Pastures and Climate Extremes: Impacts of warming and drought on the productivity and resilience of key pasture species in a field experiment

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Abstract

Shifts in the timing and frequency of climate extremes, such as drought and heatwaves, can generate sustained shifts in ecosystem function with important ecological and economic impacts for rangelands and managed pastures. The Pastures and Climate Extremes experiment (PACE) in southeast Australia used a factorial combination of elevated temperature (ambient +3 °C) and winter/spring extreme drought (60% rainfall reduction) to evaluate the impacts of increased frequency of climate extremes on pasture productivity and subsequent summer/autumn recovery. The experiment included nine species comprising three plant functional groups (C_3 grasses, C_4 grasses, and legumes) in monoculture and three two-species mixtures. The winter/spring drought resulted in productivity declines of up to 73% (*Digitaria eriantha*) during the 6-month treatment period, with nine of the twelve plantings exhibiting significant yield reductions. Functional group identity was not an important predictor of yield response to drought. Many species recovered rapidly once the drought ended, although there were carry-over effects on warm season (summer/autumn) growth for four species/mixtures, spanning all functional groups. Cool season drought translated into significant reductions in annual biomass production for four species/mixtures, ranging from 33% (*Medicago sativa*) to 70% (*Festuca arundinacea*). Additionally, warming had neutral to negative effects on productivity during both winter/spring and summer/autumn periods, resulting in annual yield declines of up to 58%, driven at least partially by indirect effects on soil water content. The combination of winter/spring drought and year-round warming resulted in net yield reductions that were either additive or less-than-additive, compared to ambient plots. This study demonstrates that predicted extreme climate conditions will have substantial negative impacts on productivity of common pasture and rangeland species.

Key words (6-10)

Climate warming, drought, grassland, rangeland, aboveground production, resistance and resilience, PACE research facility

1 Introduction

Climate change is identified as a dominant driver of ecosystem change across the globe (Sage, 2019; Steffen et al., 2015). Exposure to high temperatures or severe drought has been shown to disrupt physiological function and alter plant species interactions, ultimately driving changes in productivity and ecological processes such as nutrient and water cycling (Backhaus et al., 2014; Frank et al., 2015; Ma et al., 2015; Parmesan et al., 2000). Predicting how altered climate will impact these processes is difficult as climate extremes likely play a significant role in driving change in ecosystem function whereas models tend to focus on differences in mean annual temperature or precipitation (Easterling et al., 2000; Jentsch et al., 2009; Kreyling et al., 2008a). Despite a recent increase in the number of studies focusing on climate extremes (De Boeck et al., 2019, 2015; Hanson and Walker, 2019; Knapp et al., 2017), relatively few have addressed the ecological implications of seasonal shifts in patterns of extreme conditions for contrasting plant functional groups (i.e. C3 vs. C4, legumes; Beier et al., 2012). This is especially true for studies considering the impact of multiple climate variables simultaneously (Beier et al., 2012).

Ecosystems differ considerably in their sensitivity to drought. Managed grasslands and rangelands dominated by temperate grasses are generally considered to be drought sensitive, while tropical grasslands and legumes tend to be more resistant (Adams et al., 2016; Arredondo et al., 2016; Pearcy et al., 1987; Pearcy and Ehleringer, 1984; Wilcox et al., 2016). Ecosystem and plant responses to drought can be considered in terms of resistance - defined as the degree to which processes of interest remain unchanged during drought - or resilience, considered as the time required for recovery to pre-drought conditions (Kreyling et al., 2017; Pimm, 1984). Many studies have examined the potential for resistance versus resilience trade-offs among species in the context of drought (Hoover et al., 2014; Mitchell et

al., 2016) and there are a wide range of plant traits hypothesized to drive these responses. Examples include photosynthetic pathways and phenology (C_3 vs. C_4 grasses), growth forms (grass vs. forb), life history (perennial vs. annual) and ecosystem factors such as community species richness or functional diversity; indeed species- and/or functional group diversity is typically associated with both higher productivity and increased stress resistance in herbaceous communities, compared to lower diversity systems (Isbell et al., 2015; Vitasse et al., 2019; Vogel et al., 2012). Assessing both ecosystem resistance and resilience can be difficult in field settings due to requirements for long-term monitoring, inter-annual variability in abiotic conditions and ecological processes such as succession. Consequently, resilience has been assessed in less than half of all studies evaluating ecological consequences of an extreme event (Maxwell et al., 2019), although this aspect of plant response is key to understanding long-term impacts and consequences for ecosystem services.

In addition to changing rainfall regimes, rising temperatures are predicted to have direct and indirect impacts on many ecosystem processes (Bai et al., 2013; Novem Auyeung et al., 2013; Song et al., 2019). Direct impacts range from shifts in the timing of peak productivity relative to the start of the growing season (typically earlier) to extending the length of the growing season such that production occurs earlier and/or later in the year (Keatinge et al., 1998; Walker et al., 2006). The majority of field-based temperature manipulations have been carried out in temperate or cold-climate ecosystems where low temperatures constrain growth for at least a portion of the year. These studies often find increased total productivity and shifts in growth phenology associated with warming (Aerts et al., 2006; Kueppers et al., 2017; Lu et al., 2013; Walker et al., 2006), although there are exceptions (Arnone et al., 2011; Deutsch et al., 2011; Dukes et al., 2005). Warming experiments in warm-temperate or subtropical climates with comparatively short mild winters and hot summers are relatively

rare but needed to test whether climate warming exceeds optimal temperatures for growth (Dukes et al., 2005; Song et al., 2019; Volder et al., 2013).

Plant functional groups are predicted to differ in their response to warming, with warm-season species such as tropical grasses likely to benefit from increased winter or spring temperatures, while temperate grasses may be particularly vulnerable to higher temperatures (Munson and Long, 2017). Legume response to warming is likely to vary between seasons. For example, as with grasses, warming during the cooler months can bring temperatures closer to thermal optima (Peng et al., 2020; Sanz-Sáez et al., 2012; Whittington et al., 2013). However, higher summer temperatures may result in growth reductions as a consequence of thermal constraints on nitrogen fixation and increased respiratory carbon losses as temperatures exceed temperature optima for photosynthesis (Aranjuelo et al., 2007; Whittington et al., 2012). Understanding how warmer temperatures will affect the timing and amount of different grassland species' biomass production across seasons is an important knowledge gap in the context of both managed pastures and native grassland ecology.

While studies considering the impact of either precipitation or temperature on plant physiology and ecosystem function are valuable, it is important to note that warmer temperatures associated with extreme heatwaves frequently co-occur with drought (Boer et al., 2020; Dai, 2011; De Boeck et al., 2010; Yuan et al., 2016). Consequently, it is necessary to evaluate the impacts of co-occurring climate extremes on plant community structure and ecosystem function (Hoeppner and Dukes, 2012; Sherry et al., 2008). The **PA**stures and **C**limate **E**xtremes (PACE) field experiment sought to address this key area of research by exposing pasture and rangeland plant species to extreme winter and spring drought (60% rainfall reduction), in combination with elevated temperature (ambient + 3°C). Climate

models predict that temperate/sub-tropical Australia will be subject to large reductions in winter and spring rainfall (CSIRO, 2020). Increasing frequency and severity of drought is a consistent prediction for many grassland regions across the globe. Given the importance of pastures and rangelands for sustaining food security (Godde et al., 2020; Nábrádi, 2016; O'Mara, 2012), we established a large-scale, field experiment (the PACE facility) to evaluate plant species' responses to extreme winter/spring rainfall reduction and year-round warming, including intensification of heatwaves. Specifically, we asked: 1) How does extreme winter/spring drought affect species' productivity in monoculture and two-species mixtures? 2) Do the effects of winter/spring drought persist through the following summer and autumn (i.e. species' drought resilience) and what is the effect on annual productivity? 3) How does warming affect species' productivity in combination with drought? and, 4) Are there consistent functional group differences in response to drought and warming among pasture species? Here, we show that tropical and temperate grasses and legumes exhibited large and, in some cases persistent, reductions in productivity associated with both drought and elevated temperatures, and highlight the role of species mixtures in mitigating some of the effects of climate extremes on pasture productivity.

2 Methods

2.1 Site description

The PAstures and Climate Extremes (PACE) facility was constructed in 2017 at the Hawkesbury Campus of Western Sydney University, in Richmond, NSW, Australia (S33.60972, E150.73833, elevation 25 m). Mean annual precipitation at this location is 800 mm (Australian Government Bureau of Meteorology, Richmond - UWS Hawkesbury Station 1980-2010); however, there is large inter-annual variability (between 500 mm and over 1400 mm over the past 30 years). Winter/spring precipitation accounts for 40% of annual rainfall.

Mean annual temperature is 17.2 °C, with the monthly maximum and minimum occurring in January (22.9° C) and July (10.2° C), respectively. The site is fenced to prevent access by large herbivores. The soil is a loamy sand with a volumetric water holding capacity of 15-20% (**Table S1**).

The field facility comprised six replicate polytunnel shelters constructed from galvanized steel frames. These were covered with a single layer of polyethylene 180-micron plastic (Argosee, Australia) to intercept all ambient precipitation, although the long sides were open to a height of 1.5 m to allow free flow of air (**Figure 1**). Shelters were 48 m long by 8 m wide, with a maximum height of 4.6 m, and were oriented along a SW-NE axis with the open ends facing into the direction of the prevailing wind. Each shelter had eight treatment plots (4 m by 4 m; **Figure 1**) that were further subdivided into four subplots (**Figure 1B; Figure S1**), with different grassland species or two-species mixtures (hereafter referred to as "plantings") assigned at the subplot level (total 192 subplots). All surface soils were rotary-tilled to a depth of 12 cm to homogenize the upper soil profile prior to pasture establishment. Additionally, all 4 x 4 m plots had a full root barrier installed to a depth of 90 cm to ensure hydrological isolation between treatments and the 2 x 2 m subplots had an additional root barrier between them to a depth of 30 cm to minimise root ingress.

Nine plant species were grown in monoculture subplots along with three sets of two-species mixtures, for a total of twelve different plantings replicated in six independent shelters. Mixed two-species plots were included to examine drought resistance and resilience of a range of functional group pairings, compared to their respective monocultures. Species encompassed a range of functional diversity (C_3/C_4 grasses, legumes, annuals and perennials) and origins (native grasses, tropical pasture, temperate pasture; **Table 1**) that are all

commonly used in improved grasslands (pastures) or rangelands. For comparisons among common groupings, we considered three plant functional groups - legumes, C_3 grasses (temperate) and C_4 grasses (tropical); a fourth category comprised the mixed two-species plantings. Sward establishment was initiated during early spring 2017 (**Table S2**). Initial sowing included a fertilizer addition of diammonium phosphate (DAP;110 kg ha^{-1}), and swards were subsequently managed via hand-weeding, herbicide and, where needed, insecticide application to maintain target species following industry practice. Plantings with a legume component received appropriate rhizobium inoculant during sward establishment: ALOSCA granular inoculant for *Biserrula* subplots (Group BS; ALOSCA Technologies, Western Australia, Australia); Easy Rhiz soluble legume inoculant and protecting agent to *Medicago* subplots (Group AL; New Edge Microbials, New South Wales, Australia); and NoduleN for the *Trifolium* subplots (Group C; New Edge Microbials). Plantings received top-up fertilization seasonally to replace nutrients removed from the soil (55 kg ha^{-1}; Cal-Gran Aftergraze, Incitec Pivot Fertilisers, Australia).

2.2 Experimental treatments

All 12 planting combinations were exposed to a winter/spring drought regime implemented with reduced irrigation (Drought), and a subset of four plantings also received a warming treatment in a factorial combination with drought (**Figure S1**). The drought treatment comprised a control (Control: C) and a drought (Drought: D) watering regime that was applied during the 6-month austral winter/spring period (1 June to 30 November). For the following 6-month summer/autumn period (1 December to 31 May) all plots received the control irrigation amount. A 60% reduction in winter/spring rainfall was chosen for the drought manipulation as representing the upper end of climate model predictions for end-of-century seasonal rainfall change for south-eastern Australia, under RCP8.5 (CSIRO, 2020).

Furthermore, a 60% reduction in winter/spring was also in line with historical climate extremes for key pasture growing regions across south-eastern Australia (BOM, 2019); this treatment therefore represented historically relevant rainfall extremes, which are predicted to increase in both frequency and duration. The control was set to represent a typical precipitation regime for the local area, accounting for long-term patterns in seasonality and in the statistical distribution of event sizes and timing within seasons (**Figure S2**). The drought treatment was applied across all plantings of a species/mixture once swards were fully established, which generated staggered starting times and durations of drought among different species/mixtures (**Table 1)**.

Four plantings consisting of two monocultures (*Festuca, Medicago*) and two two-species mixtures (*Phalaris/Trifolium and Themeda/Rhytidosperma*) were also exposed to a warming treatment in a factorial combination with the winter/spring drought. These four plantings were grouped together as 2 x 2 m subplots in a single 4 x 4 m plot. The warming treatment comprised a year-round temperature increase of +3 °C (**Table 1**) achieved using infra-red (IR) heaters. Elevated temperatures (eT) were applied to two 4 x 4 m plots within each shelter; one plot received the control irrigation (eT-C) the other plot the drought treatment (eT-D) and these were paired with two ambient temperature (aT) plots, one receiving control irrigation (aT-C) and the other the drought treatment (aT-D). Each warmed plot had a heating array comprising eight 1000W ceramic heaters (FTE 1000W, Ceramicx, Ireland) mounted on an aluminium frame (4 m x 4 m) suspended 1.4 m above ground level (**Figure 1C**). Lamps were angled to give uniform coverage of IR radiation across the four composite subplots. The power level to the heating lamps was adjusted each minute, via pulse width modulation using a solid-state relay controlled by a data logger (CR1000, Campbell Scientific) using a proportional-integral control algorithm. Target temperatures for these plots were controlled

via feedback from IR-sensors (SI-100, Apogee Instruments, Logan, UT, USA) mounted at a height of 3.8 m, recording canopy surface temperatures every five minutes. The ambient + 3 °C warming treatment was applied with reference to canopy temperatures for the relevant control and drought treatments (i.e. aT-C paired to eT-C and aT-D paired to eT-D) to account for differences in soil moisture which can have an indirect effect on surface temperature.

2.3 Environmental monitoring

Each shelter had a data logger (CR1000, Campbell Scientific) that recorded environmental conditions and regulated the heating lamps. Soil moisture sensors (16 per shelter; Time Domain Reflectometers; CS616, Campbell Scientific) recorded soil moisture (0-15 cm) every 15 min in all six replicates of four different species monoculture subplots and treatment combinations (**Table S3**); in the *Medicago* subplot type soil moisture was also monitored at a second depth (15-30 cm). Soil temperature probes (T107, Campbell Scientific) were installed into the top 6-12 cm of the soil of eight subplots per shelter (all four drought and warming treatment combinations of *Festuca* and *Medicago*) to record soil temperature every 15 min (**Table S3**). Air temperature and humidity sensors (Series RHP-2O3B, Dwyer Instruments Inc, USA) mounted in force-ventilated radiation shields were installed inside three of the rainout shelters at 0.6 m height, with records collected every 5 min to determine shelter effects on environmental conditions. Additionally, three sets of sensors were installed at the same height outside the shelters. Photosynthetically active radiation (PAR) was recorded at 5-min intervals using PAR sensors (Apogee quantum sensor, USA) installed at a height of 6 m outside two shelters, with two additional sensors located within shelters at a height of 3 m.

2.4 Biomass harvests

All subplots were regularly harvested to determine aboveground productivity during active growing periods. This ‘surrogate grazing’ involved use of hand shears and a sickle mower. Timing of harvests was based on grazing recommendations for individual species and mixtures (Clements et al., 2003); hence, we conducted 3-5 harvests per year for perennial species (Clark et al., 2016) and 2-3 harvests for annual species that died back at the end of spring. Plants were cut to 5 cm above the soil surface and weighed (fresh and dry mass), with a sub-sample of harvested material sorted to determine the proportion of live and dead biomass as well as the weed fraction from each subplot. All materials were oven-dried at 70 °C for at least 48 hours.

2.5 Calculations and statistical analyses

The response of temperature and soil water content to applied drought and warming treatments were determined based on subplot-level (soil moisture, soil temperature) or plot-level (surface temperature) daily mean values. Aboveground production responses were determined based on subplot totals, summed across all harvests conducted within three defined time periods. Data were analysed separately for the 6-month winter/spring drought period (Drought period), the following 6-month summer/autumn recovery period (Recovery period), and for the combined 12-month period from June 2018-May 2019 (Annual).

Statistical analyses of treatment effects were carried out using linear mixed effects models with climate treatments (‘drought’: D or C, ‘warming’: aT or eT) as fixed effects and random effects defined as ‘subplot nested within plot’ or ‘plot’ (to account for non-independence among continuous measurements) nested within ‘shelter’ (to account for the blocked design), and ‘date’ (to account for temporal variation). Soil moisture data in *Medicago* subplots were

also analysed for differences between upper (0-15 cm) and lower (15-30 cm) depths among climate treatments by including ‘depth’ as an additional fixed effect. Climate treatment effects on aboveground production were analysed using two different linear mixed effects models based on our hypotheses comparing responses among different functional plant groups, and mixtures, using a ‘functional group’ categorical predictor fixed effect. For these analyses, ‘drought’ and ‘warming’ treatments were included as fixed effects; ‘planting type’ was also included as random effect for models examining differences among ‘functional groups’ as a fixed effect, to account for variability within plantings and ‘plot nested within shelter’ was included as a nested random effect for all models. Aboveground production was transformed using the natural logarithm to meet assumptions of normality where indicated in statistical tables. All analyses were conducted in R version 4.0.0 (R Core Team, 2020) using the package lme4 (Bates, 2015). Pairwise comparisons to determine treatment effects on temperature of soil or canopy and soil water content, or aboveground production among plantings or functional groups, were conducted using the R package emmeans (Length, 2019) and using the Tukey method for *P*-value adjustment.

To compare responses to drought among species/mixtures (i.e. “plantings”) and functional groups, log response ratios between control and droughted subplots paired within a shelter were calculated on aboveground production data for each period (winter/spring, summer/autumn, and annual). These ratios were used to evaluate differences in the effect of drought among 1) plantings and 2) functional groups using linear mixed effects models, with both specified as fixed effects. Random effects included ‘shelter’ for both models, while the model for 2) also included ‘planting type’ as an independent random effect. We additionally calculated mean treatment effect size (Equation 1) for each species on log-transformed production, with mean treatment level effects back-transformed and scaled such that 0 values

indicate no yield reduction. Standard error for the mean effect size was calculated as the product of the back-transformed mean and the standard error of the effect size.

$$\textit{Equation 1.} \qquad \textit{Effect size} = e^{\left(\ln\left(\frac{Drought}{Control}\right)-1\right)}$$

Finally, to account for differences in drought duration among plantings (Table 1), we calculated a drought sensitivity metric to provide a standardized comparison of production responses as a function of the amount of rainfall withheld (mm), compared with control treatments during the six-month winter/spring drought and annual periods (Smith et al., 2017; Equation 2). Drought sensitivity responses were also analysed using linear mixed effects models following the statistical model structure of the log response ratios above to examine differences among plantings and functional groups.

$$\textit{Equation 2.} \qquad \textit{Sensitivity Index} = -\frac{\textit{Control production- drought production (kg ha}^{-1}\textit{)}}{\textit{Control irrigation-drought irrigation (mm)}}$$

Interactive effects underlying the effect of warming on drought responses, the effect of drought on warming responses, and the effect of warming on drought effects, were calculated as the ratio between single factor treatment effects within a shelter for each period (Dieleman et al., 2012). These ratios were calculated such that the effect of drought was examined by comparing the effect size (Equation 1) for each warming level (aT-D / aT-C, eT-D / eT-C), the effect of warming was examined as the effect size for each drought level (eT-C / aT-C, eT-D / aT-D) and the effect of warming on the drought response as the ratio between these two effects ((eT-D / aT-D)/(eT-C / aT-C)).

3 Results

3.1 Drought and warming treatment effects on environmental conditions

Experimental drought and warming treatments significantly altered soil water content and temperature during the winter/spring period when drought was applied. This effect lasted

into the summer/autumn drought recovery period resulting in overall treatment differences in soil moisture, soil temperature and surface temperature at the annual scale (**Figure 2**, **Figure S3-6**, **Tables S4**, **S5**). During the winter/spring period, droughted subplots of *Biserrula* and *Festuca* had significantly reduced soil moisture in the upper 15 cm (**Figure 2**; **Table S4**; $P < 0.001$) compared with controls, while *Lolium* and *Medicago* soils were unaffected ($P = 0.12$, $P = 0.16$, respectively). Additionally, soil moisture contents in all droughted subplots were less variable throughout the winter/spring drought treatment period compared to their respective control subplots (**Figure 2A, B**). There were no residual effects of drought on soil moisture during the subsequent summer/autumn period for the two cool season annuals (*Biserrula* and *Lolium*, the latter effectively functioning as an annual at the study site due to high summertime temperatures; **Figure S2B**). However, both *Festuca* and *Medicago* had higher soil moisture in formerly droughted, compared to control, subplots throughout summer/autumn (*Festuca*: $P = 0.01$, *Medicago*: $P = 0.02$; **Figure 2B**, **Figure S2B**). Across the full 12-month period, only *Medicago* plantings exhibited a significant drought treatment effect, with droughted subplots having higher soil moisture levels than controls ($P = 0.05$; **Figure S2C**).

Soil moisture was only moderately affected by the warming treatment applied to *Festuca* and *Medicago*, with eT reducing soil moisture during the winter/spring drought period for *Medicago* ($P = 0.03$; **Figure S2A**), although there were intermittent short-term positive effects of warming on soil moisture following irrigation events in *Festuca* (**Figure 2B**). There was no significant effect of the warming treatment on soil moisture during the summer/autumn period for either of the monitored species, nor interactions with the drought treatment. Additionally, differences in soil moisture between upper (0-10 cm) and lower (15-

30 cm) depths for *Medicago* soils varied among the different drought and warming treatments throughout the drought and recovery periods (**Figure S4**).

Plot-level surface temperatures of the plant canopy and soil surface were consistently increased by both drought ($P < 0.001$, + 0.9 °C) and warming ($P < 0.001$, + 3.0 °C) treatment, and interactive effects between drought and warming were not significant (**Figure S5**; **Table S4**). Additionally, warming altered the temperature range within plots (**Figure S5**; **Table S5**). The warmed monoculture plots of *Festuca* and *Medicago* had no days when minimum temperatures fell below freezing (compared to three such days in ambient plots) and only 20 days when temperatures fell below 5 °C (compared to 62 days in ambient plots). At the other end of the scale, the warming treatment resulted in an additional 28 days when summer temperatures exceeded 40 °C and an extra 23 days where temperatures exceeded 45 °C (**Figure 2C, D**). Subsurface soil temperatures were also affected by treatments, with both drought (*Festuca*) and warming (*Festuca* and *Medicago*) consistently increasing average temperatures (**Figure S6**). Overall, soil temperature responses were similar among species, although drought amplified the warming effect in *Festuca* but not *Medicago* soils.

3.2 Aboveground productivity response to drought

During the 6-month winter/spring drought period, total productivity ranged from 1,800 to 7,400 kg ha^{-1} under control conditions (**Figure 3A**). In the control treatment, the most productive plantings were *Themeda*, *Themeda*/*Rytidosperma*, *Phalaris* and *Chloris*, while *Lolium* and *Biserrula* produced the least biomass. Droughted subplots were significantly less productive than their respective controls, with an average yield reduction of ~40% across the twelve plantings (**Figure 3B**; **Table 2**). There was also a significant interaction between drought and planting type on production, reflecting both differences in drought response and

drought duration, the latter associated with the length of time taken for initial sward establishment before imposition of the drought treatment (**Table 2**). Production in nine of the twelve plantings was significantly reduced by drought. The remaining three included the legume monoculture *Biserrula* (P = 0.15), which only had three months of drought, and two that had only a one-month drought (*Rytidosperma*: P = 0.96 and *Phalaris/Trifolium*: P = 0.77).

The drought effect size, quantified as the log response ratio between control and droughted subplots compared during the 6-month winter/spring treatment period, varied among plantings (**Table 3**) with those that received the full six months of drought generally showing the greatest loss of productivity (e.g. *Digitaria:* 70% and *Fescue:* 59% yield reduction). An exception to this pattern was *Chloris*, which also received six months of drought, but exhibited only a 37% reduction. In contrast, *Phalaris* received only one month of drought treatment but had yield reductions of 34% (**Figure 3B**). This latter result suggests a high drought-sensitivity for *Phalaris*, as was evident when standardizing the change in productivity between control and droughted subplots by the amount of irrigation withheld during the winter/spring drought treatment period (i.e. the species' "drought sensitivity" - **Figure 3C**). Indeed, drought sensitivities ranged from high (*Digitaria*, *Phalaris* and *Themeda)*, with 6-month winter/spring yield losses of ~ 20 kg ha^{-1} mm^{-1}, to low (*Biserrula*, *Medicago*, *Rytidosperma*, and the *Phalaris*/*Trifolium* mixture; **Figure 3C**), with an overall average 6-month loss of ~9 kg ha^{-1} mm^{-1} across the twelve plantings. The potential benefit of growing grasses in two-species mixtures versus in monoculture with respect to drought effects on winter/spring production was species-dependent. For the C_3 grass-legume mixture, the drought associated decline in winter/spring productivity was lower than that measured in the dominant grass monoculture (**Figure 3B**; *Phalaris* in *Phalaris*/*Trifolium* mixture). Once

this effect was standardized by the amount of water withheld, the *Phalaris*/*Trifolium* mixed species plots had significantly lower drought sensitivity than the *Phalaris* monoculture (**Figure 3C**; $P = 0.04$). In contrast, for both the grass-grass mixture (*Themeda*/*Rytidosperma*) and the C_4 grass-legume mixture (*Digitaria*/*Biserrula*), the drought sensitivity of mixtures was intermediate between that of the component species (**Figure 3C**).

Plant functional group was not a significant predictor of winter/spring yield reduction under drought treatment (**Table 3**), nor of drought sensitivity as measured by yield loss per mm irrigation withheld (**Table 4**), although it is noteworthy that all subplots dominated by C_4 grasses experienced significant cool season biomass reductions under drought. During the summer/autumn (drought recovery) period, the 6-month productivity of perennial species ranged from 1,300-10,500 kg ha^{-1} in control subplots and 470-7,800 kg ha^{-1} in formerly droughted subplots. This variation reflects the differing growth phenologies among the C_3 and C_4 species, as well as their varying capacities for recovery following the end of the experimental drought (**Figure 4A**). Four plantings experienced significant carry-over effects of drought, including *Medicago*, *Themeda*, *Themeda*/*Rytidosperma* and *Festuca*, (**Figure 4A**), the latter exhibiting the largest 6-month summer/autumn yield reduction in formerly droughted plots (i.e. lowest resilience, (**Table 3**; **Figure 4B**). There were no significant differences among functional groups in terms of carry-over effects of drought on summer/autumn productivity (**Table 3**).

Annual biomass production among perennial plantings reflected their combined drought resistance in terms of 6-month yield reduction during the winter/spring drought and capacity to recover production in the following 6-month summer/autumn, once conditions improved. Annual productivity varied almost four-fold (from 4,300-16,500 kg $ha^{-1}yr^{-1}$) in control

subplots among the twelve plantings and by a factor of six (1,700-10,700 kg $ha^{-1}yr^{-1}$; **Figure 4C**) in the droughted subplots. Four of the perennial species experienced significant drought-related yield reductions across the full 12 months of the study (**Figure 4C**). Although there were no significant differences in annual productivity) among functional groups, C_4 grass species were more consistently affected by drought compared to temperate C_3 grasses, the latter group including species that were strongly negatively affected (*Festuca*) and others that were not (*Rytidosperma*; **Figure 4D**).

Table 1. Plant species traits and treatment details for the PACE experiment

Planting	Species*	Origin	Growth Form	Photosynthetic pathways	Drought Started#	Warming Started
Festuca	*F. arundinacea*	Temperate, introduced	Grass	C_3	01/06/2018	16/04/2018
Lolium	*L. perenne*	Temperate, introduced	Grass	C_3	23/08/2018	NA
Phalaris	*P. aquatica*	Temperate, introduced	Grass	C_3	14/10/2018	NA
Rytidosperma	*R. caespitosum*	Temperate, native	Grass	C_3	14/10/2018	NA
Chloris	*C. gayana*	Tropical, introduced	Grass	C_4	01/06/2018	NA
Digitaria	*D. eriantha*	Tropical, introduced	Grass	C_4	01/06/2018	NA
Themeda	*T. triandra*	Tropical, native	Grass	C_4	01/06/2018	NA
Biserrula	*B. pelecinus*	Temperate, introduced	Legume	C_3	23/08/2018	NA
Medicago	*M. sativa*	Temperate, introduced	Legume	C_3	23/08/2018	16/04/2018
Digitaria/ *Biserrula*	*D. eriantha*, *B. pelecinus*	Tropical/temperate, introduced mixture	Grass Legume	C_4 C_3	23/08/2018	NA
Phalaris/ *Trifolium*	*P. aquatica*, *T. subterraneum*	Temperate, introduced mixture	Grass Legume	C_3 C_3	14/10/2018	16/04/2018
Themeda/ *Rytidosperma*	*R. caespitosum*, *T. triandra*	Tropical/temperate, native mixture	Grass Grass	C_3 C_4	01/06/2018	16/04/2018

**Plantings referenced by genus name in the text*

 # Date (dd/mm/year) of first watering event with 60% reduced irrigation input for drought plots

Table 2. Linear mixed effects model output for aboveground productivity during the 6-month winter/spring drought period (June-Nov. 2018), the 6-month summer/autumn (drought-recovery) period (Dec. 2018- May 2019 and annually (June 2018-May 2019).

Period	Fixed Effects	F value	*P* value	R^2m[#]	R^2c[§]
Drought*	Drought	100.9	<0.01	0.66	0.71
	Plantings[^]	17.0	< 0.01		
	Drought x Plantings	3.9	< 0.01		
Recovery	Drought	9.4	0.01	0.86	0.86
	Plantings	75.3	<0.01		
	Drought x Plantings	2.4	0.01		
Annual*	Drought	48.7	<0.01	0.81	0.83
	Plantings	51.8	<0.01		
	Drought x Plantings	4.5	<0.01		

**Biomass data were log transformed to meet assumptions of constant variance*
[^]Refers to different species/mixture types
[#]R^2m indicates marginal error associated with linear model fixed effects
[§]R^2c indicates conditional error or the total variation described by the full model including nested random effects (plots within a shelter).

Table 3. Linear mixed effects model output for comparison of log response ratios (LRR) and sensitivity of aboveground production in response to drought treatment among plantings (i.e. different species/mixtures) and functional groups (FG) for the 6-month winter/spring drought period, the 6-month summer/autumn (drought-recovery) period and the entire 12 months (annual).

Response	Period	Fixed Effects	F value	*P* value	R^2m	R^2c
LRR	Drought	Plantings*	5.1	<0.01	0.43	0.46
		FG*[#]	1.1	0.39	0.12	0.49
	Recovery	Plantings*	14.2	<0.01	0.67	0.69
		FG*[#]	0.2	0.87	0.04	0.64
	Annual	Plantings*	8.1	<0.01	0.55	0.55
		FG*[#]	0.4	0.75	0.08	0.63
Sensitivity	Drought	Plantings*	3.1	<0.01	0.31	0.35
		FG*[#]	1.1	0.40	0.09	0.34
	Annual	Plantings*	2.9	<0.01	0.30	0.34
		FG*[#]	0.4	0.76	0.04	0.35

**Includes shelter as a random effect*
[#] Includes plantings as a random effect

3.3 Effects of warming and drought-warming interaction on aboveground biomass production

The effects of warming varied across time periods and among the four different planting types, with significant warming x planting interactions in each period (**Table 4**). Warming resulted in a significant decline (28 %) in winter/spring productivity in *Phalaris*/*Trifolium*

(**Figure 5A, Figure 6B**; **Table 4**) that translated to net annual reductions (29 %) associated with warming (**Figure 5C**). In contrast, warming reduced productivity for *Festuca* during the 6-month summer/autumn warm season (**Figure 5B**), but not during the winter/spring months, an effect that also resulted in net annual reductions in aboveground productivity for this species (**Figure 5C**). Importantly, no plantings experienced a significant productivity benefit associated with warmer temperatures at any time period (**Figure 6B**).

There was a significant interaction between warming and drought treatments for aboveground productivity during the winter/spring period and at the annual scale; there were also significant three-way interactions between drought, warming, and planting type (**Table 4**) across both 6-month time periods and the entire year, highlighting the species-contingency of climate treatment impacts on plant productivity. During the summer/autumn, warming amplified the carry-over effects of winter/spring drought on *Festuca* (**Figure 5B**) with formerly droughted and warmed subplots producing significantly less biomass than other treatments. In contrast, for winter/spring and annual *Festuca* productivity, warming partially offset the negative effects of drought (winter/spring- aT: -63% yield, eT: -22% yield, **Figure 6A**). There was no evidence of greater-than-additive (i.e. synergistic) impacts (**Figures 5A, 6C**) of the combined climate manipulation treatments for any species.

Table 4. Linear mixed effects model output for aboveground production in response to drought (D) and warming (W) treatments among plantings (P)

Period	**Fixed Effects**	**F value**	***P* value**	**R^2m**	**R^2c**
Drought[*#]	Drought	61.4	*<0.01*	0.66	0.72
	Warming	2.0	0.16		
	Planting	36.9	*<0.01*		
	D * W	3.9	0.05		
	D * P	8.3	*<0.01*		
	W * P	4.3	*0.01*		
	D * W * P	3.5	*0.02*		
Recovery[*#]	Drought	37.1	*<0.01*	0.88	0.88
	Warming	44.3	*<0.01*		
	Planting	136.2	*<0.01*		
	D * W	3.0	0.10		
	D * P	27.5	*<0.01*		
	W * P	26.0	*<0.01*		
	D * W* P	4.6	*0.01*		
Annual[*#]	Drought	45.7	*<0.01*	0.86	0.88
	Warming	17.0	*<0.01*		
	Planting	180.9	*<0.01*		
	D * W	6.3	*0.01*		
	D * P	9.3	*<0.01*		
	T * P	4.4	*0.01*		
	D * W * P	3.6	*0.02*		

**Includes plots within shelter as a nested random effect*
[#] Log transformation applied

4 Discussion

Projections of future climate change, including increases in the frequency and magnitude of extreme climate events, are likely to disrupt ecosystem functioning (Jentsch and Beierkuhnlein, 2008; Knapp et al., 2008; Nijp et al., 2015), with important consequences for pastures and rangelands (Godde et al., 2020; Jiménez et al., 2011). We found that most of the C_3 and C_4 pasture species and mixtures exposed to extreme winter/spring drought experienced significant reductions in cool season productivity, with declines of up to 73%, relative to controls. Grass-legume plantings were more drought-resistant than their respective monocultures, significantly so for one species pair. Despite substantial impacts of winter/spring drought on cool season production, most species recovered quickly, with only four plantings experiencing carry-over effects into the subsequent summer/autumn. We found no evidence of a positive effect of warming on temperate species' productivity during the 6-month winter/spring period and instead observed significant reductions in productivity across the year for two of the four plantings exposed to increased temperatures. Furthermore, the combination of warming and drought generally resulted in additive or less-than-additive effects on biomass production, although always with net negative impacts, relative to controls.

4.1 Productivity responses to winter/spring drought

Decades of research focused on examining grassland responses to various drought regimes have emphasized the importance of regional climate context (Heisler-White et al., 2009; Knapp et al., 2017; Slette et al., 2019) and of standardizing observed drought effects relative to the amount of precipitation applied and the magnitude of drought imposed (Felton et al., 2020; Gao et al., 2019; Knapp et al., 2015). When we accounted for differences in drought duration by expressing yield reductions relative to the magnitude of rainfall reduction (Smith

et al., 2017; Wilcox et al., 2017), *Phalaris* and *Themeda* emerged as the more drought-sensitive species, while *Rytidosperma* and the *Phalaris*/*Trifolium* mixture were least affected; all species sensitivities (in terms of yield reductions per rainfall reduction) were, however, within the range reported from grassland studies elsewhere (Wilcox et al., 2017).

On average, cool season growth of C_4 grasses was more affected by winter/spring drought than legumes, with C_3 grasses showing the greatest range of responses. Interestingly, significant effects of cool season drought on the (predominately summer active) C_4 grasses also translated to declines in annual biomass production, demonstrating strong, negative effects of drought occurring prior to the main period of active growth in these tropical grasses. These apparent ecological mis-matches are often difficult to observe in temperate systems where the majority of growth occurs during a well-defined warm season (Knapp et al., 2015). There is, however, evidence for winter precipitation offsetting the effects of spring/summer drought (Fry et al., 2013), as well as cool season rainfall driving soil water storage and long-term patterns of productivity in semi-arid grasslands and regions with more continuous patterns of plant growth (Derner et al., 2020). These findings have important implications for the seasonality of plant productivity and subsequent short-term stocking decisions made by land managers when faced with extreme climate conditions (Murray-Tortarolo and Jaramillo, 2019). Locally in south eastern Australia, projections for increased severity of winter/spring drought (CSIRO, 2020) are likely to have large impacts on the seasonality of pasture and rangeland productivity, and similar shifts in precipitation may have far reaching implications for livestock production around the world (Derner et al., 2020).

Other plant functional groups at PACE had less consistent drought responses, including contrasting responses between legume species and high variability among the C_3 grasses.

Deep tap roots for the legume *Medicago* may have allowed access to deep soil water supporting sustained growth during dry periods or, alternatively, facilitated shifts in moisture depth profiles due to hydraulic lift (Li et al., 2012; Nie et al., 2015; Raza et al., 2013) thereby reducing drought effects at the sward level (Liste and White, 2008; Pang et al., 2013). Even so, this species experienced significant declines in productivity in all time periods, although total production was still comparable to C_3 grasses under control conditions. On the other hand, *Biserrula*, also a deep-rooted legume (Haling et al., 2016; Loi et al., 2005), experienced a strong effect of the drought treatment on soil moisture without a significant reduction in biomass. Differences in growth phenology relative to the timing of drought may explain this disparity as *Biserrula*, an annual species, reached peak growth in early spring when the drought treatment was first implemented for this species, suggesting that residual soil water from winter may have been sufficient to support strong early growth despite the spring drought (Fay et al., 2000; Hofer et al., 2017). These differences in legume response, along with the large effects of winter/spring drought on cool season productivity of our tropical grasses- effects that persisted during the more productive, warm season for one (*Themeda*) of the three C_4 species - provide support for the importance of drought timing in relation to species growth phenology (Wilcox et al., 2017; Yao et al., 2019) rather than functional group classifications.

Grass-legume mixtures were generally more drought resistant in terms of maintaining production during drought than their respective dominant monocultures, a phenomenon that has been observed in other systems contrasting different levels of species- (Bloor and Bardgett, 2012; Isbell et al., 2015) or functional diversity (Gherardi and Sala, 2015; Jentsch et al., 2009; Kreyling et al., 2008b). The lack of difference in drought response for *Themeda* grown in (grass-grass) mixture *versus* monoculture suggests that increasing the number of

species was less important than increasing functional diversity. Increased functional diversity, typically involving legume-grass mixtures, is a management strategy used widely in pasture systems to increase soil nitrogen (N) availability and improve the nutritional quality of companion grasses (Nyfeler et al., 2011; Suter et al., 2015). While we have not examined the mechanism(s) for reduced sensitivity of production to drought here, legume-associated increases in N availability and its uptake by grasses could potentially improve productivity under drier conditions by increasing photosynthesis and hence water-use efficiency (Abid et al., 2016; Adams et al., 2016; Hofer et al., 2017). This management strategy therefore has the potential to reduce climate change-driven losses in productivity and promote sustainable pastures under future, more variable climates.

4.2 Species recovery following drought and effects on annual productivity

Despite global interest in the resistance of ecosystems to extreme drought, far fewer studies have examined the factors driving post-drought recovery or resilience (Maxwell et al., 2019), especially among seasons in a year. Recovery of the original community following drought can be rapid (Hoover et al., 2014; Nicholas et al., 2004; Power et al., 2016), prolonged (Niu et al., 2014) or may never occur (Smith, 2011), with such differences often reflecting the severity and duration of the drought, land-use history and management regimes (Ruppert et al., 2015; Vogel et al., 2012). In our experiment, six of the ten perennial pastures fully recovered from winter/spring drought during the following summer and autumn. Monoculture plantings that showed full recovery included *Chloris* and *Digitaria*, both C_4 summer-active grasses, as well as the two temperate C_3 grasses that experienced a short (one-month) duration drought (*Phalaris* and *Rytidosperma*). Previous studies imposing short-duration or mild/moderate drought conditions also observed full recovery for temperate grassland species (Nicholas et al., 2004). The predominantly spring-focussed growth

phenology of these temperate grasses - partly associated with very warm summer temperatures at the experimental site - likely contributed to the minimal legacy effects of winter/spring drought observed in this study. On the other hand, the complete recovery of the two C_4 grasses suggests that these species may be particularly well-adapted to maintain summer production and thus cover a summer feed-gap for livestock (Johnston, 1996), even in the context of predicted increases in the severity and duration of winter/spring drought. Extreme drought experiments conducted in North American grasslands have also shown rapid recovery in aboveground productivity for C_4-dominated systems (Hoover et al., 2014), providing further support for a role for these grasses in maintaining year-round forage production under future, drier climates (Godde et al., 2020).

Annual productivity is one of the most commonly used metrics for assessing ecosystem responses to environmental drivers (Gao et al., 2019; Huxman et al., 2004). Despite generally high levels of drought resilience, four plantings experienced significant drought-associated declines in annual yield. These included species with wide geographic distributions (*Festuca* and *Medicago*), as well as an Australia native grass (*Themeda*), such that our findings are likely to be broadly applicable to a wide range of grasslands. Climate-associated declines in seasonal- and annual productivity have been widely reported (Godde et al., 2020; McKeon et al., 2009; Murray-Tortarolo and Jaramillo, 2020); increased understanding of these patterns will help guide climate risk management strategies such as stocking rates of livestock, as well as sustainability initiatives such as carbon farming (Kragt et al., 2012).

4.3 Plant responses to warming and drought x warming interactions

Model predictions of beneficial impacts of warming on grassland productivity globally (Gao et al., 2016) and locally (Cullen et al., 2009), especially during cool season months in higher

latitude ecosystems (Mori et al., 2014; Naudts et al., 2011), were not borne out in our study. This was despite an increase in winter growing degree days and a reduction in frost exposure, changes that are expected to increase winter and spring growth (Chang et al., 2017; Piao et al., 2019). While our cool season findings were unexpected, they do, however, align with model simulations of the effects of moderate (+3 °C) warming on Australian rangelands (McKeon et al., 2009).

Treatment-related increases in maximum temperatures and the intensity and duration of summer heatwave events were expected to reduce summer productivity as species exceeded physiological thresholds, especially for temperate species (Reyer et al., 2013). The observed neutral (*Medicago* and *Themeda/Rytidosperma*) to negative (*Festuca* and *Phalaris/Trifolium*) impacts of warming during cool and warm seasons is likely to result from both direct (physiological) and indirect (soil moisture/VPD) mechanisms. Indeed, we found that warmed plots had consistently lower soil water contents, associated with temperature-driven increases in evapotranspiration (Brookshire and Weaver, 2015; Gao et al., 2016; Kuster et al., 2013). This connection between temperature and evapotranspiration is likely to amplify the intensity of ecological drought under future climates (Adams et al., 2009; Dai, 2011; De Boeck et al., 2016; Dreesen et al., 2012). Interestingly, the combination of drought and warming in our study resulted in additive or less-than-additive (although still net negative) effects on productivity for all four plantings, that varied by season. Similar less-than-additive temperature and drought interactions have been observed in temperate grasslands and more generally across major biomes in meta-analyses (De Boeck et al., 2011; Song et al., 2019; Wu et al., 2011). Further work investigating the mechanisms and nature of these interactions will help refine predictions relating to multiple, co-occurring changes in future climate. This study provides important, new experimental, field-based data on the realized effects of

extreme drought and continuous warming on the productivity of a variety of commonly used pasture/rangeland species. These data add to information from modelling studies (Cullen et al., 2009; Kaine and Tozer, 2005) and comparisons across precipitation gradients (Clark et al., 2016) to quantify impacts of future and more extreme rainfall regimes on the productivity of the pasture and rangeland feed base that underpins livestock grazing in many parts of the world (Godde et al., 2020). Future work with these species will investigate relationships between productivity responses and plant traits and strategies relating to the acquisition and use of water (root traits, plant-microbial interactions, plant hydraulics) and carbon (above- versus below-ground allocation, vegetative versus reproductive growth, root and crown carbohydrate storage), to elucidate mechanisms responsible for species differences in sensitivity. This information will be key to extrapolating findings from this study to a wider range of locations and grassland species, including many of international relevance in production systems across the globe.

5 Conclusions

This paper introduces a new experimental facility used to simulate future, more extreme climates, under field conditions. Our findings of consistent negative effects of winter/spring drought and year-round warming on many of the pasture species, including two native rangeland grasses, that play a crucial role in livestock and dairy industries highlights the challenges associated with future climate risk management for both pasture-related industries and native grasslands. Observed productivity declines associated with warming, even in the cooler winter/spring months, indicate the important role of temperature in altering ecosystem water balance, and associated increases in the severity of ecological drought in a future, warmer world. This is likely to be an issue for many grassland systems across the globe, as higher temperatures exacerbate the effects of predicted increases in the magnitude, frequency

and duration of meteorological drought. Species with physiological, morphological and/or phenological traits that support sustained productivity under more challenging climate conditions will become increasingly important as climate variability and extremes undermine the future performance of traditional pasture and rangeland species.

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Figure Captions

Figure 1. The Pastures and Climate Extremes (PACE) field facility located at Western Sydney University in Richmond, NSW Australia. A) There were six open-sided polytunnels, each with eight experimental plots; B) Experimental plots (4 x 4 m) received a drought, warming, or drought + warming treatment and were each divided into four discrete 2 x 2 m subplots comprising nine different pasture species in monoculture or three select two-species mixtures; C) Heater (infra-red: IR) arrays were mounted above the vegetation canopy and warm the plot surface an average of 3 °C above paired ambient temperature plots.

Figure 2. Experimental treatment effects of winter/spring drought (control: C, drought: D) applied during the period between 1 June to 30 November 2018 and year-round warming (ambient temperature: aT, elevated temperature: eT) treatments on soil moisture (panels A and B) and plot surface temperature (panels C and D) averaged across the six shelters, from 1 June 2018 to 31 May 2019. A) Average soil moisture content in *Festuca* subplots (additional species are shown in Figure S2) with 95% confidence intervals as well as individual irrigation events as daily rainfall totals for control (black) and droughted (red) plots over the entire year; B) Treatment differences in soil moisture from aT-C plots over time in the *Festuca* subplots, noting the winter/spring drought treatment period between 1 June and 30 November 2018 and subsequent summer/autumn without drought treatment; C) Daily maximum plot surface temperature, relative to maximum air temperature (black line) and 40 °C (representing extreme temperatures, dashed lines); D) Daily minimum temperature compared with minimum air temperature (black line) and 0 °C (dashed lines).

Figure 3. A) Aboveground production summed for all harvests during the 6-month winter/spring drought period. Values shown are means ± 1 standard error (control = solid symbol, droughted = outline); B) drought effect size (log response ratio of drought vs control production during the 6-month drought treatment period), and C) drought sensitivity (yield reduction in the drought treatment relative to controls per mm irrigation withheld, to account for varying lengths of drought treatments among planting types, see Table 1). Values for panels B and C are mean values with 95% confidence intervals and same letter designations indicate non-significant differences among plantings. Abbreviations are as follows: *Biserrula* (Bis), *Chloris* (Chl), *Digitaria* (Dig), *Digitaria & Biserrula* mixture (DigBis), *Festuca* (Fes), *Lolium* (Lol), *Medicago* (Med), *Phalaris* (Pha), *Phalaris & Trifolium* mixture (PhaTri), *Rytidosperma* (Ryt), *Themeda* (The), *Themeda* & *Rytidosperma* mixture (TheRyt). Significant pairwise comparisons for the effect of drought treatment are indicated as follows: NS= not significant, # = $P < 0.1$, * $P < 0.05$, ** $P = <0.01$, *** $P = < 0.001$.

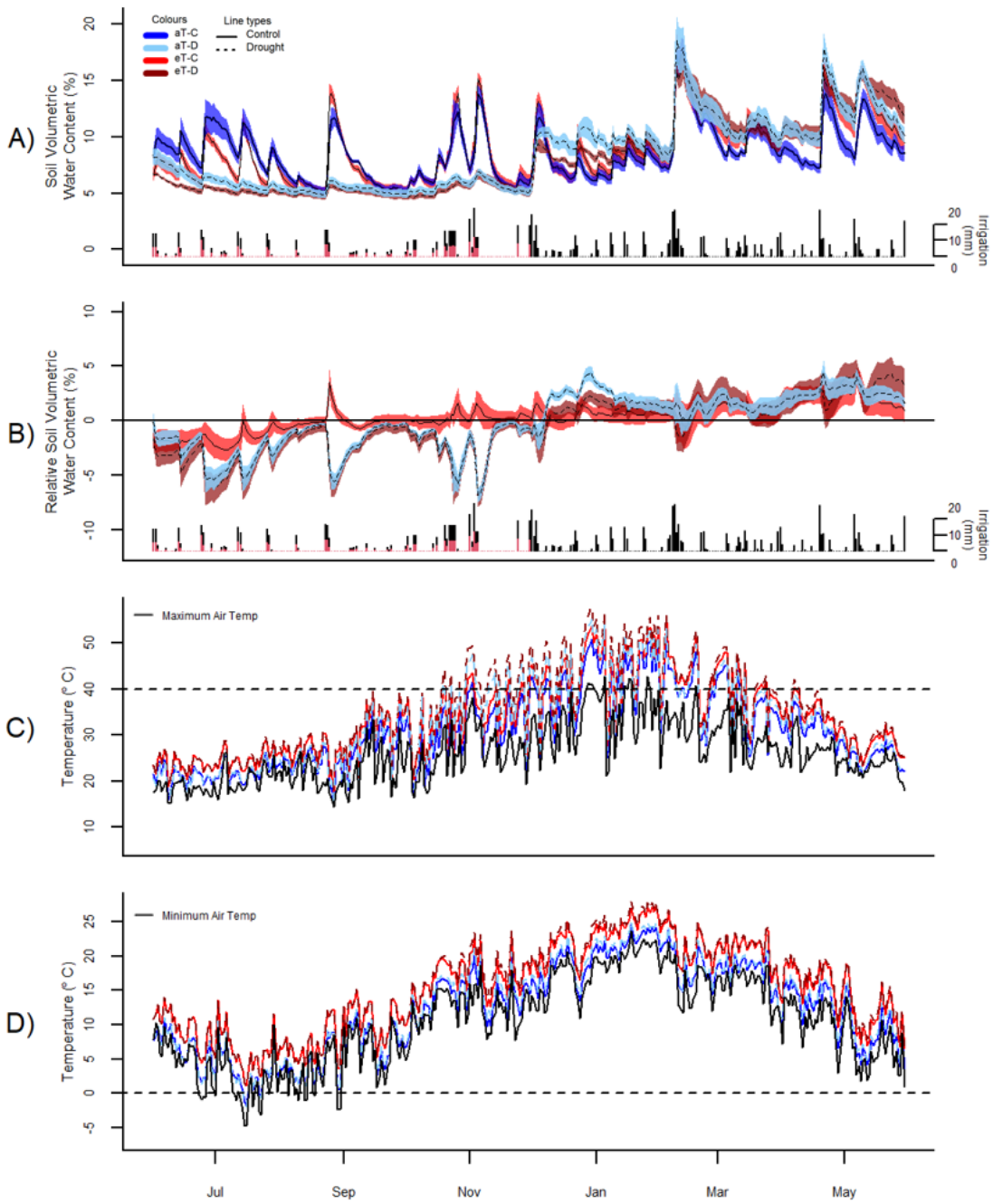
Figure 4. A) Aboveground production summed for all harvests during the 6-month summer/autumn recovery period following the winter/spring drought treatment (control = solid symbol, formerly droughted = outline), B) effect size of summer/autumn legacy effects of winter/spring drought on productivity (shown as log response ratios), C) annual aboveground production summed for all harvests June 2018-May 2019 and D) effect size (log response ratios) of winter/spring drought on total annual productivity (note that for panels C and D annual species are not included, as annual totals are the same as winter/spring values). Panels B and D are back-transformed, following analysis on log-transformed data. All symbols and abbreviations follow Figure 3.

Figure 5. Aboveground production for individual plantings exposed to drought (control: C and droughted: D) and warming (ambient: aT and elevated: eT) treatments during A) the 6-month winter/spring drought period (June 1st- Nov 30th 2018), B) the subsequent

summer/autumn recovery period (Dec 1st 2018- May 31st 2019), and C) annual production. Drt and W indicate significant drought and warming effects, respectively. Values are means ± 1 SE and all spp. abbreviations and significance levels follow Fig. 3.

Figure 6. Treatment effect sizes during the winter/spring drought period for A) drought under ambient (aT) and elevated (eT) temperatures, B) warming, under control (C) and droughted (D) conditions, and C) the effect of warming on biomass responses to drought (for panel C, positive values indicate a reduction in drought impact under warming) among plantings exposed to both drought and warming. Values shown are means with 95% confidence intervals and all spp. abbreviations follow Fig 3.

Figure 1. The Pastures and Climate Extremes (PACE) field facility located at Western Sydney University in Richmond, NSW Australia. A) There were six open-sided polytunnels, each with eight experimental plots; B) Experimental plots (4 x 4 m) received a drought, warming, or drought + warming treatment and were each divided into four discrete 2 x 2 m subplots comprising nine different pasture species in monoculture or three select two-species mixtures; C) Heater (infra-red: IR) arrays were mounted above the vegetation canopy and warm the plot surface an average of 3 °C above paired ambient temperature plots



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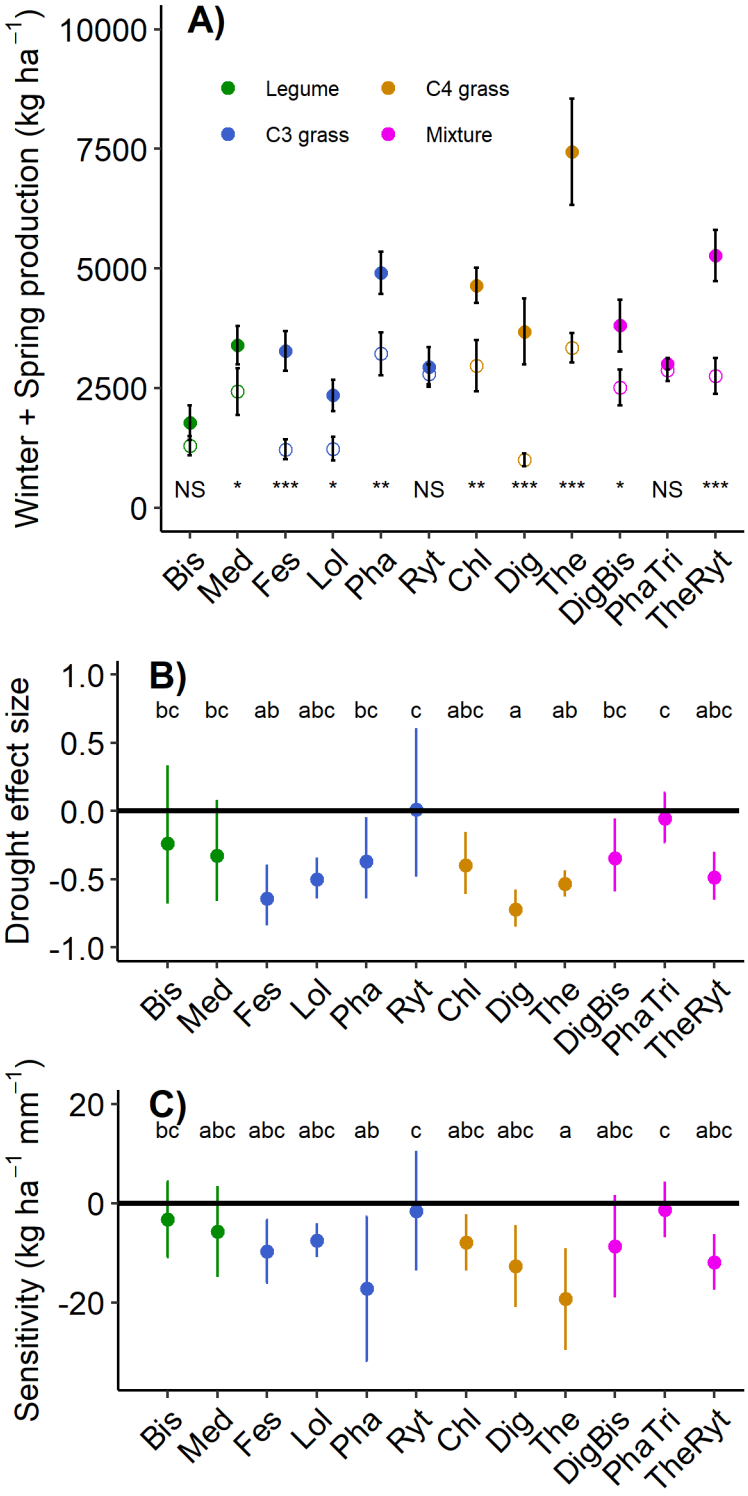

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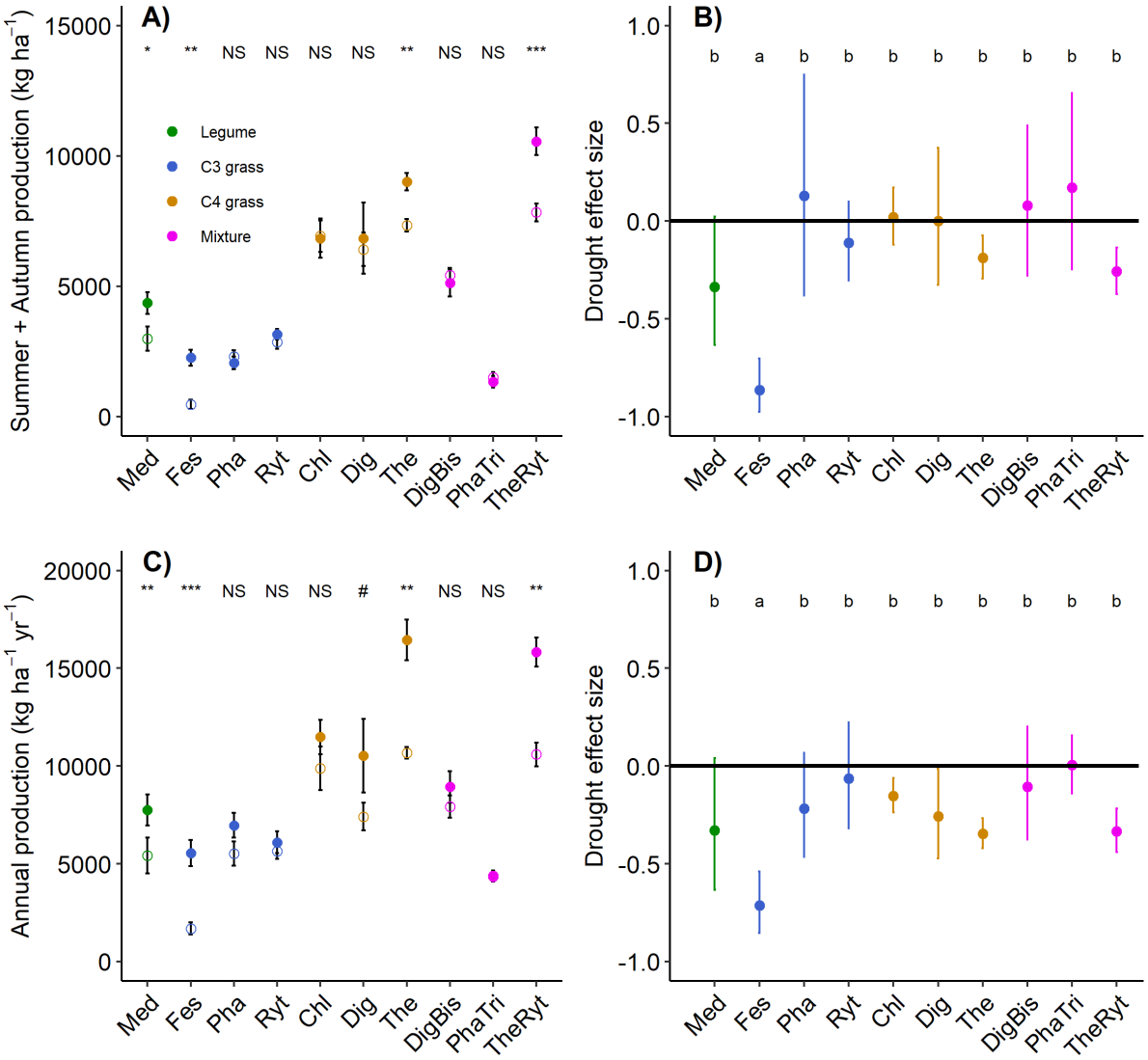

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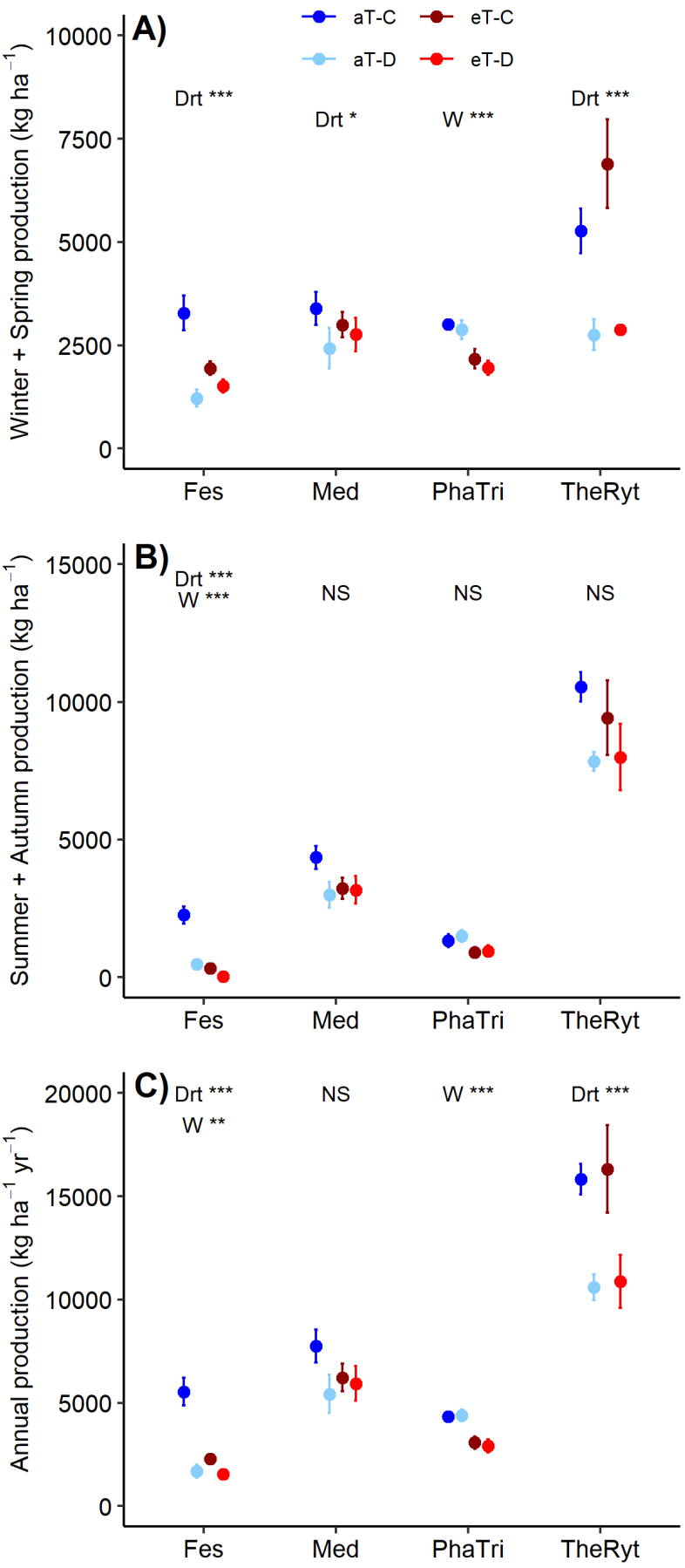

Figure 5. Aboveground production for individual plantings exposed to drought (control: C and droughted: D) and warming (ambient: aT and elevated: eT) treatments during A) the 6-month winter/spring drought period (June 1st-Nov 30th 2018), B) the subsequent summer/autumn recovery period (Dec 1st 2018-May 31st 2019), and C) annual production. Drt and W indicate significant drought and warming effects, respectively. Values are means ± 1 SE and all spp. abbreviations and significance levels follow Fig. 3.

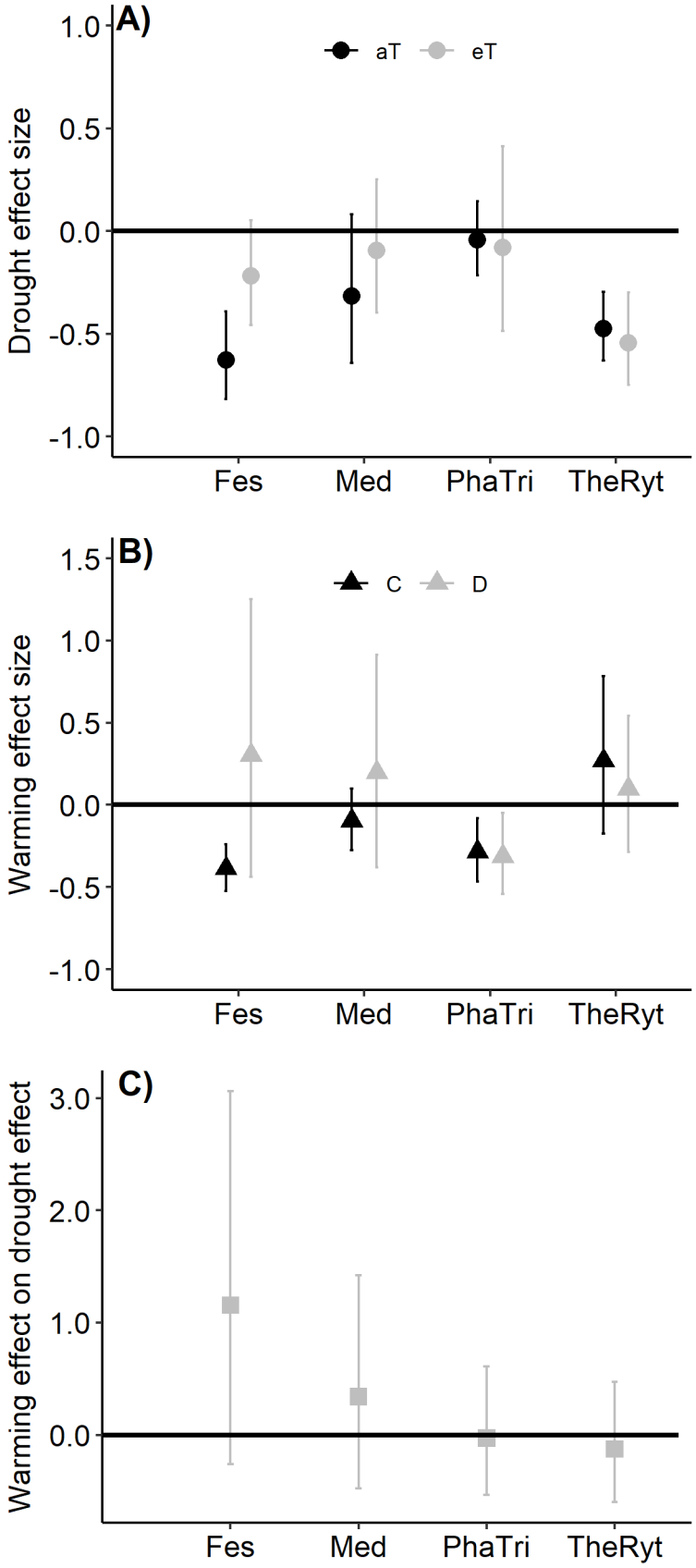

Figure 6. Treatment effect sizes among plantings exposed to both drought and warming during the winter/spring drought period for A) drought under ambient (aT) and elevated (eT) temperatures, B) warming under control (C) and drought (D) conditions and C) the effect of warming on biomass responses to rainfall (positive values indicate a reduction in drought impacts under warming). Values shown are means with 95% confidence intervals and all spp. abbreviations follow Fig 3.