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Warming Reduces Net Carbon Gain and Productivity in *Medicago sativa* L. and *Festuca arundinacea*

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Abstract: High temperature stress imposes constraints on the productivity of agricultural systems, such as pastures, and predicted increases in global temperatures are set to exacerbate these limitations. Here, we sought to understand the impact of warmer growth temperature on gas exchange and net primary productivity for two widely cultivated pasture species. We grew a C_3 legume, *Medicago sativa* (lucerne), and a C_3 grass, *Festuca arundinacea* Schreb. (tall fescue), in a climate-controlled facility exposed to two temperature treatments (ambient: 26 °C, aT; elevated: 30 °C, eT). Soil water was maintained at non-limiting conditions in both temperature treatments to control for the confounding effects of warming on soil moisture. We found that warming reduced photosynthetic capacity and increased leaf dark respiration (R_{dark}) in lucerne, while tall fescue showed little physiological change at the leaf level, but increased ecosystem respiration (R_{eco}). Growth temperature had no significant impact on the thermal optimum of photosynthesis (T_{opt}) or water use efficiency in either species. Both species exhibited significant reductions in productivity with warming; lucerne had greater reductions in shoot biomass, while tall fescue had greater reductions in root biomass. Our results highlight the potential for significant declines in pasture productivity associated with even modest increases in average temperature and highlights the need for suitable management strategies and implementation of more heat-resistant cultivars. Improvements in photosynthetic performance for greater heat tolerance in lucerne, and traits associated with biomass allocation and root performance at higher temperatures in tall fescue, should be the focus for improving high temperature resistance in these plant species.

Keywords: photosynthesis; respiration; climate change; pasture; water use efficiency; temperature

1. Introduction

Natural and anthropogenic factors have accelerated climate change, with global surface temperatures predicted to increase by 1.1–6.4 °C by 2100 [1]. Global warming can have significant impacts on plant carbon (C) assimilation (photosynthesis) and C loss (respiration) because these processes are highly temperature sensitive [2–4]. Photosynthesis and respiration regulate net primary productivity of ecosystems and the balance between these two processes determines whether an ecosystem is a net C sink or source [5]. High temperatures already impose major limitations on the productivity of temperate agricultural systems including pastures [6,7], and the response of these systems to predicted increases in global temperature will vary in both magnitude and direction across biomes, depending on species composition and prevailing climatic conditions [8–13]. A large

proportion of Australian pastures are currently growing in areas that experience temperatures well above thermal limits for optimal productivity [7] and further increases in temperature may significantly reduce photosynthetic rate, growth and forage quality [6].

Photosynthesis typically exhibits a peaked relationship, and is maximal at an optimum temperature (T_{opt}) [2]. This form of relationship is mainly driven by the influence of temperature on RuBP carboxylation (V_c) and RuBP regeneration (J). V_c is dependent on Rubisco activity, which is highly sensitive to, and increases with, temperature; however, the affinity of Rubisco for CO_2 and the solubility of CO_2 both decrease with temperature, decreasing potential V_c by driving higher rates of photorespiration [14]. While J is generally related to V_c, the correlation between the two can be influenced by the sensitivity of J to light availability and leaf nutrient status [15–17]. Importantly, the temperature response of photosynthesis varies significantly among plant species [18], as does the capacity of species to physiologically adjust photosynthesis to growth temperature [9,12,19–21], with some species exhibiting no adjustment [10,22,23]. Ultimately, species adaptation of photosynthetic capacity to warming is dependent on the current temperature regime of its present climate; species from cold environments may exhibit an increase in photosynthesis under warming, while species from warm environments may exceed T_{opt} and exhibit a reduction in photosynthesis [4,24]. Furthermore, species from habitats with higher temperature variation often have a greater ability to acclimate to warming than those from climates with minimal temperature variation [25,26]. In drier environments, an indirect decrease in photosynthetic capacity may also be incurred via warming due to higher evaporative demand and consequent reductions in soil moisture [27,28].

Autotrophic respiration is generally regarded as more temperature sensitive, with a higher Q_{10}, than photosynthesis [17,29]; reflecting temperature-driven increases in enzyme activity and photorespiration. This is especially true at higher temperatures with studies on cotton showing that respiration has a Q_{10} of 1.5–1.86 between 28 & 42 °C, while photosynthesis has a negative Q_{10} in this temperature range [30]. The response of respiration to temperature can, however, be dynamic and can vary depending on species [31], growth temperature [3,32–35], substrate availability [36], leaf age [37], soil water content [34,38], soil nutrient status [39], light environment [3,40] and canopy position [41,42]. Additionally, respiration has been shown to acclimate to growth temperature over the long-term [3,22,43–45], although this varies depending on the duration of exposure [14,46]. Most long-term studies investigating the temperature response of respiration have been conducted on trees and, given the varied possible mechanisms for changes in respiration with increasing temperature, this limits our ability to predict the respiratory response of grassland or pasture systems in a warmer future.

The magnitude and direction of change in rates of photosynthesis and respiration under warming, and the balance between the two processes (R:P), will have significant ramifications for ecosystem productivity and the global carbon cycle in the future. Globally, warming has been shown to increase photosynthesis and respiration by 6% and 33%, respectively, although the response varies substantially as a function of plant species, functional group and environmental conditions such as soil moisture and prevailing temperature regimes [4]. Liang et al. (2013) found that on a global scale, warming significantly increased respiration in C_3 species but had no clear impact on photosynthesis, while respiration and photosynthesis increased similarly in C_4 species under warming, possibly due to their higher T_{opt} [9,12,47]. This suggests that C_3 plants may be more negatively impacted by rising temperatures than C_4 species [48]. Furthermore, C_3 forbs showed a greater increase in respiration under warming (57%) compared to C_3 grasses (20%). Liang et al. (2013) also found that stimulation of photosynthetic rates by warming declined with increasing temperature, but no such relationship was found for respiratory responses. Hence, at higher temperatures, photosynthetic upregulation as a result of warming may be insufficient to compensate for temperature driven increases in respiration.

While numerous studies have investigated the impact of warming on photosynthesis and respiration, relatively few have simultaneously analysed both parameters, especially in the context of pastures [23]. These few studies have investigated the response of photosynthesis and respiration

to water stress [49], N fertilisation [50,51], shading [52], or only investigated daytime respiration [46]. Importantly, the responses of photosynthesis and respiration to temperature can be confounded by the effect of temperature on evapotranspiration and plant water status [53], which were rarely accounted for in previous studies.

Increases in air temperature will also affect the hydrological cycle, increasing aridity and drought frequency; hence, understanding plant-water relations in the context of warming is needed for predicting shifts in plant productivity. The ratio of carbon assimilated per unit of water lost, commonly referred to as plant water use efficiency (WUE), is a key ecosystem property linking global carbon and water cycles [54]; high WUE is a desirable trait in plant cultivar selection and breeding [55] as it may reduce the need for costly irrigation. Temperature can significantly influence plant WUE as warming results in higher evaporative demand and therefore increases transpiration rates, but may have little to no impact on photosynthetic carbon uptake [56,57], effectively reducing WUE. WUE can be estimated at a physiological level using leaf gas exchange measurements and is usually defined as the ratio of net light saturated photosynthesis (A_{sat}) to stomatal conductance for water vapour (g_s)—intrinsic water-use efficiency (WUE_i; [58]) or the ratio of A_{sat} to transpiration (E)—instantaneous water-use efficiency (WUE_{inst}; [59]). These metrics are however, significantly impacted by atmospheric vapour pressure deficit (VPD) [60], which is known to increase with temperature, potentially confounding the direct impacts of temperature. In order to address this issue, we used the optimal stomatal behavior parameter *g1*, which is inversely related to the marginal cost of water and VPD [61]. It has been shown that *g1* is representative of plant water use strategy across plant functional types and ecosystems, and therefore allows WUEi to be compared across environmental conditions [61].

Here, we investigated the effects of warming on the photosynthetic capacity, leaf dark respiration (R_{dark}), daytime ecosystem respiration (R_{eco}), WUE and productivity of lucerne and tall fescue. Lucerne is a temperate legume and is the most important and most widely grown forage legume in the world with ~32 Mha cultivated [62,63]. Lucerne provides high-quality feed for livestock and fixes atmospheric N_2, thereby improving soil nutrient status, making it important for pasture productivity worldwide [64]. Tall fescue is highly productive and used extensively for forage in all classes of livestock and is adapted to a wide range of growing conditions [14,65]. We grew seedlings of lucerne and tall fescue in a climate-controlled facility in ambient temperature (26 °C, aT) or ambient temperature +4 °C (eT); aT represented the average daily maximum temperature for Richmond, NSW, Australia over the last 20 years, and eT represented the predicted maximum temperature increase of 4 °C for this region, within this century [7]. We hypothesized that warming would increase leaf level photosynthesis, but that concurrent increases in respiration would lead to a reduction in overall leaf-level C uptake, with resulting declines in productivity. We also hypothesised that tall fescue would be less negatively affected by warming because it has a higher T_{opt} than lucerne [49,66]. Finally, we hypothesised that increased evaporative demand under eT would lead to higher levels of water loss via transpiration and an overall reduction in WUE for both species.

2. Materials and Methods

2.1. Study Species and Experimental Design

We used seedlings of lucerne (*Medicago sativa*, Cultivar: SARDI 7 Series 2) and tall fescue (*Festuca arundinacea* Schreb., Cultivar: Quantum II MaxP), which are two extensively cultivated C_3 pasture species with significant economic value [62,67,68]. These cultivars are widely grown across eastern Australia and have recommended optimum growth temperatures of 15–25 °C and 15–30 °C, respectively [66,69]. The experiment was conducted between April and August 2018, in four environmentally-controlled glasshouse chambers (two for each temperature treatment) at Western Sydney University's Hawkesbury campus in New South Wales, Australia (latitude −33.611141, longitude 150.745315). Temperature was controlled either under ambient (aT; 26/18 °C day/night) or elevated (eT; 30/22 °C day/night) conditions. Plants were grown using a 15:9 light: dark cycle, achieved

using natural daylight supplemented with fluorescent lamps that provided a photosynthetic photon flux density (PPFD) of 300–400 µmol m^{-2} s^{-1}. Humidity was controlled at 60%, thereby generating VPD of ~1.35 kPa (aT) and 1.7 kPa (eT).

Soil was collected from the field at Western Sydney University (sandy-loam texture with a pH ~5.6), sieved (5 mm), and mixed with quartz sand (soil to sand ratio of 7:3, *v*/*v*). Plastic pots (3.7 L, 15 cm diameter, 24 cm height) were filled with ~3.9 kg soil mixture. Seeds were surface sterilized with a 1.25% bleach solution for 10 min, then rinsed 10 times with deionized water, and germinated in Petri dishes with sterilized water for 1 week (Zhang et al., 2020 *in review*). Five seedlings were transplanted into each pot and then thinned to four healthy individuals per pot after 2 weeks. All lucerne individuals were inoculated with Easy Rhiz soluble legume inoculant (Group AL, New Edge Microbials, NSW, Australia) and assessed for nodulation during the final harvest to ensure all lucerne individuals were well inoculated. Plants were watered using an automated irrigation system, with top-up hand watering conducted every other day to ensure soil water was maintained at similar levels between temperature treatments (80% field capacity), and was non-limiting for growth. Overall, the experiment contained 4 treatment combinations (2 temperatures × 2 species) and eight replicates for each treatment (divided between two growth chambers), generating 32 pots in total.

During the experiment, pots were randomly reallocated among positions within chambers every two weeks to minimize potential within-chamber effects. To mimic standard practices in pasture management associated with cut-and-carry operations, aboveground plant material was clipped ~5 cm above the soil surface at 8 weeks after planting (WAP). At this time, fertiliser was added in the form of KNO_3 and KH_2PO_4, at a rate equivalent to 30 kg N ha^{-1} and 5 kg P ha^{-1}. Plants were then allowed to regrow for a further 8 weeks before they were harvested.

2.2. Photosynthetic Capacity

Gas exchange measurements were conducted on attached, recently fully expanded leaves (RFEL) using a portable open gas exchange system (LI-6400XT, LI-COR Inc., Lincoln, NE, USA). Leaf areas for all leaf samples of lucerne used in gas exchange analyses were calculated by capturing high resolution photographs on a pre-calibrated surface and then analysing leaf area using Image J (National Institutes of Health). Leaf area for tall fescue was kept constant by filling the cuvette during each measurement, taking care to prevent overlapping of leaves.

The response of net photosynthesis (A) to intercellular CO_2 concentration (Ci) was measured thirteen WAP (weeks after planting) or 5 weeks after clipping. Measurements were taken between 10:00 and 15:00 AEST, at a saturating PPFD of 1800 µmol m^{-2} s^{-1}, and at treatment specific mid-day air temperatures (26 or 30 °C). Leaf-to-air vapour pressure deficit (VPD_L) levels were on average ~1.2 kPa and ~1.6 kPa for plants under aT and eT, respectively. Steady state measurements of light-saturated photosynthesis (A_{sat}; µmol m^{-2} s^{-1}), stomatal conductance (g_s; mol m^{-2} s^{-1}) and transpiration (E; mmol m^{-2} s^{-1}) were conducted at the beginning of each A/Ci curve at a cuvette reference [CO_2] (C_r) of 420 µmol CO_2 mol^{-1} [70]. A/Ci curves were subsequently conducted by measuring A_{sat} at 15 additional C_r points (5, 50, 100, 150, 200, 250, 300, 420, 500, 650, 800, 1000, 1250, 1500 and 1800 µmol CO_2 mol^{-1}) and each leaf was allowed ~2 min to equilibrate to each C_a before conducting measurements [71]. Time constraints resulted in measurements only being conducted on 6 of the 8 replicate plants per species, per temperature treatment, giving a total of 24 plants. A/Ci curves were parameterized using the Farquhar, von Caemmerer & Berry model of C_3 photosynthesis [2] for maximum rate of Rubisco carboxylation (V_{cmax}; µmol m^{-2} s^{-1}) and the apparent maximum rate of electron transport for RuBP regeneration (J_{max}; µmol m^{-2} s^{-1}). Analyses were conducted using the *fitaci* function within the *plantecophys* package [72] in R version 4.0 (R Development Core Team, 2020) without constraining mesophyll conductance [73]. To make V_{cmax} and J_{max} values comparable across species and growth temperatures, estimated V_{cmax} and J_{max} values were corrected for temperature and expressed at 25 °C using the default *Tcorrect* parameters included in the *fitaci* function. This allows for V_{cmax} and J_{max} values to be expressed at a common temperature

using modified Arrhenius-type equations that involve previously determined values for activation energy (J mol^{-1}), delta S (J mol^{-1} K^{-1}) and peakedness of the curve (EdV) [12], for more details see https://github.com/RemkoDuursma/plantecophys/blob/master/vignettes/new_T_responses.Rmd. CO_2-saturated assimilation rates (A_{max}) were determined at a C_i of 1500 µmol CO_2 mol^{-1} by fitting each A/Ci data set to the Farquhar, von Caemmerer & Berry model [2].

The responses of leaf photosynthesis (A) to irradiance (photosynthetic photon flux density (PPFD)) were measured immediately following the completion of A/Ci curves on the same leaves. A/PPFD curves were measured by first exposing each leaf to a PPFD of 1800 mmol m^{-2} s^{-1} with sample chamber [CO_2] (C_s) at 400 µmol CO_2 mol^{-1} [74] until steady state of net CO_2 fixation was reached. Irradiance was then reduced in a stepwise manner and A was measured at 13 additional PPFD points (1400, 1200, 1000, 600, 300, 200, 150, 100, 80, 60, 40, 20 & 0 µmol m^{-2} s^{-1}). Each leaf was allowed ~2 min to equilibrate to each PPFD before measurements were taken. Measurements were conducted on 6 replicate plants per species per temperature treatment for a total of 24 plants. A/PPFD curve parameters were estimated using nonlinear least squares regression of a nonrectangular hyperbola (Equation (1); [74,75]) using the *nlsLM* function within the *minpack.lm* package in R version 4.0 (R Development Core Team, Vienna, Austria, 2020).

$$A_{net} = \frac{\mathbf{\Phi}PPFD + A_{max-light} - \sqrt{\left(\mathbf{\Phi}PPFD + A_{max-light}\right)^2 - 4\varnothing\mathbf{\Phi}PPFD\left(A_{max-light}\right)}}{2\varnothing} - R_d \quad (1)$$

where A_{net} and $A_{max\text{-}light}$ are the area-based net and maximum gross photosynthetic rates (µmol m^{-2} s^{-1}) respectively, $\mathbf{\Phi}$ is the apparent quantum yield (mol CO_2 mol^{-1} photons); R_d is the daytime dark respiration rate (A_{net} at PPFD = 0 µmol m^{-2} s^{-1}); $\emptyset$ is the curve convexity (dimensionless). The light saturation point (LSP) was estimated as the PPFD when 80% of A_{max} (model asymptote) was achieved and the light compensation point (LCP) was estimated from the *x*-axis intercept (A_{net} = 0) [75].

The responses of A_{sat} to leaf temperature (A/T curves) were measured 1 week after A/Ci curves were measured (14 WAP) on the same individuals used for A/Ci curves (6 replicates per species per treatment). Measurements were taken at a PPFD of 1800 µmol m^{-2} s^{-1} and 420 µmol CO_2 mol^{-1}. All plants to be measured were transferred to an empty glasshouse chamber, which was maintained at 10 °C, on the night before measurement. The A/T curves began at 09:00 and A_{sat} was measured on all plants at 10 °C. A/T curves were subsequently analysed by measuring A_{sat} at 6 additional temperatures (15, 20, 25, 30, 35 and 40 °C) by raising the temperature of the glasshouse chamber and the block temperature of the leaf gas exchange cuvette in a step-wise manner. Temperatures were raised every hour, and plants were allowed to acclimate to each temperature for a minimum of 30 min before measurements were taken.

The A/T curves were fit with an empirical temperature response function (Equation (2); [76,77]) which describes the temperature response in terms of the optimum (T_{opt}) and minimum temperatures, and the curvature coefficient q. All analyses were conducted using the *nls* function in R.

$$f_T(T) = \begin{cases} 0, & T \le T_{mx} \\ \left(\frac{T - T_{mn}}{T_r - T_{mn}}\right)^q \left(\frac{(1+q)T_{opt} - T_{mn} - qT}{(1+q)T_{opt} - T_{mn} - qT}\right), & T_{mn} < T < T_{mx} \\ 0, & T_{mn} \ge T_{mx} \end{cases} \quad (2)$$

Here T_{mn} and T_{mx} are the minimum and maximum temperatures respectively, while T_r is a reference temperature (20 °C) and q is the curvature coefficient [77].

Spot measurements of leaf gas exchange were conducted three times during the experiment: (1) 8 WAP, immediately prior to plants being clipped; (2) 12 WAP, one month following clipping; and (3) 16 WAP, at the end of the experiment. Measurements of A_{sat}, stomatal conductance (g_s) and transpiration (*E*) were conducted on RFEL at respective mid-day growth temperatures (26 or 30 °C) using a photosynthetic photon flux density (PPFD) of 1800 µmol m^{-2} s^{-1}, a reference [CO_2] of 400 µmol CO_2 mol^{-1} and a flow rate of 500 µmol s^{-1}. VPD_L was maintained between 1–2.0 kPa and each leaf

was allowed 5–10 min to equilibrate before measurements were taken [71]. Measurements were taken between 10:00 and 15:00 AEST and conducted on the same four replicate individuals of each treatment at each time point.

2.3. Respiration

Leaf dark respiration (R_{dark}) was measured using a portable open gas exchange system (LI-6400XT, Li-Cor, Lincoln, NE, USA) on the week following the measurements of A/T curves on the same individuals (15 WAP). All measurements were conducted at night in the dark between 22:00 and 24:00 on RFEL at respective night-time air temperatures (18 or 22 °C for aT and eT, respectively) using a photosynthetic photon flux density (PPFD) of 0 µmol m^{-2} s^{-1}, a reference [CO_2] of 420 µmol CO_2 mol^{-1}, humidity maintained at ambient chamber conditions and a flow rate of 300 µmol s^{-1}. Ecosystem respiration (R_{eco}) was analysed one day before the final harvest (16 WAP) on 4 replicates of each species under each temperature treatment. Each pot was fitted with a removable, airtight chamber, composed of a non-transparent PVC tube (15 cm in diameter × 35 cm in height, 7 L volume), allowing the headspace to be closed for gas measurements [78]. The measurement chambers were installed on each pot, water was added to the bottom tray during measurement to ensure no gas leakage occurred, and 20 mL gas was sampled after 0, 15 and 30 min using a syringe. Each gas sample was stored in a 12 mL vial and transported to the laboratory. All gas samples were analysed using a headspace autosampler (Teledyne Tekmar, Mason, OH, USA) connected to a 5890-gas chromatograph (Agilent/Hewlett-Packard, Palo Alto, CA, USA) equipped with a thermal conductivity detector (TCD) to quantify the concentration of CO_2 (Zhang et al., *in review* 2020). Rates of CO_2 flux were determined by measuring the change in gas concentration over time within the headspace (Collier, Ruark, Oates, Jokela, & Dell, 2014). All measurements were standardized by the total dry biomass (both aboveground and belowground biomass) within each pot.

2.4. Leaf Level Water Use Efficiency (WUE)

Instantaneous WUE (WUE_{inst}) was calculated from gas exchange measurements as the ratio of carbon assimilated (A_{sat}) to water lost through transpiration (E) [79]. Intrinsic WUE (WUEi) was calculated as the ratio of A_{sat} to g_s. Calculations of WUE are influenced by atmospheric vapour pressure deficit (VPD). In order to account for this, we used the *g1* parameter from a model of stomatal conductance that accounts for VPD (Equation (3); [61]):

$$g_s = 1.6\left(1+\frac{g_1}{\sqrt{D}}\right)\frac{A}{C_s} \quad (3)$$

where C_s and D (kPa) are the CO_2 concentration and the VPD at the leaf surface, respectively, and A is the net assimilation rate [80].

2.5. Biomass and Shoot Nutrients

During the final harvest, plant shoots were cut at the soil surface, and placed in paper bags. The pots were completely emptied, then roots were washed and collected from the soil and placed in paper bags. All samples were dried at 65 °C for 48 h and weighed and a subset of the dried shoot biomass was separated, weighed and then ground to a fine powder using a mixer mill (Retsch® MM200; Haan, Germany). The ground sample was analysed for P concentrations using an Epsilon-3× X-ray fluorescence spectrometer (PANalytical, EA Almelo, The Netherlands) as described in [81]. C and N concentrations were measured using an isotope-ratio mass spectrometer (Stable Isotope Facility, UC Davis, Davis, CA, USA; IRMS; Deltaplus XP and Delta C prototype Finnigan MAT, respectively, Finnigan MAT, Bremen, Germany; 0.1‰ precision). Due to the internal airflow system in our glasshouse, where expelled CO_2 from each chamber is recycled and CO_2 concentration is controlled by the addition of fresh air, the proportion of fresh air to expired air varied between chambers. Hence,

the isotopic value from the respired CO_2 and fresh air varied, and therefore the plant isotopic value could not be interpreted and was excluded from the study.

2.6. Statistics

All statistical analyses were carried out using the software R version 4.0.0 (R Core Development Team 2020). In order to calculate species differences and any interaction between temperature and species, we applied a two-way ANOVA with temperature and species as fixed effects and chamber as a random effect, using the "*lmer*" function from the R-package 'lme4' [82]. We tested for statistical differences between temperature treatments by conducting pair-wise t-tests for each species using the "*emmeans*" function from the R-package "emmeans" [83]. All data were analysed for normality and homoscedasticity and, where necessary log-transformed to fit these assumptions.

3. Results

3.1. Carbon Balance

At the leaf level, we observed a significant interaction between species and growth temperature for A_{sat} ($p = 0.03$; Table 1); warming resulted in a small (non-significant) increase in A_{sat} for tall fescue (+11%; Figure 1a), but significantly reduced A_{sat} for lucerne (−31%, $p = 0.03$). At the leaf level, warming had no significant impact on R_{dark} in tall fescue, but significantly increased R_{dark} in lucerne by 173% ($p = 0.02$; Figure 1b). Overall, we found that warming significantly increased the ratio of R_{dark} to A_{sat} in lucerne by 218% ($p = 0.01$; Figure 1c), but had no significant impact in tall fescue. At the whole pot level, warming did not affect the R_{eco} for lucerne, but led to a 56% increase in tall fescue ($p = 0.03$; Figure 1d).

Table 1. F values of linear mixed effects models and their interactions on parameters for lucerne (*Medicago sativa*) and tall fescue (*Festuca arundinacea*), with Species (S) and growth temperature (T) as fixed effects and growth chamber as the random effect. Statistical significance denoted by * ($p < 0.05$), ** ($p < 0.01$) & *** ($p < 0.001$).

Variable [#]		S	T	S:T
Photosynthetic Capacity	A_{sat}	35.77 ***	3.01	5.59 *
	g_s	8.91 **	0.03	0.46
	E	20.56 ***	2.05	0.06
	T_{opt}	3.13	0.13	0.7
	A_{opt}	48.77 ***	2.74	0.76
	A_{max}	27.63 ***	0.25	4.65
	V_{cmax} ^	33.89 ***	0.77	3.96
	J_{max} ^	35.1 ***	0.16	5.59 *
	J_{max}:V_{cmax}	2.63	1.31	0.07
	V_{cmax25} ^	35.37 ***	6.63	3.24
	J_{max25} ^	34.57 ***	2.59	5.36 *
	J_{max25}:V_{cmax25}	4.13	2.28	0.21
Respiration	R_{dark}	8.22 *	8.26	2.03
	R_{eco} ^	11.95 **	5.91	2.46
Carbon Balance	R_{dark}:A_{sat}	0.07	11.08	3.75
WUE	A_{sat}/E	1.78	2.33	0.74
	A_{sat}/g_s	1.97	0.95	1.06
Biomass	Shoot Biomass	579.58 ***	112.26 **	30.01 ***
	Root biomass ^	236.34 ***	44.49 *	2.67
	Root:Shoot	39.53 ***	5.24	1.84
	Total Biomass	602.31 ***	107.86 *	30.51 ***
Leaf Stoichiometry	N ^	487.9 ***	17.77	0.214
	P	13.17 ***	0.99	7.49 *
	N:P	76.66 ***	5.69	6.07 *
	C:N	848.6 ***	36.3 *	0.4

^ Variables were log transformed to meet assumptions of normality. [#] G1 is a modelled output parameter, hence could not be tested for statistical significance.

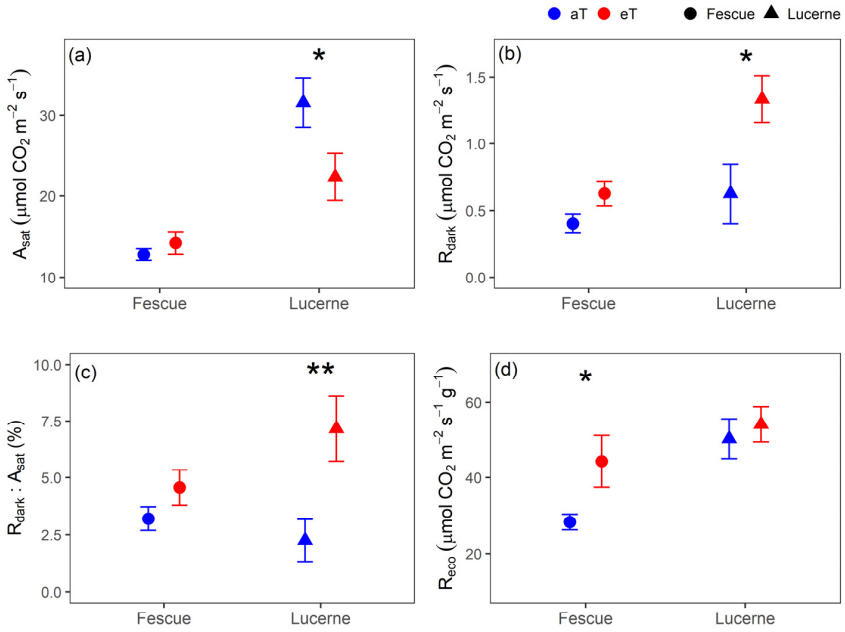

Figure 1. (**a**) Average rates of light saturated photosynthesis at ambient [CO_2] (A_{sat}), (**b**) leaf respiration during the night (R_{dark}), (**c**) the ratio of A_{sat} to R_{dark} and (**d**) total CO_2 flux from each pot per g of dry total biomass (R_{eco}) for tall fescue (circles) and lucerne (triangles) grown under 26 °C (aT, blue) and 30 °C (eT, red). Error bars indicate ± standard error. Statistically significant differences between temperature treatments are portrayed as * ($p < 0.05$), ** ($p < 0.01$).

3.2. Productivity

Warming significantly reduced shoot biomass for both tall fescue (−30.8%, $p = 0.006$: Figure 2a) and lucerne (−34%, $p < 0.001$), and root biomass in tall fescue (57.9%, $p < 0.001$: Figure 2b) and in lucerne (40.4%, $p = 0.01$). Warming also reduced the root to shoot ratio for tall fescue (37%, $p = 0.04$: Figure 2c) but had no significant impact in lucerne. Overall, warming reduced total biomass by 39% ($p = 0.007$: Figure 2d) and 37% ($p < 0.001$) for tall fescue and lucerne, respectively.

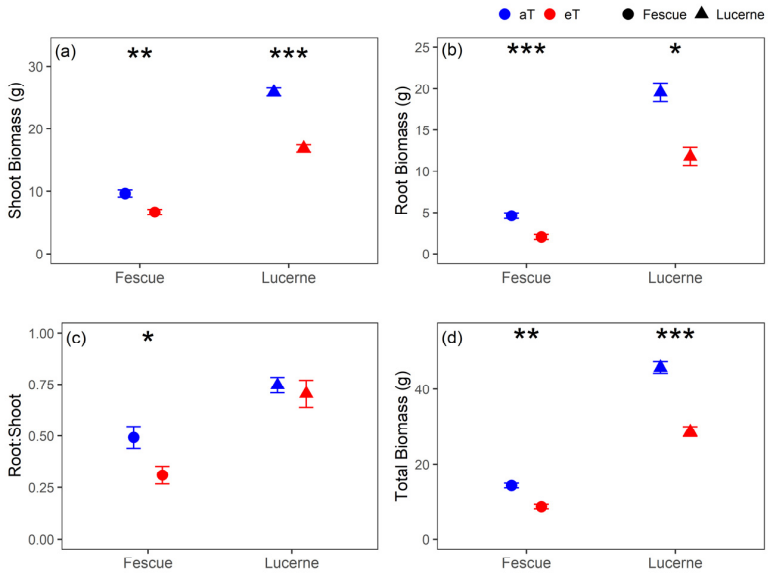

Figure 2. Total dry shoot (**a**) and root biomass (**b**), root to shoot ratio (**c**) and total biomass (**d**) for tall fescue (circles) and lucerne (triangles) grown under 26 °C (aT, blue) and 30 °C (eT, red). Error bars indicate ± standard error ($n = 8$). Statistically significant differences between temperature treatments are portrayed as * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$).

3.3. Photosynthetic Capacity

Warming had no significant impact on V_{cmax} (Figure 3a) or J_{max} (Figure 3b) for both species, but led to a significant decline in V_{cmax25} (−44%: Figure 3b) and J_{max25} (−33%: Figure 3d) for lucerne. Warming had no significant impact on A_{max} (Figure 3g; Table 1), apparent quantum efficiency (Φ) (Supplementary Materials Table S1), $A_{max\text{-}light}$ or light compensation point (LCP) (μmol m^{-2} s^{-1}) for either species. We did, however, observe a significant interaction between species and temperature for A_{max} (Table 1; $p = 0.046$), J_{max} ($p = 0.03$) and J_{max25} ($p = 0.033$): Tall fescue exhibited an increase in A_{max} (+22%: Figure 3g), J_{max} (+21%: Figure 3c) and J_{max25} (+6%: Figure 3d), but lucerne exhibited a decrease in A_{max} (−19%), J_{max} (−31%) and J_{max25} (−33%) under eT. We also observed a significant interaction between species and temperature for V_{cmax25} ($p = 0.012$): lucerne exhibited a much larger decrease in V_{cmax25} (−46%: Figure 3b) than tall fescue (−18%). Warming had no significant impact on J_{max}: V_{cmax} at the growth temperature (Figure 3e) or when corrected to 25 °C (Figure 3f) for both species. Spot measurement of gas exchange conducted throughout the experiment showed no significant change in rates of A_{sat} between temperature treatments for both species (Figure S1).

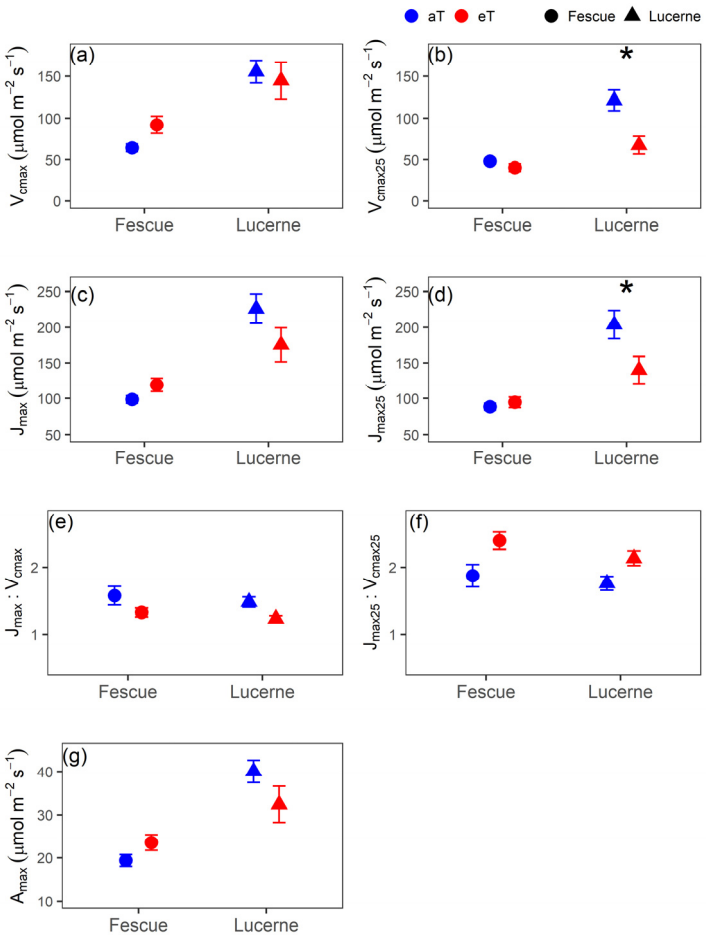

Figure 3. Maximum rate of carboxylation by Rubisco (V_{cmax}) at growth temperature (**a**) and at 25 °C (**b**). Maximum rate of electron transport (J_{max}) at measurement temperature (**c**) and at 25 °C (**d**). Ratio of J_{max} to V_{cmax} at measurement temperature (**e**) and at 25 °C (**f**). (**g**) Maximum rates of light saturated photosynthesis at saturating [CO_2] (1500 ppm) (A_{max}). Values shown are means for tall fescue (circles) and lucerne (triangles) grown under 26 °C (aT, blue) and 30 °C (eT, red). Error bars indicate ± standard error ($n = 6$). Statistically significant differences between temperature treatments are portrayed as * ($p < 0.05$).

Growth temperature had no significant impact on the short-term temperature response of photosynthesis for either species (Figure 4; Table 1). T_{opt} in tall fescue grown under aT and eT was ~29 °C and 28 °C, respectively, while T_{opt} in lucerne was ~30 °C for individuals grown under both aT and eT. We observed no significant difference in the T_{opt} between species and no interaction between species and growth temperature.

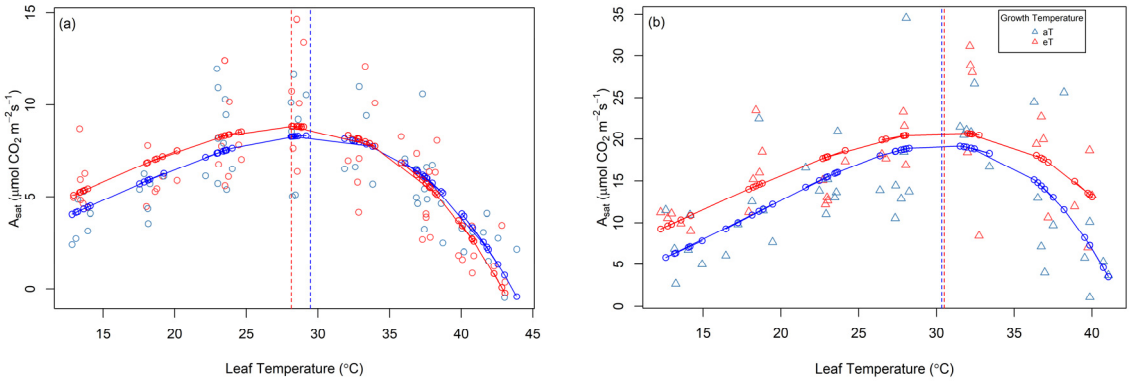

Figure 4. Short-term temperature response of light-saturated net photosynthesis (A_{sat}) for (**a**) tall fescue and (**b**) lucerne grown under 26 °C (aT, blue) and 30 °C (eT, red). Blue and red lines indicate the temperature response function for the 26 °C and 30 °C growth temperature treatments, respectively. Vertical dashed lines represent the T_{opt} for each species grown under aT (blue) and eT (red).

3.4. WUE

Despite a small trend toward a reduction in WUE for both species under warming, no significant change in WUE_i (Figure 5a) or WUE_{inst} (Figure 5b) was observed in either species (Table 1). We also observed no significant change in WUE_i normalised for VPD and expressed as g_1 (Figure 5c).

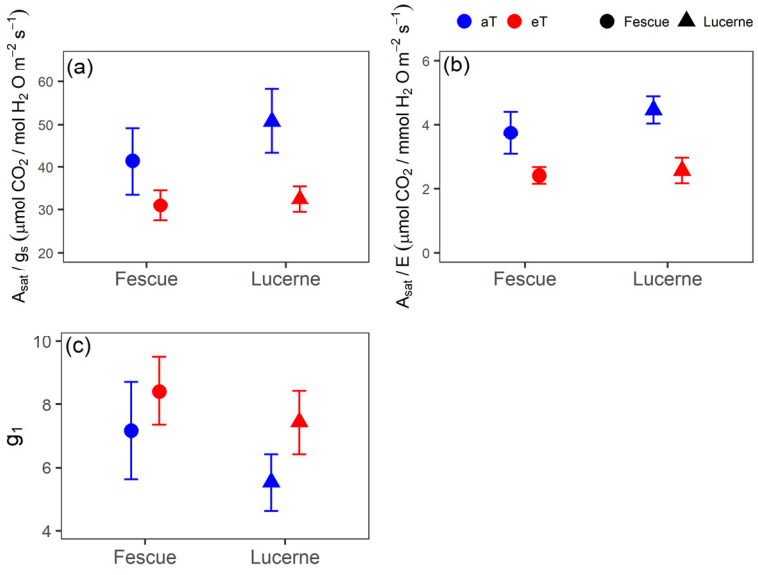

Figure 5. Water use efficiency parameters for tall fescue (circles) and lucerne (triangles) grown under 26 °C (aT, blue) and 30 °C (eT, red). (**a**) Ratio of light-saturated photosynthesis at ambient [CO_2] (A_{sat}) to stomatal conductance (g_s) (WUE_i), (**b**) Ratio of A_{sat} to transpiration (E) (WUE_{inst}), (**c**) model fit parameter using Equation (1) (g_1). Values shown are means and error bars indicate ± standard error (n = 6).

3.5. Shoot Stoichiometry

Warming had no significant impact on shoot N for tall fescue, but led to a 38% increase in lucerne (Figure 6a, $p = 0.049$). Warming had no impact on shoot P for either species, but caused a significant increase in N:P ratio (+69%, $p = 0.043$) for tall fescue. Both tall fescue and lucerne incurred a significant reduction in C:N ratio by 26% (Figure 6d, $p = 0.009$) and 21% ($p = 0.026$), respectively.

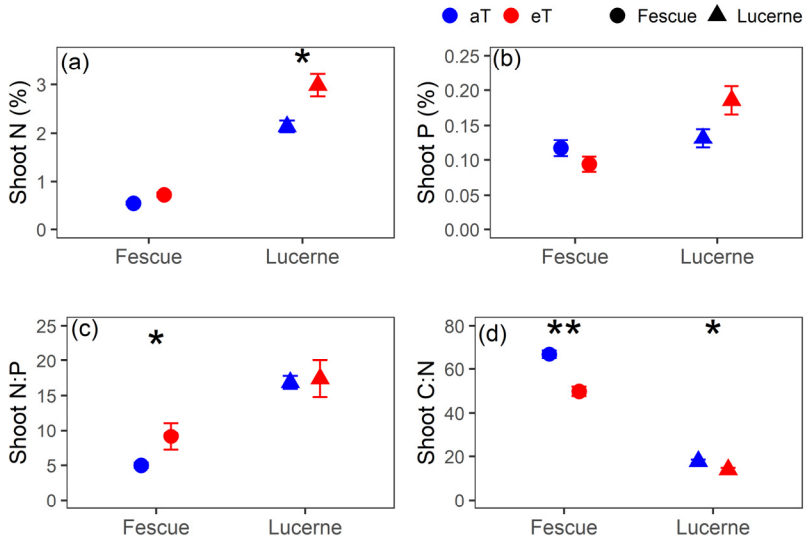

Figure 6. Shoot nutrient stoichiometry (**a**), Shoot N (**b**) P (**c**) N:P ratio (**d**) C:N ratio for tall fescue (circles) and lucerne (triangles) grown under 26 °C (aT, blue) and 30 °C (eT, red). Error bars indicate ± standard error. Statistically significant differences between temperature treatments are portrayed as * ($p < 0.05$), ** ($p < 0.01$).

4. Discussion

Here we sought to investigate the effect of climate model-predicted increases in temperature on the physiology and productivity of two widely cultivated, and economically important [62,67,68], pasture species. We found that a 4 °C increase in growth temperature had a more significant impact on the temperate legume (lucerne) than on the C_3 grass (tall fescue), despite similar climate niches in pastures. Lucerne experienced reductions in photosynthetic capacity and increased R_{dark} under eT, while tall fescue showed an increase in R_{eco} despite little change in physiological function at the leaf level. The results for lucerne support our first hypothesis, that photosynthetic upregulation under warming would be counterbalanced by a corresponding increase in respiration rates; however, this was not observed in tall fescue. Despite some physiological adjustment in tall fescue, both species exhibited significant declines in biomass productivity, contrary to our second hypothesis that tall fescue would be less negatively impacted than lucerne, due to its higher normal growing temperature of 15–30 °C. We also found little evidence to support our third hypothesis, that warming would lead to a reduction in plant water use efficiency.

Despite numerous global predictions suggesting widespread gains in photosynthesis with increasing temperatures, research examining these relationships in temperate pastures and related species have shown mixed results [84–86]. Here, we observed a significant interaction between species and growth temperature; lucerne exhibited a reduction in photosynthetic capacity under eT, while tall fescue exhibited a small increase. Our findings are in line with previous studies on tall fescue that observed little change in photosynthetic capacity between 25 to 30 °C [46] or found an increase in photosynthesis between 15–35 °C over the short term [14,87]. Studies have however, found marked reductions in photosynthetic capacity for tall fescue after long-term exposure to 35 °C [88], even in a putative heat-tolerant cultivar [6]. Our results for lucerne disagree with previous literature, which suggests that lucerne has a broad temperature optimum and experiences little to no change

in carbon assimilation between 5–30 °C [20,47,84,89,90] and others who observed the highest rate of photosynthesis at 34 °C [91]. Our results do, however, agree with those of Pearson & Hunt (1972) [92] who found a steady decline in photosynthesis between 10 & 40 °C. Differences in these studies may be due to differences in light intensity, other environmental conditions and timing of measurements. Furthermore, many of the earlier experiments were conducted at the whole pot level and may not account for temperature-derived changes in soil C flux. Our results for lucerne are similar to field-based experiments, in which experimental warming increased photosynthesis in the grass *Festuca ovina*, but reduced photosynthesis in lucerne [23].

We found little evidence of photosynthetic acclimation with both species having a similar T_{opt} of ~30 °C at both growth temperatures. Our results agree with Brown and Radcliffe (1986), who observed a T_{opt} for photosynthesis of 30 °C. Therefore, air temperatures that generate leaf temperatures above 30 °C will most likely lead to reductions in photosynthesis. Our results are in contrast to previous studies on similar species, which observed that T_{opt} of photosynthesis was influenced to a greater degree by growth temperature than either species or climate-of-origin, with plants grown under lower temperatures showing markedly different T_{opt} when grown at temperatures ranging from 15 to 35 °C [48,85,87,89].

At the leaf level, warming significantly increased R_{dark} in lucerne, but had no impact on tall fescue. This is in line with previous long-term studies on lucerne, which observed a 54% increase in R_{dark} when grown at 25 & 30 °C [93] and a 60% increase in respiration when lucerne was grown at 21 °C and 34 °C [91]. A previous study on tall fescue by Yu et al., (2012) [46] observed an increase in day-time respiration when plants were exposed to an increase in temperature from 25 °C to 30 °C; however, this effect disappeared after 28 days of high temperature exposure. Our results are similar to a meta-analysis [4] which found that warming, ranging from 0.5 to 29.6 °C, generally led to a greater increase in respiration for C_3 forbs (+57%) than grasses (+20%).

At the level of the plant-root-soil system, we found warming significantly increased R_{eco} for tall fescue but had no impact on lucerne. Given little change in leaf-level respiration (R_{dark}), the increase in R_{eco} for fescue under eT may be driven by increased respiration belowground (i.e., root or microbial respiration). Previous studies have shown contradictory results, with a recent meta-analysis suggesting a general increase in belowground respiration with temperature [94] while other studies have found no consistent effect [95,96] acclimation over time [97] or a reduction in respiration under warming [98]. Many of these studies, however, did not control for changes in soil water content or plant biomass in response to warming. Furthermore, previous studies have found that warming significantly increases belowground C allocation via root exudates under N limiting conditions [99–101]. In our study, tall fescue was severely limited by N while this was not the case in lucerne, due to high levels of nodulation and N fixing activity in lucerne (personal communication H. Zhang). The paradigm that short-term stimulation of respiration under warming declines with exposure time, and that respiration acclimates to growth temperature over the long-term [3,8,22,43–45], was not observed in our species after four months of growth at warmer temperatures.

Our results indicate that warming amplified net C loss for both species, but in different ways: via belowground respiration in tall fescue and via leaf respiration in lucerne and, the overall trend towards a reduction in net C was highlighted by the significant reductions in biomass for both species. Our results for lucerne are similar to studies that suggested an optimum temperature for growth between 15–25 °C in the daytime and 10–20 °C in the night-time [14,89,91], but contrasts with studies showing no reduction in growth between 10–30 °C, with marked reductions being observed only at temperatures around 40 °C [92,102,103]. Previous studies on tall fescue have observed similar trends with festucoid species observed to have an optimum growth temperature between 20–27 °C [85,87,104,105]. The significant declines in biomass for tall fescue, despite little change in photosynthetic capacity, suggests that whole-plant productivity may be more sink-limited than source-limited [106], with productivity regulated by tiller production & leaf canopy orientation [107]. The significant decline in productivity for both species under warming may also be linked to the

significant reduction we observed in C:N ratio, which suggests a decline in long term nitrogen use efficiency [108].

Growth temperature had no significant impact on leaf level water use efficiency in either species. This may be due to our careful control of soil moisture, thereby removing potential indirect effects of temperature on WUE via changes in soil moisture and the transient effect of temperature on g_s which disappeared over the long-term [6]. Our results are consistent with other long-term studies in cotton (*Gossypium hirsutum* L.) grown at 28 and 32 °C [109] and in soybean [*Glycine max* (L.) Merr.] grown at 28 and 32 °C [110], while field studies on rice observed a reduction in WUE between 26 & 30 °C [111]. Short-term studies on tall fescue have observed a decrease in WUE_{inst} in plants exposed to high temperature stress (35 °C) of 20 days when compared to those grown at 20 °C [6], while Yu et al., 2012 found no significant change in WUE for tall fescue grown at 30 °C after 28 days of exposure, when compared to those grown at 25 °C.

5. Conclusions

For plants to successfully acclimate to higher growth temperature, they must increase photosynthetic capacity to counteract temperature-driven increases in respiration. Numerous studies have suggested that warming may have a stimulatory impact on photosynthetic capacity globally, leading to enhanced net C balance of leaves and increasing primary productivity and terrestrial biomass (see Liang et al. 2013 and references therein).

However, our results obtained under controlled environment conditions in a greenhouse suggest that in the warm climate of Australia, an increase in temperature may lead to an overall reduction in net C balance and large reductions in the productivity of pasture systems. Breeding and development of more heat-tolerant cultivars of economically important pasture species may be required to maintain current levels of pasture productivity.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-4395/10/10/1601/s1, Figure S1: Average rates of light saturated photosynthesis (A_{sat}) at 8, 12 & 15 weeks after planting (WAP) for tall fescue (circles) and lucerne (triangles) grown under ambient (aT 26/18 °C day/night, blue) and elevated (eT 30/22 °C day/night, red) temperatures. Green line indicates point at which all individuals were clipped to 5 cm height. Error bars indicate ± standard error; Table S1: Parameters of A-PPFD curves for tall fescue (*Festuca arundinacea*) and lucerne (*Medicago sativa*) grown under aT (26 °C) and eT (30 °C). Parameters include maximum net photosynthesis at maximum PPFD level ($A_{max\text{-}light}$) (μmol CO_2 m^{-2} s^{-1}), apparent quantum efficiency (Φ) (μmol CO_2 μmol^{-1} photon), light compensation point (LCP) (μmol m^{-2} s^{-1}) and light saturating point (LSP) (μmol m^{-2} s^{-1}). Each value is the mean ± S.E (n = 6).

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References

1. Bernstein, L.; Bosch, P.; Canziani, O.; Chen, Z.; Christ, R.; Davidson, O.; Hare, W.; Huq, S.; Karoly, D.; Kattsov, V.; et al. *Climate Change 2007: Synthesis Report: An Assessment of the Intergovernmental Panel on Climate Change*; IPCC: Geneva, Switzerland, 2008.
2. Farquhar, G.D.; Von Caemmerer, S.; Berry, J.A. A Biochemical Model of Photosynthetic CO_2 Assimilation. *Planta* **1980**, *90*, 78–90. [CrossRef] [PubMed]
3. Atkin, O.K.; Tjoelker, M.G. Thermal Acclimation and the Dynamic Response of Plant Respiration to Temperature. *Trends Plant Sci.* **2003**, *8*, 343–351. [CrossRef]

4. Liang, J.; Xia, J.; Liu, L.; Wan, S. Global Patterns of the Responses of Leaf-Level Photosynthesis and Respiration in Terrestrial Plants to Experimental Warming. *J. Plant Ecol.* **2013**, *6*, 437–447. [CrossRef]
5. Ryan, E.M.; Ogle, K.; Peltier, D.; Walker, A.P.; De Kauwe, M.G.; Medlyn, B.E.; Williams, D.G.; Parton, W.; Asao, S.; Guenet, B.; et al. Gross Primary Production Responses to Warming, Elevated CO_2, and Irrigation: Quantifying the Drivers of Ecosystem Physiology in a Semiarid Grassland. *Glob. Chang. Biol.* **2017**, *23*, 3092–3106. [CrossRef] [PubMed]
6. Cui, L.; Li, J.; Fan, Y.; Xu, S.; Zhang, Z. High Temperature Effects on Photosynthesis, PSII Functionality and Antioxidant Activity of Two *Festuca arundinacea* Cultivars with Different Heat Susceptibility. *Bot. Stud.* **2006**, *47*, 61–69.
7. Cullen, B.R.; Johnson, I.R.; Eckard, R.J.; Lodge, G.M.; Walker, R.G.; Rawnsley, R.P.; McCaskill, M.R. Climate Change Effects on Pasture Systems in South-Eastern Australia. *Crop Pasture Sci.* **2009**, *60*, 933–942. [CrossRef]
8. Aspinwall, M.J.; Varhammar, A.; Blackman, C.J.; Tjoelker, M.G.; Ahrens, C.; Byrne, M.; Tissue, D.T.; Rymer, P.D. Adaptation and Acclimation Both Influence Photosynthetic and Respiratory Temperature Responses in *Corymbia calophylla*. *Tree Physiol.* **2017**, *37*, 1095–1112. [CrossRef] [PubMed]
9. Berry, J.; Bjorkman, O. Photosynthetic Response and Adaptation to Temperature in Higher Plants. *Annu. Rev. Plant Physiol.* **1980**, *31*, 491–543. [CrossRef]
10. Drake, J.E.; Aspinwall, M.J.; Pfautsch, S.; Rymer, P.D.; Reich, P.B.; Smith, R.A.; Crous, K.Y.; Tissue, D.T.; Ghannoum, O.; Tjoelker, M.G. The Capacity to Cope with Climate Warming Declines from Temperate to Tropical Latitudes in Two Widely Distributed Eucalyptus Species. *Glob. Chang. Biol.* **2015**, *21*, 459–472. [CrossRef]
11. Ishikawa, K.; Onoda, Y.; Hikosaka, K. Intraspecific Variation in Temperature Dependence of Gas Exchange Characteristics among *Plantago asiatica* Ecotypes from Different Temperature Regimes. *New Phytol.* **2007**, *172*, 356–364. [CrossRef]
12. Kumarathunge, D.P.; Medlyn, B.E.; Drake, J.E.; Tjoelker, M.G.; Aspinwall, M.J.; Battaglia, M.; Cano, F.J.; Kelsey, C.R.; Cavaleri, M.A.; Cernusak, L.A.; et al. Acclimation and Adaptation Components of the Temperature Dependence of Plant Photosynthesis at the Global Scale. *New Phytol.* **2018**, *222*, 768–784. [CrossRef]
13. Way, D.A.; Yamori, W. Thermal Acclimation of Photosynthesis: On the Importance of Adjusting Our Definitions and Accounting for Thermal Acclimation of Respiration. *Photosynth. Res.* **2014**, *119*, 89–100. [CrossRef] [PubMed]
14. Brown, R.H.; Morgan, J.A. Photosynthesis of Grass Species Differing in Carbon Dioxide Fixation Pathways' VI. Differential effects of temperature and light intensity on photorespiration in C_3, C_4, and intermediate species. *Plant Physiol.* **1980**, *66*, 541–544. [CrossRef] [PubMed]
15. Walker, A.P.; Beckerman, A.P.; Gu, L.; Kattge, J.; Cernusak, L.A.; Domingues, T.F.; Scales, J.C.; Wohlfahrt, G.; Wullschleger, S.D.; Woodward, F.I. The Relationship of Leaf Photosynthetic Traits—V_{cmax} and J_{max}—to Leaf Nitrogen, Leaf Phosphorus, and Specific Leaf Area: A Meta-Analysis and Modeling Study. *Ecol. Evol.* **2014**, *4*, 3218–3235. [CrossRef]
16. Medlyn, B.E.; Dreyer, E.; Ellsworth, D.; Forstreuter, M.; Harley, P.C.; Kirschbaum, M.U.F.; Le Roux, X.; Montpied, P.; Strassemeyer, J.; Walcroft, A.; et al. Temperature Response of Parameters of a Biochemically Based Model of Photosynthesis. II. A Review of Experimental Data. *Plant Cell Environ.* **2002**, *25*, 1167–1179. [CrossRef]
17. Joseph, T.; Whitehead, D.; Turnbull, M.H. Soil Water Availability Influences the Temperature Response of Photosynthesis and Respiration in a Grass and a Woody Shrub. *Funct. Plant Biol.* **2014**, *41*, 468–481. [CrossRef]
18. Hikosaka, K.; Ishikawa, K.; Borjigidai, A.; Muller, O.; Onoda, Y. Temperature Acclimation of Photosynthesis: Mechanisms Involved in the Changes in Temperature Dependence of Photosynthetic Rate. *J. Exp. Bot.* **2006**, *57*, 291–302. [CrossRef] [PubMed]
19. Wright, I.J.; Reich, P.B.; Atkin, O.K.; Lusk, C.H.; Tjoelker, M.G.; Westoby, M. Irradiance, Temperature and Rainfall Influence Leaf Dark Respiration in Woody Plants: Evidence from Comparisons across 20 Sites. *New Phytol.* **2006**, *169*, 309–319. [CrossRef]
20. Brown, R.H.; Bouton, J.H.; Rigsby, L.; Rigler, M. Photosynthesis of Grass Species Differing in Carbon Dioxide Fixation Pathways. *Plant Physiol.* **1983**, *71*, 425–431. [CrossRef]

21. Way, D.A.; Sage, R.F. Thermal Acclimation of Photosynthesis in Black Spruce [*Picea mariana* (Mill.) B.S.P.]. *Plant Cell Environ.* **2008**, *31*, 1250–1262. [CrossRef] [PubMed]
22. Ow, L.F.; Whitehead, D.; Walcroft, A.S.; Turnbull, M.H. Thermal Acclimation of Respiration but Not Photosynthesis in *Pinus radiata*. *Funct. Plant Biol.* **2008**, *35*, 448–461. [CrossRef] [PubMed]
23. Valencia, E.; Quero, J.L.; Maestre, F.T. Functional Leaf and Size Traits Determine the Photosynthetic Response of 10 Dryland Species to Warming. *J. Plant Ecol.* **2016**, *9*, 773–783. [CrossRef]
24. Parmesan, C. Influences of Species, Latitudes and Methodologies on Estimates of Phenological Response to Global Warming. *Glob. Chang. Biol.* **2007**, *13*, 1860–1872. [CrossRef]
25. Holmgren, M.; Gómez-Aparicio, L.; Quero, J.L.; Valladares, F. Non-Linear Effects of Drought under Shade: Reconciling Physiological and Ecological Models in Plant Communities. *Oecologia* **2012**, *169*, 293–305. [CrossRef]
26. Xiong, F.S.; Mueller, E.C.; Day, T.A. Photosynthetic and Respiratory Acclimation and Growth Response of Antarctic Vascular Plants to Contrasting Temperature Regimes. *Am. J. Bot.* **2000**, *87*, 700–710. [CrossRef]
27. Dermody, O.; Weltzin, J.F.; Engel, E.C.; Allen, P.; Norby, R.J. How Do Elevated [CO_2], Warming, and Reduced Precipitation Interact to Affect Soil Moisture and LAI in an Old Field Ecosystem? *Plant Soil* **2007**, *301*, 255–266. [CrossRef]
28. Gunderson, C.A.; O'hara, K.H.; Campion, C.M.; Walker, A.V.; Edwards, N.T. Thermal Plasticity of Photosynthesis: The Role of Acclimation in Forest Responses to a Warming Climate. *Glob. Chang. Biol.* **2010**, *16*, 2272–2286. [CrossRef]
29. AMTHOR, J.S. Respiration in a Future, Higher-CO_2 World. *Plant Cell Environ.* **1991**, *14*, 13–20. [CrossRef]
30. Salvucci, M.E.; Crafts-Brandner, S.J. Inhibition of Photosynthesis by Heat Stress: The Activation State of Rubisco as a Limiting Factor in Photosynthesis. *Physiol. Plant.* **2004**, *120*, 179–186. [CrossRef]
31. Lewis, J.D.; Phillips, N.G.; Logan, B.A.; Hricko, C.R.; Tissue, D.T. Leaf Photosynthesis, Respiration and Stomatal Conductance in Six Eucalyptus Species Native to Mesic and Xeric Environments Growing in a Common Garden. *Tree Physiol.* **2011**, *31*, 997–1006. [CrossRef]
32. Atkin, O.K.; Holly, C.; Ball, M.C. Acclimation of Snow Gum (*Eucalyptus pauciflora*) Leaf Respiration to Seasonal and Diurnal Variations in Temperature: The Importance of Changes in the Capacity and Temperature Sensitivity of Respiration. *Plant Cell Environ.* **2000**, *23*, 15–26. [CrossRef]
33. Tjoelker, M.G.; Oleksyn, J.; Reich, P.B. Modelling Respiration of Vegetation: Evidence for a General Temperature-Dependent Q_{10}. *Glob. Chang. Biol.* **2001**, *7*, 223–230. [CrossRef]
34. Turnbull, M.H.; Whitehead, D.; Tissue, D.T.; Schuster, W.S.F.; Brown, K.J.; Griffin, K.L. Responses of Leaf Respiration to Temperature and Leaf Characteristics in Three Deciduous Tree Species Vary with Site Water Availability. *Tree Physiol.* **2001**, *21*, 571–578. [CrossRef] [PubMed]
35. Whitehead, D.; Griffin, K.L.; Turnbull, M.H.; Tissue, D.T.; Engel, V.C.; Brown, K.J.; Schuster, W.S.F.; Walcroft, A.S. Response of Total Night-Time Respiration to Differences in Total Daily Photosynthesis for Leaves in a *Quercus rubra* L. Canopy: Implications for Modelling Canopy CO_2 Exchange. *Glob. Chang. Biol.* **2004**, *10*, 925–938. [CrossRef]
36. Katja, H.; Irina, B.; Hiie, I.; Olav, K.; Tiit, P.; Bahtijor, R.; Mari, T.; Ülo, N. Temperature Responses of Dark Respiration in Relation to Leaf Sugar Concentration. *Physiol. Plant.* **2012**, *144*, 320–334. [CrossRef]
37. Rodríguez-Calcerrada, J.; Limousin, J.M.; Martin-Stpaul, N.K.; Jaeger, C.; Rambal, S. Gas Exchange and Leaf Aging in an Evergreen Oak: Causes and Consequences for Leaf Carbon Balance and Canopy Respiration. *Tree Physiol.* **2012**, *32*, 464–477. [CrossRef]
38. Xu, C.Y.; Griffin, K.L. Seasonal Variation in the Temperature Response of Leaf Respiration in *Quercus rubra*: Foliage Respiration and Leaf Properties. *Funct. Ecol.* **2006**, *20*, 778–789. [CrossRef]
39. Turnbull, M.H.; Tissue, D.T.; Griffin, K.L.; Richardson, S.J.; Peltzer, D.A.; Whitehead, D. Respiration Characteristics in Temperate Rainforest Tree Species Differ along a Long-Term Soil-Development Chronosequence. *Oecologia* **2005**, *143*, 271–279. [CrossRef]
40. Slot, M.; Zaragoza-Castells, J.; Atkin, O.K. Transient Shade and Drought Have Divergent Impacts on the Temperature Sensitivity of Dark Respiration in Leaves of *Geum urbanum*. *Funct. Plant Biol.* **2008**, *35*, 1135–1146. [CrossRef]
41. Griffin, K.L.; Turnbull, M.; Murthy, R. Canopy Position Affects the Temperature Response of Leaf Respiration in *Populus deltoides*. *New Phytol.* **2002**, *154*, 609–619. [CrossRef]

42. Turnbull, M.H.; Whitehead, D.; Tissue, D.T.; Schuster, W.S.F.; Brown, K.J.; Griffin, K.L. Scaling Foliar Respiration in Two Contrasting Forest Canopies. *Funct. Ecol.* **2003**, *17*, 101–114. [CrossRef]
43. Atkin, O.K.; Bruhn, D.; Hurry, V.M.; Tjoelker, M.G. Evans Review No. 2—The Hot and the Cold: Unravelling the Variable Response of Plant Respiration to Temperature. *Funct. Plant Biol.* **2005**, *32*, 87–105. [CrossRef]
44. Way, D.A.; Oren, R. Differential Responses to Changes in Growth Temperature between Trees from Different Functional Groups and Biomes: A Review and Synthesis of Data. *Tree Physiol.* **2010**, *30*, 669–688. [CrossRef]
45. Wythers, K.R.; Reich, P.B.; Tjoelker, M.G.; Bolstad, P.B. Foliar Respiration Acclimation to Temperature and Temperature Variable Q_{10} Alter Ecosytem Carbon Balance. *Glob. Chang. Biol.* **2005**, *11*, 435–449. [CrossRef]
46. Yu, J.; Chen, L.; Xu, M.; Huang, B. Effects of Elevated CO_2 on Physiological Responses of Tall Fescue to Elevated Temperature, Drought Stress, and the Combined Stresses. *Crop Sci.* **2012**, *52*, 1848–1858. [CrossRef]
47. Vong, N.Q.; Murata, Y. Studies on the Physiological Characteristics of C_3 and C_4 Crop Species: I. The Effects of Air Temperature on the Apparent Photosynthesis, Dark Respiration, and Nutrient Absorption of Some Crops. *Jpn. J. Crop Sci.* **1977**, *46*, 45–52. [CrossRef]
48. Bolton, J.K.; Harold Brown, R. Photosynthesis of Grass Species Differing in Carbon Dioxide Fixation Pathways. V. Response of *Panicum maximum*, *Panicum milioides*, and Tall Fescue (*Festuca arundinacea*) to Nitrogen Nutrition. *Plant Physiol.* **1980**, *66*, 97–100. [CrossRef]
49. Huang, B.; Fu, J. Photosynthesis, Respiration, and Carbon Allocation of Two Cool-Season Perennial Grasses in Response to Surface Soil Drying. *Plant Soil* **2000**, *227*, 17–26. [CrossRef]
50. Bélanger, G.; Gastal, F.; Warembourg, F.R. Carbon Balance of Tall Fescue (*Festuca arundinacea* Schreb.): Effects of Nitrogen Fertilization and the Growing Season. *Ann. Bot.* **1994**, *74*, 653–659. [CrossRef]
51. Skinner, R.H. Nitrogen Fertilization Effects on Pasture Photosynthesis, Respiration, and Ecosystem Carbon Content. *Agric. Ecosyst. Environ.* **2013**, *172*, 35–41. [CrossRef]
52. Ludlow, M.M. Studies on the Productivity of Tropical Pasture Plants. V.* Effect of Shading on Growth, Photosynthesis and Respiration in Two Grasses and Two Legumes. *Aust. J. Agric. Res.* **1974**, *25*, 425–433. [CrossRef]
53. Kumarathunge, D.P.; Drake, J.E.; Tjoelker, M.G.; López, R.; Pfautsch, S.; Vårhammar, A.; Medlyn, B.E. The Temperature Optima for Tree Seedling Photosynthesis and Growth Depend on Water Inputs. *Glob. Chang. Biol.* **2020**, *26*, 2544–2560. [CrossRef] [PubMed]
54. Tarin, T.; Nolan, R.H.; Medlyn, B.E.; Cleverly, J.; Eamus, D. Water-Use Efficiency in a Semi-Arid Woodland with High Rainfall Variability. *Glob. Chang. Biol.* **2020**, *26*, 496–508. [CrossRef] [PubMed]
55. Yoo, C.Y.; Pence, H.E.; Hasegawa, P.M.; Mickelbart, M.V. Regulation of Transpiration to Improve Crop Water Use. *Crit. Rev. Plant Sci.* **2009**, *28*, 410–431. [CrossRef]
56. Will, R.E.; Wilson, S.M.; Zou, C.B.; Hennessey, T.C. Increased Vapor Pressure Deficit Due to Higher Temperature Leads to Greater Transpiration and Faster Mortality during Drought for Tree Seedlings Common to the Forest-Grassland Ecotone. *New Phytol.* **2013**, *200*, 366–374. [CrossRef] [PubMed]
57. Duan, H.; Duursma, R.A.; Huang, G.; Smith, R.A.; Choat, B.; O'Grady, A.P.; Tissue, D.T. Elevated [CO_2] Does Not Ameliorate the Negative Effects of Elevated Temperature on Drought-Induced Mortality in *Eucalyptus radiata* Seedlings. *Plant Cell Environ.* **2014**, *37*, 1598–1613. [CrossRef]
58. Von Caemmerer, S.; Farquhar, G.D. Some Relationships between the Biochemistry of Photosynthesis and the Gas Exchange of Leaves. *Planta* **1981**, *153*, 376–387. [CrossRef]
59. Fischer, R.; Turner, N.C. Plant productivity in the arid and semiarid zones. *Ann. Rev. Plant Physiol.* **1978**, *29*, 277–317. [CrossRef]
60. Monteith, J.L.; Greenwood, D.J. How Do Crops Manipulate Water Supply and Demand? *Philos. Trans. R. Soc. Lond. Ser. A Math. Phys. Sci.* **1986**, *316*, 245–259. [CrossRef]
61. Medlyn, B.E.; Duursma, R.A.; Eamus, D.; Ellsworth, D.S.; Prentice, I.C.; Barton, C.V.M.; Crous, K.Y.; De Angelis, P.; Freeman, M.; Wingate, L. Reconciling the Optimal and Empirical Approaches to Modelling Stomatal Conductance. *Glob. Chang. Biol.* **2011**, *17*, 2134–2144. [CrossRef]
62. Bouton, J.H. An Overview of the Role of Lucerne (*Medicago sativa* L.) in Pastoral Agriculture. *Crop Pasture Sci.* **2012**, *63*, 734–738. [CrossRef]
63. Yang, S.; Gao, M.; Xu, C.; Gao, J.; Deshpande, S.; Lin, S.; Roe, B.A.; Zhu, H. Alfalfa Benefits from *Medicago truncatula*: The RCT1 Gene from *M. truncatula* Confers Broad-Spectrum Resistance to Anthracnose in Alfalfa. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 12164–12169. [CrossRef]

64. Wigley, K.; Ridgway, H.J.; Humphries, A.W.; Ballard, R.A.; Moot, D.J. Increased Lucerne Nodulation in Acid Soils with *Sinorhizobium meliloti* and Lucerne Tolerant to Low PH and High Aluminium. *Crop Pasture Sci.* **2018**, *69*, 1031–1040. [CrossRef]
65. Kørup, K.; Lærke, P.E.; Baadsgaard, H.; Andersen, M.N.; Kristensen, K.; Münnich, C.; Didion, T.; Jensen, E.S.; Mårtensson, L.M.; Jørgensen, U. Biomass Production and Water Use Efficiency in Perennial Grasses during and after Drought Stress. *GCB Bioenergy* **2018**, *10*, 12–27. [CrossRef]
66. Mcdonald, W.; Nikandrow, A.; Bishop, A.; Lattimore, M.; Gardner, P.; Williams, R.; Hyson, L. *Lucerne for Pasture and Fodder*; NSW Agriculture: Orange, NSW, Australia, 2003; Agfact P2. 2.25.
67. Harris, C.; Clark, S.; Culvenor, R.; Li, G.; Gardner, M.; Hayes, R.; Nie, Z.; Norton, M.; Clark, B. New Tall Fescue Cultivars for Medium to Low Rainfall Environments in Southern Australia. In Proceedings of the 16th Australian Agronomy Conference on Capturing Opportunities and Overcoming Obstacles in Australian Agronomy, Armidale, NSW, Australia, 14–18 October 2012.
68. Yang, F.; Li, J.; Gan, X.; Qian, Y.; Wu, X.; Yang, Q. Assessing Nutritional Status of *Festuca arundinacea* by Monitoring Photosynthetic Pigments from Hyperspectral Data. *Comput. Electron. Agric.* **2010**, *70*, 52–59. [CrossRef]
69. Hill, M.J.; Pearson, C.J.; Kirby, A.C. Germination and Seedling Growth of Prairie Grass, Tall Fescue and Italian Ryegrass at Different Temperatures. *Aust. J. Agric. Res.* **1985**, *36*, 13–24. [CrossRef]
70. Aspinwall, M.J.; Drake, J.E.; Campany, C.; Vårhammar, A.; Ghannoum, O.; Tissue, D.T.; Reich, P.B.; Tjoelker, M.G. Convergent Acclimation of Leaf Photosynthesis and Respiration to Prevailing Ambient Temperatures under Current and Warmer Climates in *Eucalyptus tereticornis*. *New Phytol.* **2016**, *212*, 354–367. [CrossRef]
71. Ghannoum, O.; Phillips, N.G.; Sears, M.A.; Logan, B.A.; Lewis, J.D.; Conroy, J.P.; Tissue, D.T. Photosynthetic Responses of Two Eucalypts to Industrial-Age Changes in Atmospheric [CO_2] and Temperature. *Plant Cell Environ.* **2010**, *33*, 1671–1681. [CrossRef] [PubMed]
72. Duursma, R.A. Plantecophys—An R Package for Analysing and Modelling Leaf Gas Exchange Data. *PLoS ONE* **2015**, *10*, e0143346. [CrossRef]
73. Sharkey, T.D.; Bernacchi, C.J.; Farquhar, G.D.; Singsaas, E.L. Fitting Photosynthetic Carbon Dioxide Response Curves for C_3 leaves. *Plant Cell Environ.* **2007**, *30*, 1035–1040. [CrossRef] [PubMed]
74. Heberling, J.M.; Fridley, J.D. Resource-Use Strategies of Native and Invasive Plants in Eastern North American Forests. *New Phytol.* **2013**, *200*, 523–533. [CrossRef]
75. Marshall, B.; Biscoe, P.V. A Model for C3 Leaves Describing the Dependence of Net Photosynthesis on Irradiance: II. Application to the Analysis of Flag Leaf Photosynthesis. *J. Exp. Bot.* **1980**, *31*, 41–48. [CrossRef]
76. Thornley, J.H.M.; France, J. Mathematical Models in Agriculture: Quantitative Methods for the Plant, Animal and Ecological Sciences. Available online: https://books.google.com.au/books?id=rlwBCRSHobcC&printsec=frontcover#v=onepage&q&f=false (accessed on 21 July 2020).
77. Johnson, I.R. *DairyMod and the SGS Pasture Model: A Mathematical Description of the Biophysical Model Structure*; IMJ Consultants: Dorrigo, NSW, Australia, 2016; Available online: http://imj.com.au/dairymod/ (accessed on 18 June 2020).
78. Bender, S.F.; Plantenga, F.; Neftel, A.; Jocher, M.; Oberholzer, H.R.; Köhl, L.; Giles, M.; Daniell, T.J.; Van Der Heijden, M.G.A. Symbiotic Relationships between Soil Fungi and Plants Reduce N_2O Emissions from Soil. *ISME J.* **2014**, *8*, 1336–1345. [CrossRef] [PubMed]
79. Zufferey, V.; Spring, J.-L.; Verdenal, T.; Dienes, A.; Belcher, S.; Lorenzini, F.; Koestel, C.; Rösti, J.; Gindro, K.; Spangenberg, J.; et al. The Influence of Water Stress on Plant Hydraulics, Gas Exchange, Berry Composition and Quality of Pinot Noir Wines in Switzerland. *Oeno One* **2017**, *51*. [CrossRef]
80. Medlyn, B.E.; De Kauwe, M.G.; Lin, Y.S.; Knauer, J.; Duursma, R.A.; Williams, C.A.; Arneth, A.; Clement, R.; Isaac, P.; Limousin, J.M.; et al. How Do Leaf and Ecosystem Measures of Water-Use Efficiency Compare? *New Phytol.* **2017**, *216*, 758–770. [CrossRef] [PubMed]
81. Hiltpold, I.; Demarta, L.; Johnson, S.N.; Moore, B.D.; Power, S.A.; Mitchell, C. Silicon and other essential element composition in roots using X-ray fluorescence spectroscopy: A high throughput approach. *Invertebr. Ecol. Australas. Grassl.* **2016**, 191–196. [CrossRef]
82. Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D. Nlme: Linear and Nonlinear Mixed Effects Models; R Package Version 3.1-117. 2014. Available online: http://CRAN.R-project.org/package=nlme (accessed on 21 August 2020).

83. Lenth, R.; Singmann, H.; Love, J.; Buerkner, P.; Herve, M. Emmeans: Estimated Marginal Means, Aka Least-Squares Means; R Package Version 1.3. 4. 2019. Available online: https://CRAN.R-project.org/package=emmeans (accessed on 21 August 2020).
84. Thomas, M.; Hill, G. Photosynthesis under Field Conditions. In *Photosynthesis in Plants*; Iowa State College Press: Ames, IA, USA, 1949; pp. 19–52.
85. Charles-edwards, D.A.; Charles-edwards, J.; Cooper, J.P. The Influence of Temperature on Photosynthesis and Transpiration in Ten Temperate Grass Varieties Grown in Four Different Environments. *J. Exp. Bot.* **1971**, *22*, 650–662. [CrossRef]
86. Farfan-Vignolo, E.R.; Asard, H. Effect of Elevated CO_2 and Temperature on the Oxidative Stress Response to Drought in *Lolium perenne* L. and *Medicago sativa* L. *Plant Physiol. Biochem.* **2012**, *59*, 55–62. [CrossRef]
87. Sasaki, H.; FuKuyama, M.; Toko, O.; Suyama, T.; Shoji, A. Effects of Increasing CO_2 Concentration and Leaf Temperature on the Photosynthesis of Tall Fescue: *Festuca arundinacea* Schreb. *Jpn. J. Grassl. Sci.* **2002**, *48*, 12–16. [CrossRef]
88. Jiang, Y.; Huang, B. Physiological Responses to Heat Stress Alone or in Combination with Drought: A Comparison between Tall Fescue and Perennial Ryegrass. *HortScience* **2001**, *36*, 682–686. [CrossRef]
89. Murata, Y.; Iyama, J.; Honma, T. Studies on the Photosynthesis of Forage Crops: IV. Influence of Air-Temperature upon the Photosynthesis and Respiration of Alfalfa and Several Southern Type Forage Crops. *Jpn. J. Crop Sci.* **1965**, *34*, 154–158. [CrossRef]
90. Brown, R.H.; Radcliffe, D.E. A Comparison of Apparent Photosynthesis in *Sericea lespedeza* and Alfalfa 1. *Crop Sci.* **1986**, *26*, 1208–1211. [CrossRef]
91. Al-hamdani, S.; Todd, G.W. Effect of Temperature Regimes on Photosynthesis, Respiration, and Growth in Alfalfa. *Proc. Okla. Acad. Sci.* **1990**, *70*, 1–4.
92. Pearson, C.J.; Hunt, L.A. Effects of Pretreatment Temperature on Carbon Dioxide Exchange in Alfalfa. *Can. J. Bot.* **1972**, *50*, 1925–1930. [CrossRef]
93. Ziska, L.H.; Bunce, J.A. Direct and Indirect Inhibition of Single Leaf Respiration by Elevated CO_2 Concentrations: Interaction with Temperature. *Physiol. Plant.* **1994**, *90*, 130–138. [CrossRef]
94. Bond-Lamberty, B.; Thomson, A. Temperature-Associated Increases in the Global Soil Respiration Record. *Nature* **2010**, *464*, 579–582. [CrossRef]
95. Rustad, L.E.; Campbell, J.L.; Marion, G.M.; Norby, R.J.; Mitchell, M.J.; Hartley, A.E.; Cornelissen, J.H.C.; Gurevitch, J.; Alward, R.; Beier, C.; et al. A Meta-Analysis of the Response of Soil Respiration, Net Nitrogen Mineralization, and Aboveground Plant Growth to Experimental Ecosystem Warming. *Oecologia* **2001**, *126*, 543–562. [CrossRef]
96. Ryan, E.M.; Ogle, K.; Zelikova, T.J.; Lecain, D.R.; Williams, D.G.; Morgan, J.A.; Pendall, E. Antecedent Moisture and Temperature Conditions Modulate the Response of Ecosystem Respiration to Elevated CO_2 and Warming. *Glob. Chang. Biol.* **2015**, *21*, 2588–2602. [CrossRef]
97. Luo, Y.; Wan, S.; Hui, D.; Wallace, L.L. Acclimatization of Soil Respiration to Warming in a Tall Grass Prairie. *Nature* **2001**, *413*, 622–625. [CrossRef]
98. Pendall, E.; Heisler-White, J.L.; Williams, D.G.; Dijkstra, F.A.; Carrillo, Y.; Morgan, J.A.; LeCain, D.R. Warming Reduces Carbon Losses from Grassland Exposed to Elevated Atmospheric Carbon Dioxide. *PLoS ONE* **2013**, *8*, e71921. [CrossRef]
99. Yin, H.; Li, Y.; Xiao, J.; Xu, Z.; Cheng, X.; Liu, Q. Enhanced Root Exudation Stimulates Soil Nitrogen Transformations in a Subalpine Coniferous Forest under Experimental Warming. *Glob. Chang. Biol.* **2013**, *19*, 2158–2167. [CrossRef]
100. Yin, H.; Xiao, J.; Li, Y.; Chen, Z.; Cheng, X.; Zhao, C.; Liu, Q. Warming Effects on Root Morphological and Physiological Traits: The Potential Consequences on Soil C Dynamics as Altered Root Exudation. *Agric. Meteorol.* **2013**, *180*, 287–296. [CrossRef]
101. Zhang, Z.; Qiao, M.; Li, D.; Yin, H.; Liu, Q. Do Warming-Induced Changes in Quantity and Stoichiometry of Root Exudation Promote Soil N Transformations via Stimulation of Soil Nitrifiers, Denitrifiers and Ammonifiers? *Eur. J. Soil Biol.* **2016**, *74*, 60–68. [CrossRef]
102. Feltner, K.C.; Massengale, M.A. Influence of Temperature and Harvest Management on Growth, Level of Carbohydrates in the Roots, and Survival of Alfalfa (*Medicago sativa* L.). *Crop Sci.* **1965**, *5*, 585–588. [CrossRef]
103. Smith, D. Influence of Temperature on the Yield and Chemical Composition of 'Vernal' Alfalfa at First Flower. *Agron. J.* **1969**, *61*, 470–472. [CrossRef]

104. Cooper, J.; Taiton, N. Light and Temperature Requirements for the Growth of Tropical and Temperate Grasses. *Herb. Abstr.* **1968**, *38*, 167–176.
105. Sinclair, T.; Fiscus, E.; Wherley, B.; Durham, M.; Rufty, T. Atmospheric Vapor Pressure Deficit Is Critical in Predicting Growth Response of "Cool-Season" Grass *Festuca arundinacea* to Temperature Change. *Planta* **2007**, *227*, 273–276. [CrossRef]
106. Nelson, C.J.; Asay, K.H.; Horst, G.L. Relationship of Leaf Photosynthesis to Forage Yield of Tall Fescue. *Crop Sci.* **1975**, *15*, 476–478. [CrossRef]
107. Kiniry, J.R.; Kim, S. A Review of Modeled Water Use Efficiency of Highly Productive Perennial Grasses Useful for Bioenergy. *Agronomy* **2020**, *10*, 328. [CrossRef]
108. Chapin, F.S.; Van Cleve, K. (Eds.) Approaches to Studying Nutrient Uptake, Use and Loss in Plants. In *Plant Physiological Ecology*; Springer: Dordrecht, The Netherlands, 2000; pp. 185–207. [CrossRef]
109. Duursma, R.A.; Payton, P.; Bange, M.P.; Broughton, K.J.; Smith, R.A.; Medlyn, B.E.; Tissue, D.T. Near-Optimal Response of Instantaneous Transpiration Efficiency to Vapour Pressure Deficit, Temperature and [CO_2] in Cotton (*Gossypium hirsutum* L.). *Agric. Meteorol.* **2013**, *168*, 168–176. [CrossRef]
110. Allen, L.H.; Pan, D.; Boote, K.J.; Pickering, N.B.; Jones, J.W. Carbon Dioxide and Temperature Effects on Evapotranspiration and Water Use Efficiency of Soybean. *Agron. J.* **2003**, *95*, 1071–1081. [CrossRef]
111. Nakagawa, H.; Hone, T.; Kim, H.Y.; Ohnishi, H.; Homma, K. Rice Responses to Elevated CO_2 Concentrations and High Temperatures. *J. Agric. Meteorol.* **1997**, *52*, 797–800. [CrossRef]