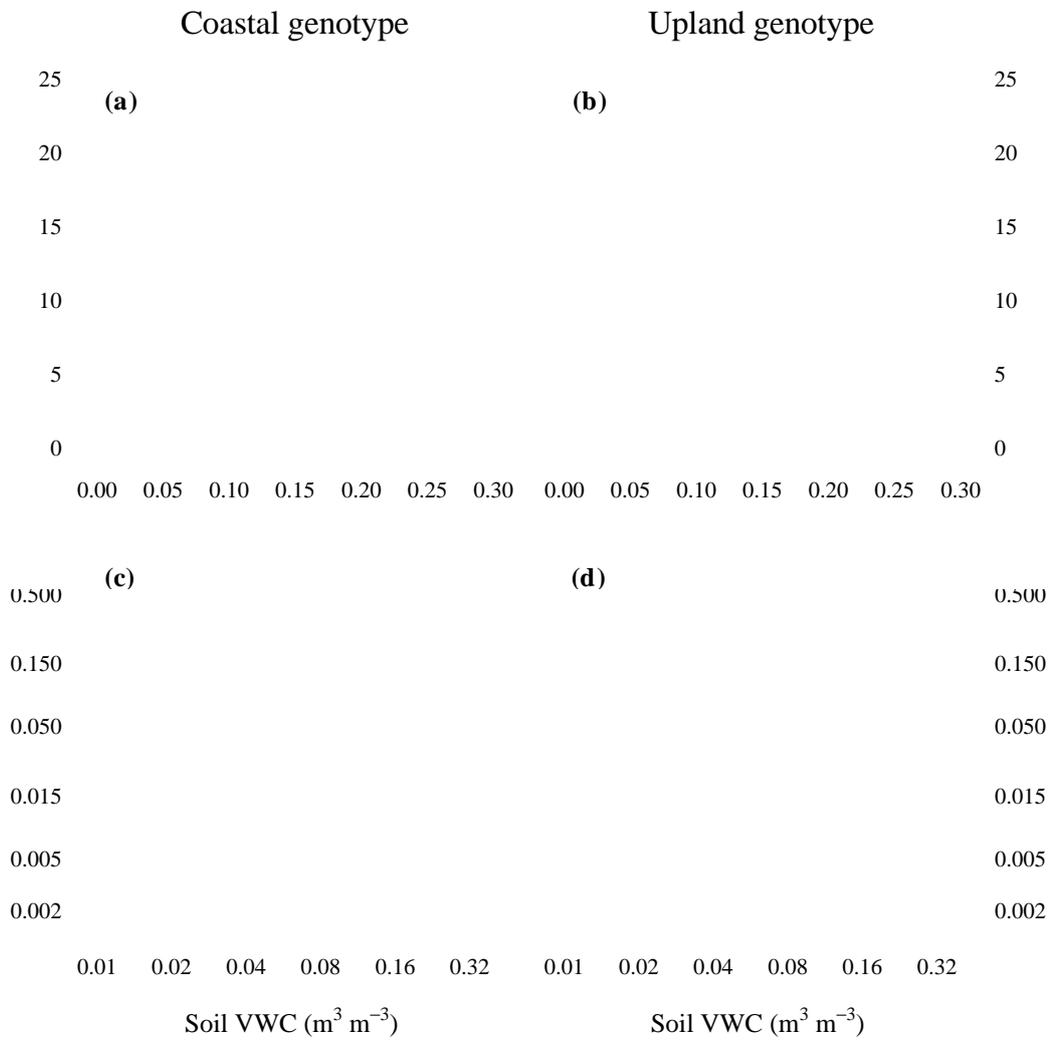


Figure Error! No text of specified style in document.-12 Light-saturated photosynthesis (A_{sat} ; a and b) and stomatal conductance (g_s ; c and d) of *Telopea speciosissima* Coastal and Upland genotypes in the *drought* treatment as a function of soil VWC exposed to *ambient* (T_A ; blue) and *elevated* (T_E ; red) temperatures and *ambient* (C_A ; circles) and *elevated* (C_E ; triangles) [CO_2]. Data are fitted for each of the four [CO_2] and temperature treatment combinations: $C_A T_A$ (the blue dash line), $C_A T_E$ (the red dash line), $C_E T_A$ (the blue solid line), and $C_E T_E$ (the red solid line). Data for A_{sat} are fitted with a three-parameter sigmoid regression, and data for g_s are fitted with a linear regression on log-log scales. Fit parameters are shown in Table 3-3 and Table 3-4, respectively.

Table Error! No text of specified style in document.-7 Summary of parameters in the fitted sigmoid regressions between light-saturated photosynthesis (A_{sat}) and soil VWC of *Telopea speciosissima* Coastal and Upland genotypes grown under the four [CO₂] and temperature treatments

Genotype	Treatment	R ²	y_{asym}		k		VWC _{mid}	
			Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Coastal 13.589	$C_A T_A$	0.768	12.254b	10.919,	189.748	46.822, 332.673	0.043	0.038, 0.048
					49.938	-4.310, 104.187	0.041	0.021, 0.062
	$C_A T_E$	0.610	10.598b	7.977, 13.220	117.169	-2.738, 237.077	0.054	0.040, 0.067
	$C_E T_A$	0.921	17.340a	16.283, 18.396	104.177	16.884, 191.469	0.050	0.042, 0.058
	$\hat{C} \hat{T}$ 16.103	0.830	13.315b	12.152, 14.479		34.022, 127.606	0.059	
Upland	$A A$				80.814			0.048, 0.069
	$C_A T_E$	0.854	12.225b	10.730, 13.721	165.537	-122.958, 454.032	0.057	0.042, 0.073
	$C_E T_A$	0.817	16.877a	15.521, 18.233	74.611	26.040, 123.182	0.062	0.052, 0.072
	$C_E T_E$	0.683	13.444b	11.672,	96.327	-45.675, 238.330	0.049	0.029, 0.069
	15.215							

The four [CO₂] and temperature treatments are: $C_A T_A$ (400 $\mu\text{l l}^{-1}$, 26 °C), $C_A T_E$ (400 $\mu\text{l l}^{-1}$, 30 °C), $C_E T_A$ (640 $\mu\text{l l}^{-1}$, 26 °C) and $C_E T_E$ (640 $\mu\text{l l}^{-1}$, 30 °C). The three-parameter sigmoid regressions were fitted as: $y = y_{\text{asym}} / (1 + e^{-(\text{VWC} - \text{VWC}_{\text{mid}}) / k})$, where y_{asym} is the estimated asymptote for each regression, VWC_{mid} is the inflection point of soil VWC (where $y = y_{\text{asym}} / 2$) and k is a scaling parameter. Adjusted R² values ($P < 0.001$ in all cases) indicate the goodness-of-fit for regressions. Different letters indicate a significant difference among [CO₂] and temperature treatments for each parameter of each genotype based on the 95% confidence interval (i.e., 95% CI).

Table Error! No text of specified style in document.-8 Summary of parameters in the fitted linear regressions between stomatal conductance (g_s) and soil VWC of *Telopea speciosissima* Coastal and Upland genotypes grown under the four [CO₂] and temperature treatments

Genotype	Treatment	R ²	m			
			Estimate	95% CI		
Coastal 1.134	$C_A T_A$	0.600	0.609	0.084,	1.520	1.052, 1.988
	$C_A T_E$	0.548	0.536	-0.255, 1.327	1.356	0.738, 1.974
	$C_E T_A$	0.797	0.846	0.463, 1.778	1.842	1.485, 2.199
	$C_E T_E$	0.759	0.669	0.297, 1.041	1.238	0.826, 1.650
		0.560	0.199	-0.237,	1.675	
Upland	$C_A T_A$					1.318, 2.032
	$C_A T_E$	0.687	0.848	0.289, 1.407	1.729	1.229, 2.230
	$C_E T_A$	0.833	0.833	-1 0.524, 1.141	-1 1.862	1.547, 2.178
	$C_E T_E$	0.734	0.284	-0.060,	1.372	1.059, 1.684
		0.628				

The four [CO₂] and temperature treatments are: $C_A T_A$ (400 μl l⁻¹, 26 °C), $C_A T_E$ (400 μl l⁻¹, 30 °C), $C_E T_A$ (640 μl l⁻¹, 26 °C) and $C_E T_E$ (640 μl l⁻¹, 30 °C). Linear regressions were fitted on log-log scales: $\log_{10}(y) = y_0 + m \times \log_{10}(\text{VWC})$, where y_0 and m are the intercept and slope for each regression, respectively. Adjusted R² values ($P < 0.001$ in all cases) indicate the goodness-of-fit for regressions. 95% CI stands for the 95% confidence interval.

Resistance to drought

The capacity of *T. speciosissima* seedlings in resisting drought stress declined with plant size (i.e., the covariate; stem volume in this case), and there was a significant effect of temperature treatment on the capacity after removing the variance accounted for by the plant size (Fig. 3-7). Compared with T_A , increase in temperature negatively affected the capacity of seedling resistance to drought, leading to a quicker closure of stomata as drought progressed. At any common plant size, T_E accelerated the rates of g_s decline under *drought*, advancing the time for *drought* seedlings to become physiologically stressed by 1.5 weeks on average (Fig. 3-7). Apart from the temperature effect, the capacity of seedling resistance to drought did not vary between genotypes or [CO₂] treatments, or among the treatment combinations.

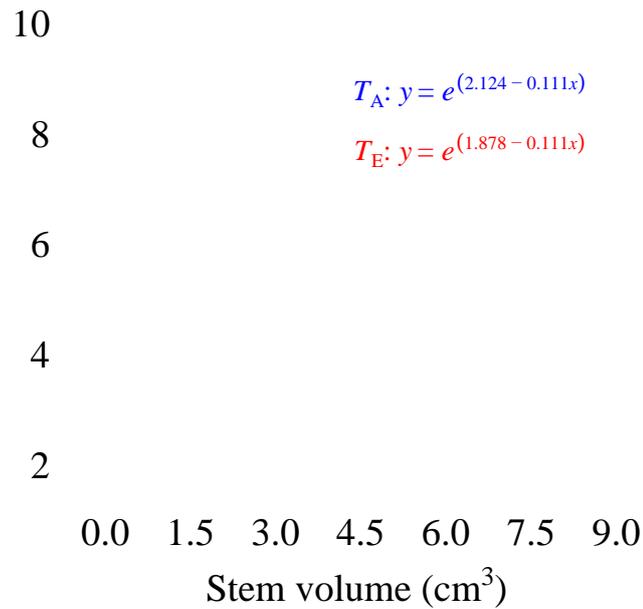


Figure Error! No text of specified style in document.-13 Drought resistance (time for a seedling becoming physiologically stressed) versus plant size (stem volume) of drought-treated *Telopea speciosissima* exposed to *ambient* (T_A ; blue) and *elevated* (T_E ; red) temperatures and *ambient* (C_A ; circles) and *elevated* (C_E ; triangles) [CO₂]. Data are fitted with exponential regressions based on a generalized linear model ($P < 0.001$, $R^2 = 0.927$). Fittings for temperature treatments are shown in the plot.

Discussion

Intraspecific variation in woody plant responses to warming and elevated [CO₂]

Significant intraspecific variation in growth plasticity between the two *T. speciosissima* genotypes was observed when responding to warming, with the Coastal genotype exhibiting greater increments in growth traits such as whole-plant dry mass, leaf area and SMF, compared to the Upland genotype. The differentiation between genotypes in growth response to warming reported here is consistent with the general prediction that plant populations may exhibit genetic variation in phenotypic plasticity (Donohue *et al.*, 2001; Alpert & Simms, 2002; Van Kleunen & Fischer, 2005; Aspinwall *et al.*, 2015). It has been

suggested that there is predictable intraspecific variation in the capacity of woody species to respond to T_E (Saxe *et al.*, 2001; Weston & Bauerle, 2007; Weston *et al.*, 2007; Way & Oren, 2010; Drake *et al.*, 2015). For example, Drake *et al.* (2015) studied 21 provenances of two widely distributed eucalyptus species (*Eucalyptus tereticornis* and *Eucalyptus grandis*) grown in conditions simulating ambient summer temperatures at seed origin and warmed temperatures (+ 3.5 °C), and found that the effect of warming on plant biomass and leaf area strongly interacted with the provenance's climate-of-origin. Similarly, I found that the growth capacity of woody plants in response to warming may vary among genotypes from contrasting climates.

Unlike other studies showing intraspecific variation in plasticity of physiological traits such as photosynthetic variables under T_E (Weston & Bauerle, 2007; Weston *et al.*, 2007; Drake *et al.*, 2015), differentiation in physiological plasticity of the two *T. speciosissima* genotypes in response to warming was largely absent in this study. T_E had similar effects on most physiological traits between the two genotypes, despite that there was significant genotype by temperature interaction on a few physiological traits including g_s , A/T_L parameter C and tuber Ss. This phenomenon suggests that the effect of warming on growth plasticity was not parallel with the effect of warming on physiological plasticity in this study. This pattern may be attributed to the difference in plant size between the two *T. speciosissima* genotypes. Under

warming, both genotypes allocated more biomass to the above-ground for vegetative growth, as indicated by the reduced Root/Shoot ratio and the increased LAR, but the magnitudes of these changes did not differ between genotypes. However, the Coastal seedlings were bigger than the Upland counterparts, and therefore the Coastal genotype allocated more mass in essence to leaves and stems under warming conditions. In such circumstances, when compared with the Upland genotype, the Coastal genotype not only had greater whole-plant leaf area, but also showed greater increase in leaf area to warming, which is possibly the primary cause of the intraspecific variation in growth (i.e., biomass) response to temperature between the two *T. speciosissima* genotypes in this study.

Despite the fact that many traits (including growth and physiology) measured in this study showed a significant response to C_E , no interaction between genotype and $[CO_2]$ was found for any of the growth or physiological traits, indicating that the two *T. speciosissima* genotypes had similar phenotypic plasticity under C_E . Although most studies on intraspecific variation in woody species responsiveness to C_E demonstrate substantial intraspecific differentiation in the responses of plant growth and/or physiology to changing $[CO_2]$ (Ceulemans *et al.*, 1996; Dickson *et al.*, 1998; Isebrands *et al.*, 2001; Mohan *et al.*, 2004; Cseke *et al.*, 2009), some studies show limited intraspecific variation in woody plant responsiveness to C_E (e.g., Cantin *et al.*, 1997). In this study, both genotypes of *T. speciosissima* were equally limited by carbon availability and therefore showed strong increases in leaf area (29%) and mass production (35%) when grown in C_E . Subsequently, rising $[CO_2]$ is not likely to generate differential responses in genotypes of *T. speciosissima* in future climates.

I did not observe significant interaction between temperature and $[CO_2]$ in most traits measured in this study, except the ratio of J_{max}/V_{cmax} and the root S_s , suggesting that the effects of T_E and C_E were generally independent in the two *T. speciosissima* genotypes. There is no clear trend in the literature for the interactive effects of temperature and $[CO_2]$ on woody plant species. Many studies show that C_E is likely to interact with T_E , synergistically affecting woody plant growth and/or physiology (Callaway *et al.*, 1994; Peltola *et al.*, 2002; Ghannoum *et al.*, 2010a; Ayub *et al.*, 2011; Wang *et al.*, 2012). However, findings from the present study are consistent with other studies indicating that the effects of increasing $[CO_2]$ and

warming are additive (Lewis *et al.*, 2001; Lloyd & Farquhar, 2008; Ghannoum *et al.*, 2010b; Lewis *et al.*, 2013). In addition, I also did not find significant interactive effects of temperature and [CO₂] on the genotypic variation in phenotypic plasticity for most traits, except in root Ss. Especially for traits that showed interaction between genotype and temperature (i.e., plant dry mass, leaf area, SMF, g_s , A/T_L parameter C and tuber Ss), genotypic variation in phenotypic plasticity under T_E was not affected by changes in [CO₂]. I suggest that the lack of interactive effects of temperature and [CO₂] on genotypic variation in phenotypic plasticity in this study may be partially due to the absence of interactive effects of temperature and [CO₂] on plant growth and physiology.

Association between phenotypic plasticity and source environment variability of woody plant

populations

Plant populations usually show genetic differentiation in phenotypic plasticity and the divergence among populations may be influenced by the pattern of environmental variation. A long-standing hypothesis suggests that greater levels of environmental variability will select for genotypes with greater phenotypic plasticity (Galloway, 1995; Ackerly *et al.*, 2000; Weinig, 2000; Donohue *et al.*, 2001; Alpert & Simms, 2002; Gianoli & Gonzalez-Teuber, 2005; Van Kleunen & Fischer, 2005). Although testing this hypothesis on woody plant species is limited, there is at least one case study that supports the theory (Drake *et al.*, 2015). Specifically, this case study on two widespread eucalyptus species (*E. tereticornis* and *E. grandis*) showed that, for both species, provenances originating from cooler and more variable temperature climates exhibited higher plasticity in growth and photosynthetic capacity under warming, when compared with provenances from warmer and more uniform temperature climates (Drake *et al.*, 2015).

Results from this study contradict the current paradigm. I observed that the Coastal genotype of *T. speciosissima* (warmer and less variable temperature environments) rather than the Upland genotype (cooler and more variable temperature environments), exhibited higher growth plasticity in response to T_E . The differentiation in phenotypic plasticity among plant populations may be associated with source environment

variability and linked to the intrinsic difference in adaptation to distinct source environments. Plant populations usually are highly adapted to local conditions, showing the greatest fitness in their home environments (Savolainen *et al.*, 2007; Hereford, 2009; Wang *et al.*, 2010). The upland region in this study is *c.* 2–5 °C cooler than the coastal region (Table 2-1), and the temperature difference between these regions has been estimated to be larger during the Last Glacial Maximum (Barrows *et al.*, 2001; Hesse *et al.*, 2003). This long-term temperature differential may have shaped and maintained the genetic differences between the coastal and upland populations of *T. speciosissima* (Rossetto *et al.*, 2011). The Upland genotype that might have been adapted to cooler temperatures, may not have the capacity to fully utilise warmer temperatures in terms of plant growth, and therefore showed lower growth plasticity in response to T_E when compared with the warmer-origin Coastal genotype. However, to more rationally explain why the results in this study contradict the long-standing paradigm, further studies with a more specific and thorough design (e.g., with both ecological and evolutionary aspects included) on *T. speciosissima* would be more informative.

3.4.1 No intraspecific variation in growth and photosynthetic responses to drought

Between the two *T. speciosissima* genotypes originating from contrasting environments with differentiated precipitation, differences in the declines of growth and photosynthesis induced by drought were largely absent across [CO₂] and temperature treatments. In addition, their sensitivity of photosynthetic traits (i.e., A_{sat} and g_s) to declines in soil water content and the capacity of plant drought resistance (measured by the time for drought treated seedlings to become physiologically stressed) also did not differ between the two genotypes. These results collectively suggest that there is no intraspecific variation in the response to drought between the *T. speciosissima* genotypes in this study, contradicting observations on other woody species, in which plant populations from different precipitation regions usually showed differentiated responses under drought conditions (e.g., Ramirez-Valiente *et al.*, 2010; McLean *et al.*, 2014; Bansal *et al.*, 2015). Specifically, these studies indicated that woody plant populations originated from more mesic regions were usually more susceptible to drought (Cregg & Zhang, 2001; Silva *et al.*, 2006; Ramirez-Valiente *et al.*, 2010; Dutkowski & Potts, 2012; Robson *et al.*, 2012), while populations from more stressful

environments tended to be less responsive to water stress (Gratani *et al.*, 2003; Baquedano *et al.*, 2008; Aranda *et al.*, 2010; Bansal *et al.*, 2015).

The lack of intraspecific variation in response to drought in this study could be attributed to the fact that there might be no inherent difference in the capacity to cope with drought between the two *T. speciosissima* genotypes. Although the Coastal and the Upland genotypes were sampled from regions with different precipitation, both regions can be characterized as high rainfall regions (more than 850 mm per year) with no difference in precipitation variability (see Huang *et al.*, 2015), suggesting the relative uniformity of precipitation conditions between the two regions. Therefore, these two genotypes might have been adapted to somewhat similar non-water-stressed environments and may not differ in their inherent capacity of coping with water deficit. Similar results were found in a drought manipulating study on provenances of two widely distributed *Eucalyptus* species, where provenances originating from contrasting environments (tropical *vs.* temperate) did not show intraspecific variation in most growth and physiological responses to drought (Huang *et al.*, unpublished data). In that study, provenances were also selected from

regions with relatively sufficient precipitation (all > 890 mm rainfalls per year) and similar precipitation variability, despite that there was significant difference in the mean annual precipitation (MAP) between them. In contrast, woody plant populations exhibiting intraspecific variation in the drought responses usually distribute across low (MAP < 400 mm), mid (MAP between 400 and 800 mm) and high (MAP > 800 mm) rainfall regions (Aranda *et al.*, 2010; Ramirez-Valiente *et al.*, 2010; McLean *et al.*, 2014; Bansal *et al.*,

2015), or at least two contrasting rainfall regions (Cregg & Zhang, 2001; Gratani *et al.*, 2003; Silva *et al.*, 2006; Robson *et al.*, 2012), suggesting that these populations may possess inherent difference in their capacity to cope with water stress due to local adaptation.

3.4.2 Effects of T_E and C_E on woody plants in response to drought

I observed a significant effect of temperature on the capacity of seedling resistance to drought after removing the variance accounted for by the plant size. For both *T. speciosissima* genotypes, T_E accelerated

the rates of g_s decline under drought conditions and thereby reduced the time for drought seedlings to become physiologically stressed. Results from this study are consistent with the prevailing findings that an increase in air temperature usually exacerbates the negative impacts of water stress on woody plants (Adams *et al.*, 2009; Allen *et al.*, 2010; Duan *et al.*, 2013, 2014, 2015; Will *et al.*, 2013; Zhao *et al.*, 2013). However, the quicker closure of stomata under T_E did not reflect in the sensitivity of g_s as a function of soil VWC in this study. For both temperature treatments, g_s positively correlated with soil water content in a similar manner, suggesting that the nature of *T. speciosissima* stomata in response to declines in soil water content was not altered by changes in temperature. Therefore, I hypothesize that the negative impacts of T_E on the drought resistance of *T. speciosissima* seedlings may be working as follows: under drought conditions, higher temperatures will accelerate transpiration water loss through the increase in vapour pressure deficits, which will in turn speed up the drawdown of soil water content and hence create a positive feedback loop to magnify or exacerbate the negative effects of drought (De Boeck *et al.*, 2011; Will *et al.*, 2013; Teskey *et al.*, 2015).

By contrast, an increase in $[CO_2]$ neither impacted the capacity of plant drought resistance, nor altered the sensitivity of A_{sat} or g_s to declines in soil water content for both *T. speciosissima* genotypes in this study. In addition, C_E did not ameliorate the negative effects of T_E on drought resistance, suggesting that C_E may be a less strong determinant than T_E on regulating plant response to drought. Observations about the effects of C_E on woody plant drought response are considerably inconsistent in literature. Some studies indicate that C_E would lead to partial closure of stomata, thereby reducing transpiration water loss and mitigating the negative effects of drought on plant performance (Ambebe & Dang, 2010; Wertin *et al.*, 2010; Duan *et al.*, 2013; Lewis *et al.*, 2013); while other studies (Duan *et al.*, 2014, 2015) suggest that C_E may only have a negligible effect on woody plant response to drought, consistent with findings of this study. The absence of $[CO_2]$ effects on *T. speciosissima* drought response may be explained by the fact that g_s in this study overall did not differ between $[CO_2]$ treatments across all experimental stages, indicating that C_E did not significantly reduce g_s to improve plant water usage and therefore did not ameliorate the negative effects of drought. Although most woody plants show a significant decrease in g_s under C_E (Wullschleger *et al.*, 2002; Ainsworth & Long, 2005; Ainsworth & Rogers, 2007; Wang *et al.*, 2012), there are some

exceptions as well (Saxe *et al.*, 1998; Ellsworth, 1999; Lewis *et al.*, 2002; Ghannoum *et al.*, 2010a; Duan *et al.*, 2014, 2015). Given the inconsistency and complexity of [CO₂] effects on plant drought response (Wullschleger *et al.*, 2002; Franks *et al.*, 2013), further studies with a systematic manner are necessary for exploring mechanisms that underpin woody plant response to drought and C_E.

In conclusion, I found that the Coastal genotype of *T. speciosissima*, which originated from warmer and less variable temperature environments, showed greater plasticity in growth with warming than the Upland genotype from cooler and more variable temperature environments. On the other hand, C_E did not expose genotypic variation in growth or physiological responses, either individually or interactively with T_E. These findings suggest that temperature will be more effective than [CO₂] in exposing intraspecific variation in growth plasticity for genetically differentiated woody plant populations under future climates. Overall, results from this study contradict the paradigm that genotypes from more variable climates will exhibit greater phenotypic plasticity in future climate regimes. The two *T. speciosissima* genotypes neither showed difference in their capacity in resisting to drought stress, nor exhibited differentiated declines in growth and photosynthesis under drought conditions across [CO₂] and temperature treatments, suggesting that there might be no inherent difference in their capacity to cope with drought. Regardless of genotype, T_E imposed a negative effect on plant drought resistance, accelerating the process of drought seedlings becoming physiologically stressed. In contrast, C_E did not affect the capacity of plant drought resistance or alter the sensitivity of photosynthesis to declines in soil water content for both *T. speciosissima* genotypes. Furthermore, C_E did not ameliorate the negative effects of T_E on drought response. Collectively, these findings suggest that woody plant populations originating from differentiated environments may not necessarily show intraspecific variation in response to drought under current climates or future climates. These results also indicate that temperature is likely to be stronger determinant than [CO₂] affecting the capacity of woody plants in resisting to drought in the context of climate change.

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