

Elevated carbon dioxide and warming impact silicon and phenolic-based defences differently in native and exotic grasses

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Abstract

Global climate change may increase invasions of exotic plant species by directly promoting the success of invasive/exotic species or by reducing the competitive abilities of native species. Changes in plant chemistry, leading to altered susceptibility to stress, could mediate these effects. Grasses are hyper-accumulators of silicon, which play a crucial function in the alleviation of diverse biotic and abiotic stresses. It is unknown how predicted increases in atmospheric carbon dioxide (CO₂) and air temperature affect silicon accumulation in grasses, especially in relation to primary and secondary metabolites. We tested how elevated CO₂ (eCO₂) (+240 ppm) and temperature (eT) (+4°C) affected chemical composition (silicon, phenolics, carbon and nitrogen) and plant growth in eight grass species, either native or exotic to Australia. eCO₂ increased phenolic concentrations by 11%, but caused silicon accumulation to decline by 12%. Moreover, declines in silicon occurred mainly in native species (−19%), but remained largely unchanged in exotic species. Conversely, eT increased silicon accumulation in native species (+19%) but decreased silicon accumulation in exotic species (−10%). Silicon and phenolic concentrations were negatively correlated with each other, potentially reflecting a defensive trade-off. Moreover, both defences were negatively correlated with plant mass, compatible with a growth-defence trade-off. Grasses responded in a species-specific manner, suggesting that the relative susceptibility of different species may differ under future climates compared to current species rankings of resource quality. For example, the native *Microlaena stipoides* was less well defended under eCO₂ in terms of both phenolics and silicon, and thus could suffer greater vulnerability to herbivores. To our knowledge, this is the first demonstration of the impacts of eCO₂ and eT on silicon accumulation in grasses. We speculate that the greater plasticity in silicon uptake shown by Australian native grasses may be partly a consequence of evolving in a low nutrient and seasonally arid environment.

KEYWORDS

defences, grasses, herbivores, phenolic acids, silica, silicon, stress, trade-offs

1 | INTRODUCTION

Up to a third of global carbon stocks are stored in grasslands, which account for up to 40% of terrestrial land mass (Gibson, 2009). This

is even higher in the Australian continent, with permanent meadows and pastures accounting for 360 million hectares, 47% of current land use (FAO, 2016). Widespread introductions of exotic grass species have occurred throughout the continent and continue to

threaten these important ecosystems (Groves & Willis, 1999). Globally, introductions of exotic plant species, both deliberate and accidental, are known to be facilitated by climate change through a range of mechanisms (Bradley, Blumenthal, Wilcove, & Ziska, 2010; Dukes, Chiariello, Loarie, & Field, 2011; Dukes & Mooney, 1999; Walther et al., 2009). Climate change, for example, can facilitate the spread of exotic species when it renders native plant species less competitive than the exotic ones, either in terms of resource acquisition or in the natives' ability to cope with biotic (e.g. herbivory) and abiotic (e.g. drought) stress (Manea, Sloane, & Leishman, 2016).

Grasses are hyper-accumulators of silicon (Si), which plays a crucial role in mitigating an extensive array of abiotic stresses, including drought, salt stress, toxic metals, nutrient deficiency (Guntzer, Keller, & Meunier, 2012; Liang, Sun, Zhu, & Christie, 2007; Ma, 2004), and biotic stresses including pathogen infection (Van Bockhaven, De Vleeschauwer, & Höfte, 2013; Wang et al., 2017) and herbivory (Cooke & Leishman, 2011; Hartley & DeGabriel, 2016; Massey, Ennos, & Hartley, 2007; Reynolds, Keeping, & Meyer, 2009). Plants acquire silicon via uptake of soluble silicic acid from the soil (Epstein, 1999) and deposit it within or between cells, in the cell wall or as discrete opaline phytoliths; such deposition varies dramatically between species and in response to damage and Si supply (Hartley, Fitt, McLarnon, & Wade, 2015). Silicon phytoliths may have abrasive effects on herbivore mouthparts and guts, leading to reduced digestive efficiency (Massey & Hartley, 2009; Reynolds, Gurr, Padula, & Zeng, 2016).

Predicted increases in concentrations of atmospheric carbon dioxide (CO₂) and air temperatures can have significant impacts on plant growth as well as primary and secondary metabolite profiles in the plant (DeLucia, Nabity, Zavala, & Berenbaum, 2012; Ode, Johnson, & Moore, 2014), potentially including silicon-based resistance in grasses although this remains largely unreported to date (Hartley & DeGabriel, 2016). To our knowledge, only two studies have explored the effects of elevated CO₂ (eCO₂) on plant silicon (Fulweiler, Maguire, Carey, & Finzi, 2014; Ryalls, Hartley, & Johnson, 2017 investigating a tree and a grass, respectively) and none have included elevated temperature (eT). Robinson, Ryan, and Newman (2012) provide the most comprehensive meta-analysis of eCO₂ impacts on plant–arthropod interactions to date. They specifically highlight silicon as a defence that could be affected by eCO₂ and eT, yet none of the studies available to them had measured silicon. Hence, as yet, evidence-based predictions on the impact of environmental change on silicon have not been possible.

What has been demonstrated is potential trade-offs between silicon and other defences. Silicon accumulation in grasses has been shown to be negatively correlated with phenolic compounds in both the shoots (Cooke & Leishman, 2012; Schaller, Brackhage, & Dudel, 2012; Simpson, Wade, Rees, Osborne, & Hartley, 2017) and roots (Frew, Powell, Sallam, Allsopp, & Johnson, 2016). Cooke and Leishman (2012) showed this convincingly using 47 plant species, and suggested that there could be a trade-off between silicon and carbon-based (e.g. phenolics and terpenoids) anti-herbivore defences in plants. Since phenolic compounds are widely reported to respond to environmental change (Robinson et al., 2012; Veteli

et al., 2007; Zvereva & Kozlov, 2006), such changes could affect silicon accumulation.

Broadly speaking, plant growth and photosynthesis increase in response to eCO₂, with stronger responses seen in C₃ than C₄ plants (Ainsworth & Rogers, 2007; Long, Ainsworth, Rogers, & Ort, 2004; Wand, Midgley, Jones, & Curtis, 1999). While both carbon and nitrogen often increase in plants grown under eCO₂, carbon concentrations often increase at an accelerated rate relative to nitrogen concentrations, leading to an increase in C:N ratios (Luo, Hui, & Zhang, 2006; Stiling & Cornelissen, 2007). This effectively reduces nitrogen concentrations, either by reallocation or dilution (DeLucia et al., 2012) although the latter mechanism has been contested (Feng et al., 2015). The most recent meta-analysis to examine the effects of eCO₂ on plant secondary metabolites reported that nitrogen-based secondary metabolites decreased (–16%), whereas total phenolics increased by 19% (Robinson et al., 2012). Elevated temperature (eT) increases growth and photosynthesis to an optimum, beyond which it has adverse effects (Newman, Anand, Henry, Hunt, & Gedalof, 2011). The impacts of eT on primary and secondary metabolites are less clear cut. The meta-analysis by Zvereva and Kozlov (2006) reported that eT led to decreased leaf soluble sugars, starch, and total non-structural carbohydrates, whereas nitrogen concentrations were unaffected. Generally, concentrations of foliar terpenes increased, whereas phenolic compounds decreased (Zvereva & Kozlov, 2006).

Studies involving the effects of both eCO₂ and eT on plant metabolism are rare compared to single factor studies (Robinson et al., 2012), despite the fact that they are predicted to increase in tandem (IPCC, 2014) and often have interactive impacts on plant chemistry when they have been investigated (e.g. Gherlenda, Haigh, Moore, Johnson, & Riegler, 2015; Murray, Ellsworth, Tissue, & Riegler, 2013; Ryalls, Moore, Riegler, Gherlenda, & Johnson, 2015). When eCO₂ and eT were considered together, for example, temperature negated the increase in leaf carbohydrates caused by eCO₂, but amplified decreases in leaf nitrogen concentrations, causing substantial increases in leaf C:N ratio (Zvereva & Kozlov, 2006). Similarly, increased concentrations of phenolics in trees under eCO₂ were reduced when eT conditions were simultaneously applied (Veteli et al., 2007; but see Veteli, Kuokkanen, Julkunen-Tiitto, Roininen, & Tahvanainen, 2002). The reasons for counteracting effects are unclear, but Kuokkanen, Julkunen-Tiitto, Keinänen, Niemelä, and Tahvanainen (2001) speculated that higher temperatures may increase losses of carbon via maintenance respiration (Amthor, 1984), potentially attenuating increased rates of carbon fixation under eCO₂.

Silicon is thought to provide plants with structural support at a lower metabolic cost than carbon-based compounds such as lignin (McNaughton, Tarrants, McNaughton, & Davis, 1985; Raven, 1983), so higher carbon availability under eCO₂ may reduce this advantage. Indeed, it has been suggested that silicification of the Poaceae during the Miocene, when atmospheric CO₂ levels were low, was a competitive strategy (Craine, 2009) that allowed grasses to maintain growth and defence (Cooke & Leishman, 2011). While this remains speculative (see recent review by Stromberg, Di Stilio, and Song (2016)), it at least raises the prospect that the reverse may occur in a high CO₂ world

and plants could reduce silicon accumulation. In support of the hypothesis that eCO₂ decreases silicon uptake is the fact that eCO₂ usually depresses the jasmonate signalling pathway in plants (Ode et al., 2014; Zavala, Nabity, & DeLucia, 2013) and, in rice at least, silicon uptake is stimulated by activation of the jasmonate pathway (Ye et al., 2013). eT often increases transpiration rates in plants and since silicon enters plants via the transpiration stream, silicon uptake may increase under eT although the link between silicon uptake and transpiration rates is subject to debate (Kumar, Milstein, Bami, Elbaum, & Elbaum, 2017; McLarnon, McQueen-Mason, Lenk, & Hartley, 2017; Quigley & Anderson, 2014). Alternatively, eT could also facilitate silicon uptake by higher metabolically driven uptake of nutrients in general (Hartley & DeGabriel, 2016).

It is widely held that silicon accumulation may be particularly beneficial to plants growing in seasonally arid environments during periods of drought (Coughenour, 1985; Stromberg et al., 2016), so it is conceivable that grasses native to Australia may adjust silicon uptake more than exotic species in response to environmental change. In terms of other chemical defences, differences between native and exotic plant species are harder to predict. The “increased competitive ability” hypothesis predicts that exotic (and especially invasive) plant species will have fewer chemical defences because they experience less herbivore pressure (Blossey & Notzold, 1995). In contrast, the novel weapons hypothesis predicts that exotic plant species have more chemical defences than invasive species, which underpins their competitive advantage (Callaway & Aschehoug, 2000). While there is support for both hypotheses, there is growing evidence for exotic invasive species having more distinct secondary metabolites (Cappuccino & Arnason, 2006; Macel, de Vos, Jansen, van der Putten, & van Dam, 2014) and in higher concentrations for phenolics (e.g. Kim & Lee, 2011). How environmental change affects such defences in relation to silicon remains untested. The objective of this study was therefore to determine how widely occurring grass species in Australia, native and exotic, would respond to predicted changes in atmospheric CO₂ and temperature, acting individually and in combination. We determined the effects of eCO₂ (+240 ppm) and eT (+4°C) on the silicon and carbon-based (phenolics) defences in eight grass species, relative to plants grown under ambient conditions. We additionally determined changes in nutritional quality (carbon and nitrogen concentrations) and plant growth.

We hypothesize that eCO₂ causes a decrease in silicon accumulation and an increase in phenolic production because of increased carbon availability and the previously observed trade-off between the two (e.g. Cooke & Leishman, 2012; Schaller et al., 2012). We predict opposing impacts of eT; increased silicon uptake (potentially via increased transpiration) and lower phenolic biosynthesis (e.g. Veteli et al., 2007; Zvereva & Kozlov, 2006). Based on this, we hypothesize that eT diminishes the impacts of eCO₂ on silicon and phenolic concentrations. We predict a negative correlation between levels of silicon and phenolic compounds in the plant and also between plant growth (mass) and defence in general. Moreover, we anticipate that Australian native species will show greater plasticity in silicon uptake compared to exotic species partly because they

have evolved in a seasonally arid and low nutrient environment. Exotic species, in contrast, will have higher concentrations of phenolics which will be more responsive to environmental change than silicon.

2 | MATERIALS AND METHODS

2.1 | Experimental procedure

Eight grass species were initially grown from seed (Sydney Seeds, Seven Hills, NSW, Australia) in Osmocote Seed Raising & Cutting Mix (Scotts, Bella Vista, NSW, Australia). These comprised 40 replicates of five introduced or exotic species: annual ryegrass (*Lolium rigidum*), cocksfoot (*Dactylis glomerata*), perennial ryegrass (*Lolium perenne*), Rhodes grass (*Chloris gayana*), tall fescue (*Festuca arundinacea*) and three species native to Australia: red grass (*Bothriochloa macra*), weeping meadow grass (*Microlaena stipoides*) and Wallaby grass (*Austrodanthonia bipartita*). Grasses were grown in 70 mm diameter pots filled with coarsely sieved local Hawkesbury soil (Barton et al., 2010).

In all, 10 plants of each species were transferred after sowing to glasshouse chambers maintained at either ambient CO₂ concentrations, aCO₂ (400 µmol/mol), or at eCO₂ (640 µmol/mol) which is broadly anticipated by 2050 (Garnaut, 2011). Temperature was maintained at either ambient temperature (aT) (26/18°C day/night on a 15:9 light:dark cycle) or eT (30/22°C day/night on a 15:9 light:dark cycle). aT (26°C) represents the average daily maximum temperature for Richmond, NSW over the last 30 years, and eT was consistent with the predicted maximum temperature increase in 4°C for this region within this century (CSIRO and Bureau of Meteorology, 2015). The environmental conditions within the chambers were logged and monitored continuously throughout the experiment to maintain temperature and CO₂ differences between chambers and temperature readings were cross-checked with transportable temperature loggers. To minimize “chamber effects” associated with using four chambers, plants were circulated within each chamber every 5 days and chambers were swapped every c. 10 days by transferring plants between chambers and adjusting the environmental conditions accordingly. While this does not eliminate pseudo-replication, using this approach in these chambers has provided almost identical empirical results to truly replicated experiments, whether replicated with chambers or experimental run (Johnson, Gherlenda, Frew, & Ryalls, 2016). Plants were grown for a further 16 weeks before being destructively harvested. Grasses were separated from the soil, washed, freeze-dried and weighed.

2.2 | Chemical analysis

Dried shoot material was ball-milled. Leaf silicon concentrations were determined by placing approximately 100 mg of ground plant material into a small mass holder (PANalytical), and then analysed with an X-ray fluorescence spectrometer (Epsilon 3^x, PANalytical), using the procedure and certified reference material described in Hiltbold et al. (2017). This method was based on the approach of Reidinger, Ramsey, and Hartley (2012). Concentrations of total

phenolics were determined using a Folin–Ciocalteu assay with gallic acid (Sigma-Aldrich, St. Louis, MO, USA) as the quantification standard (Salminen & Karonen, 2011). Foliar N and C concentrations were determined using a CHN analyser (LECO TruSpec Micro, LECO Corporation, St. Joseph, MI, USA).

2.3 | Statistical analysis

Three-way analysis of variance (ANOVA) tests were conducted on all plant responses with species, CO₂ and temperature included as individual and interactive factors. The species term was replaced with origin status (i.e. exotic or native) to test for any patterns between these two groups. Correlations between plant growth, silicon and phenolic concentrations were tested to establish potential basis for trade-offs. Because of the strong interactive effects between species and one or both environmental factors, we conducted subsequent statistical analysis for each species separately with two-way (CO₂ and temperature) ANOVAs. Unless stated in table or figure legends, analysis was conducted on untransformed data. Where appropriate, transformations were chosen to give residual diagnostic plots which best fitted a normal distribution and showed least heteroscedasticity. All analysis was conducted in GENSTAT (Version 17, VSN International, UK).

3 | RESULTS

3.1 | Responses of grouped grass species

All of the plant traits measured varied between species (Table 1). eCO₂ increased plant growth, carbon concentrations, C:N ratio and

phenolic concentrations, but caused significant declines in silicon accumulation (Table 1). There was a significant negative correlation between concentrations of phenolics and silicon (Figure 1a) and also between plant growth and concentrations of both phenolics and silicon (Figure 1b). Overall, temperature did not impact on any other plant traits but diminished CO₂-induced increases in biomass and carbon concentrations, as indicated by significant interaction terms in Table 1.

Grouping grasses according to native versus exotic status, exotic species grew c. 300% larger ($F_{1,279} = 139.67, p < .001$), had 55% lower silicon concentrations ($F_{1,279} = 318.23, p < .001$) and 33% higher concentrations of phenolics ($F_{1,279} = 44.41, p < .001$) than native species. CO₂ and temperature affected native and exotic plant traits similarly except for silicon accumulation which was much more adversely affected by CO₂ in natives (−19%) compared to invasive species (<1%) ($F_{1,279} = 11.36, p < .001$). Conversely, eT increased silicon accumulation in native species (+19%), but decreased silicon accumulation in exotic species (−10%).

Because there were significant interactive effects between species and one or more environmental factors (Table 1), analysis was conducted and reported for each species separately (Table S1). A native species, *Microlaena stipoides*, was most affected by eCO₂ and eT, whilst an exotic, *Lolium rigidum*, was the least affected.

3.2 | Silicon and phenolics

eCO₂ caused significant decreases in foliar silicon concentrations for *M. stipoides* (Figure 2a) and *A. bipartita* (Figure 2c), but increased concentrations in *C. gayana* (Figure 2b) though only at elevated temperatures. Warmer temperatures increased silicon concentrations in

TABLE 1 Plant responses to varying CO₂ and temperature across all eight grass species

Environmental factors		Plant responses (mean ± SE)					
Temperature (°C)	CO ₂	Silicon (%)	Phenolics (GAE mg/g)	Biomass (g) ^a	Carbon (%) ^b	Nitrogen (%) ^b	C:N ^c
26	aCO ₂	0.93 ± 0.06	8.05 ± 0.40	2.69 ± 0.32	41.61 ± 0.20	0.55 ± 0.33	89.24 ± 4.66
	eCO ₂	0.83 ± 0.05	8.87 ± 0.29	5.04 ± 0.68	42.35 ± 0.21	0.50 ± 0.20	100.95 ± 6.34
30	aCO ₂	1.00 ± 0.09	7.88 ± 0.40	5.01 ± 0.93	41.99 ± 0.24	0.54 ± 0.03	118.10 ± 13.52
	eCO ₂	0.88 ± 0.05	8.78 ± 0.45	3.03 ± 0.41	41.93 ± 0.16	0.52 ± 0.03	102.98 ± 6.72
Statistical analysis		F	F	F	F	F	F
Spp _(7,288)		65.39***	34.07***	242.86***	16.43***	63.09***	66.43***
CO ₂ _(1,288)		11.04***	9.67**	5.05*	5.34*	3.20	4.06*
T _(1,288)		2.13	0.14	1.91	0.01	1.38	1.35
Spp × CO ₂ _(7,288)		5.32***	2.60*	1.47	0.31	3.58***	3.58
Spp × T _(7,288)		3.74***	2.12*	8.22***	0.99	10.23***	9.99***
CO ₂ × T _(1,288)		0.13	0.01	70.99***	8.10**	2.62	3.68
Spp × CO ₂ × T _(7,288)		2.87**	4.20*	6.85***	5.06***	4.65***	3.96

Mean values ± SE shown. F values (maximum degrees of freedom shown in parentheses) shown with statistical significance indicated * $p < .05$, ** $p < .01$ or *** $p < .001$ in bold.

Spp = grass species, CO₂ = carbon dioxide and T = temperature.

^aLog + 1 transformed.

^bLogit transformed.

^cLog transformed.

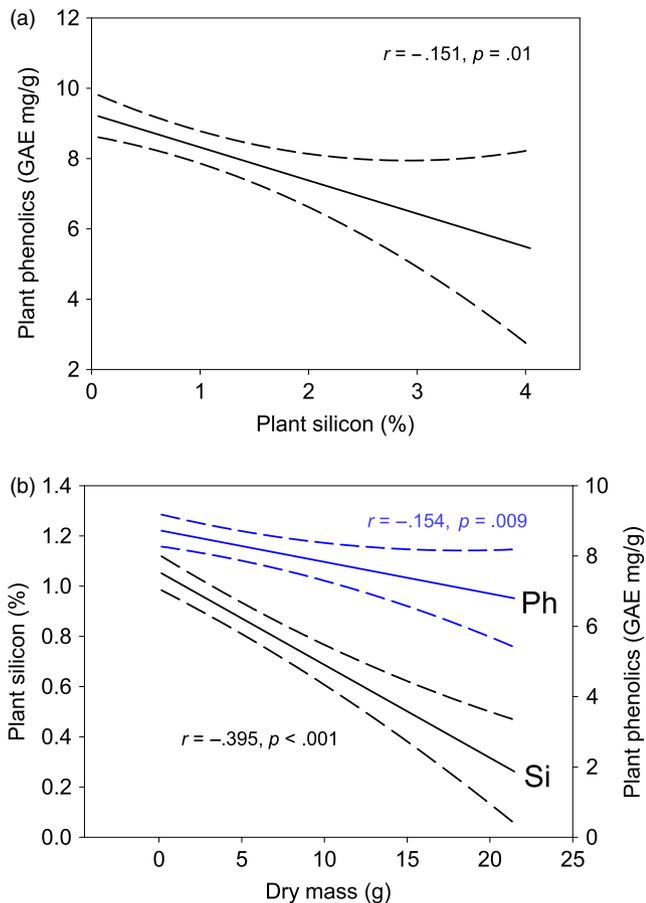


FIGURE 1 Negative correlations between (a) silicon and phenolic concentrations and (b) plant dry mass and both silicon (Si) and phenolic (Ph) concentrations. 95% confidence intervals displayed as dashed lines [Colour figure can be viewed at wileyonlinelibrary.com]

both *M. stipoides* (Figure 2a) and *B. macra* (Figure 2d). eCO₂ concentrations increased phenolic concentrations in *C. gayana* (Figure 3b), *A. bipartita* (Figure 3c), *B. macra* (Figure 3d) and *L. perenne* (Figure 3h), but decreased phenolic concentrations in *M. stipoides* (Figure 3a). Warmer temperatures caused phenolic concentrations to decline in *C. gayana* (Figure 3b), and enhance CO₂-driven increases in phenolic concentrations observed at ambient temperatures for *L. perenne* (Figure 3h) and *F. arundinacea* (Figure 3e), with the interactions operating in the opposite direction for *D. glomerata* (Figure 3f).

3.3 | Plant growth

Elevated temperature caused significant decreases in plant growth for *M. stipoides*, *F. arundinacea*, *L. rigidum* (Fig. S1a,e,g, respectively), but increased growth of *C. gayana* (Fig. S1b). eCO₂ promoted growth of *F. arundinacea* (Fig. S1e) and *A. bipartita* (Fig. S1c). Elevated temperature and CO₂ had interactive effects on several occasions. Higher temperatures reduced CO₂-driven increases in growth for *M. stipoides* (Fig. S1a), *C. gayana* (Fig. S1b), *A. bipartita* (Fig. S1c), *D. glomerata* (Fig. S1f), *L. rigidum* (Fig. S1g) and *L. perenne* (Fig. S1h).

3.4 | Primary chemistry

Elevated temperature caused a small decline in foliar carbon concentrations for *M. stipoides* (Fig. S2a), and interacted with elevated CO₂ to reduce the non-significant increase in carbon concentrations in *L. perenne* seen under elevated CO₂ (Fig. S2h). eT increased foliar nitrogen in *M. stipoides* (Fig. S3a) and *A. bipartita* (Fig. S3c) but caused declines in *C. gayana* (Fig. S3b). eCO₂ caused foliar nitrogen concentrations to decline for both *B. macra* (Fig. S3d), *F. arundinacea* (Fig. S3e) and *D. glomerata* (Fig. S3f). eT and eCO₂ interacted on three occasions, with eCO₂ slightly increasing nitrogen concentrations at ambient temperatures but decreasing concentrations at higher temperatures in *M. stipoides* (Fig. S3a). eCO₂ had exactly the opposite effect for *A. bipartita* (Fig. S3c) and *D. glomerata* (Fig. S3f); it caused concentration declines under ambient temperature conditions which were no longer manifested when temperature increased. Changing nitrogen concentrations, in response to elevated CO₂, altered foliar C:N ratio in *F. arundinacea* (Fig. S4e) and *L. rigidum* (Fig. S4g), whereas temperature effects on nitrogen concentrations caused C:N shifts in *M. stipoides* (Fig. S4a), *C. gayana* (Fig. S4b) and *A. bipartita* (Fig. S4c). Some *C. gayana* plants contained particularly low levels of nitrogen, which had a disproportionately large effect on foliar C:N.

The overall effects of eT and eCO₂ and their interactive effects are shown in Figure 4 (C:N ratios not shown).

4 | DISCUSSION

This study has shown widespread changes in the primary and secondary chemistry of both native and exotic grass species common to Australia under predicted climate and atmospheric change conditions. Collectively, eCO₂ caused silicon concentrations to decline by 12% and phenolic concentrations to increase by 11%. eT, in contrast, had no overall impact on either defence. Native and exotic species were generally affected similarly by eCO₂ and eT, except for silicon concentrations, which showed stronger declines under eCO₂ than exotic species though these effects were moderated by eT which caused silicon concentrations to increase. Examined at the species level, grasses showed more specific responses to these factors.

4.1 | Silicon

Silicon improves tolerance to abiotic stresses including heavy metal toxicity, salinity, nutrient imbalances, heat and drought (Liang et al., 2007), some of which are likely to themselves be exacerbated under future climate change (Newman et al., 2011), as well as defending plants against both pathogens (Van Bockhaven et al., 2013) and herbivores (Hartley & DeGabriel, 2016; Reynolds et al., 2009). The fact that eCO₂ caused silicon accumulation to decline overall, and very strongly in native species, may compromise the ability of these grasses to cope with the biotic and abiotic stresses in the future. While temperature was a much weaker driver of silicon concentrations, it did ameliorate CO₂-driven declines in native species to some

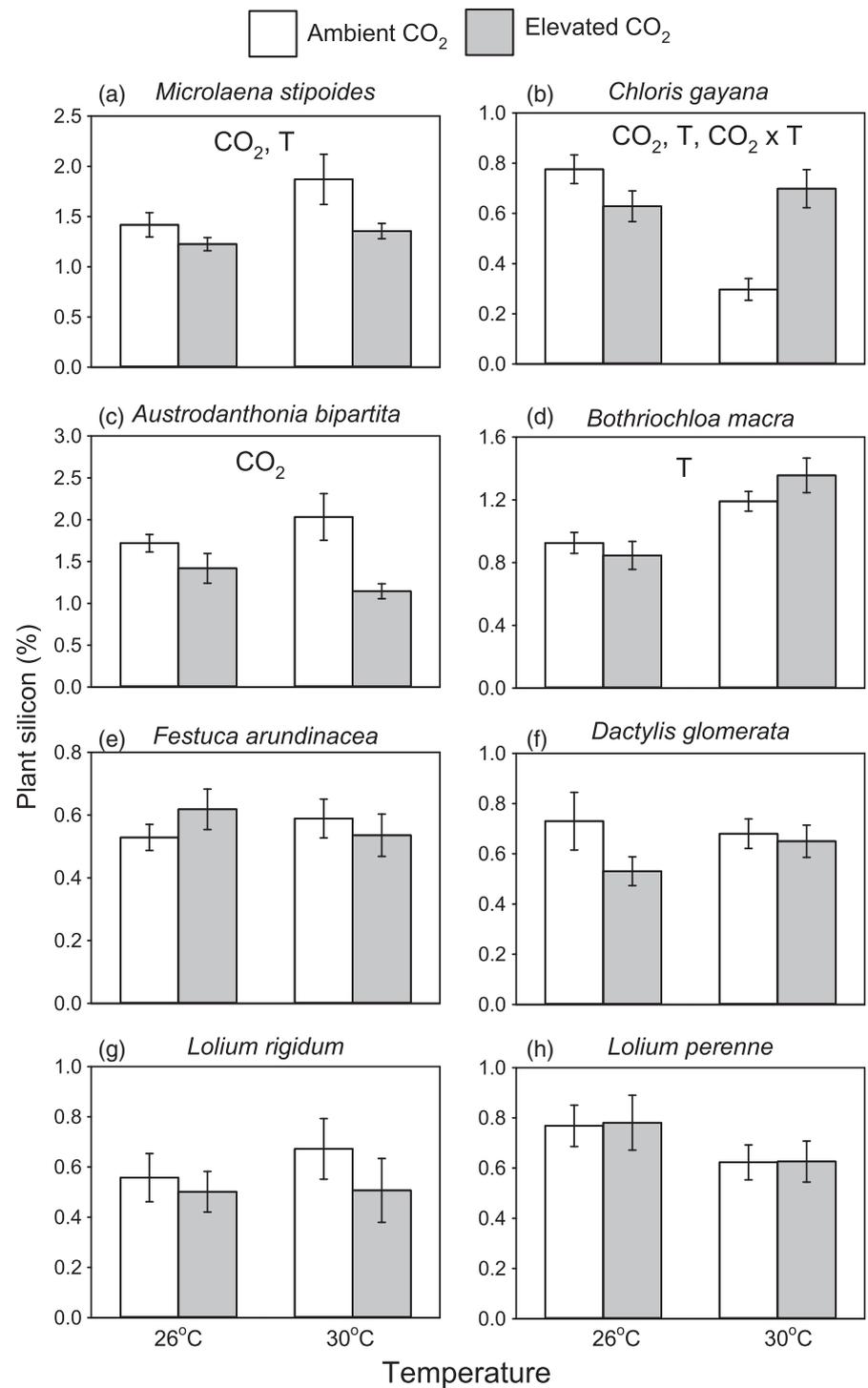


FIGURE 2 Impacts of eCO₂ and eT on shoot Si concentrations. Statistically significant ($p < .05$) impacts and interactions indicated in each panel. Mean values \pm SE shown. $N = 10$. Statistically significant terms and interactions (temperature, T , and carbon dioxide, CO₂) indicated in panels (see Table S1 for statistical analysis)

extent although it is unclear whether this would be to the extent that stress alleviation would be restored. Given that exotic species either maintained or increased silicon concentrations (albeit at lower levels) under these scenarios, this may be enough to alter the competitive balance between species.

The extent of silicon accumulation in plants appears to be related to the presence of silicon transporter genes, NIP2s in particular, which are present in plants accumulating silicon in excess of 1% of dry mass (termed "silicon competent") (Deshmukh & Bélanger, 2016).

Plants lacking functional NIP2s typically accumulate <1% silicon dry mass (Deshmukh & Bélanger, 2016). All of the native species in this study contained >1% silicon, whereas all of the exotic species contained less than 1%. It is still uncertain how and why plants have acquired and lost silicon competence (Stromberg et al., 2016), but we can conclude that the natives in the current study possessed this trait and that they showed greatest changes in silicon accumulation in response to eCO₂ and eT. It could be speculated that absorbing relatively more silicon, with greater plasticity (i.e. regulating active

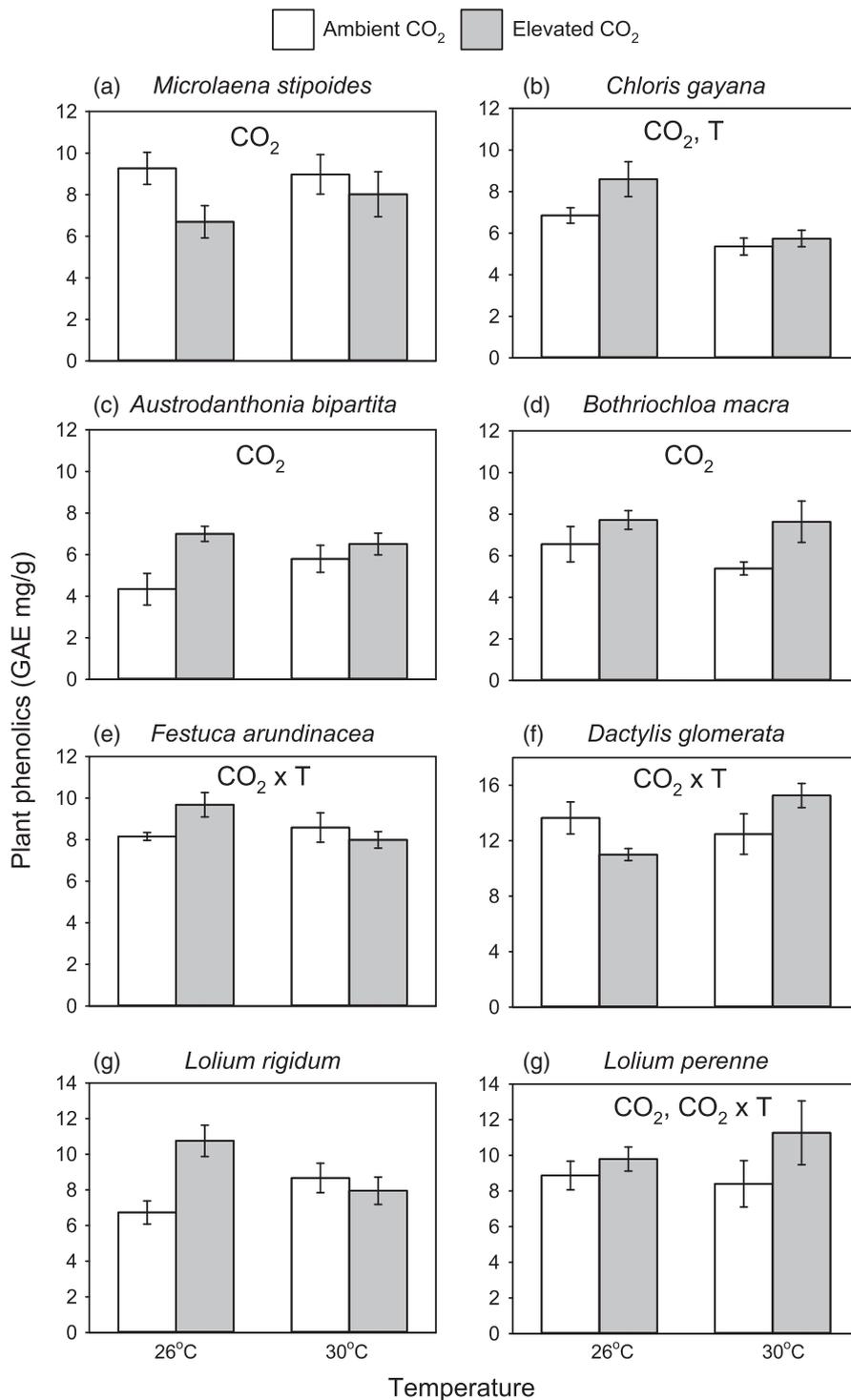


FIGURE 3 Impacts of eCO₂ and eT on shoot phenolic concentrations. Statistically significant ($p < .05$) impacts and interactions indicated in each panel. Mean values \pm SE shown. $N = 10$. Statistically significant terms and interactions (temperature, T , and carbon dioxide, CO₂) indicated in panels (see Table S1 for statistical analysis)

transporters as needed), would be a selective advantage to plants evolving in low nutrient soils and seasonally arid climates (Stromberg et al., 2016) such as Australia. As previously discussed, silicon may act as substitute for nutrient costly structural compounds (McNaughton et al., 1985; Raven, 1983) and has been widely shown to alleviate the effects of heat and drought (Liang et al., 2007). The fact that Australian natives in this study responded to warmer temperatures by increasing silicon uptake is at least compatible with this hypothesis.

4.2 | Defensive trade-offs involving silicon

While eCO₂ frequently increases defences such as phenolics (Robinson et al., 2012), negative correlations between phenolics and silicon-based defences reported here and previously (Cooke & Leishman, 2012; Frew et al., 2016; Schaller et al., 2012) could make some plants more susceptible to herbivory if silicon is the more effective defence. Cooke and Leishman (2012) demonstrated that silicon was negatively correlated with the abundance of

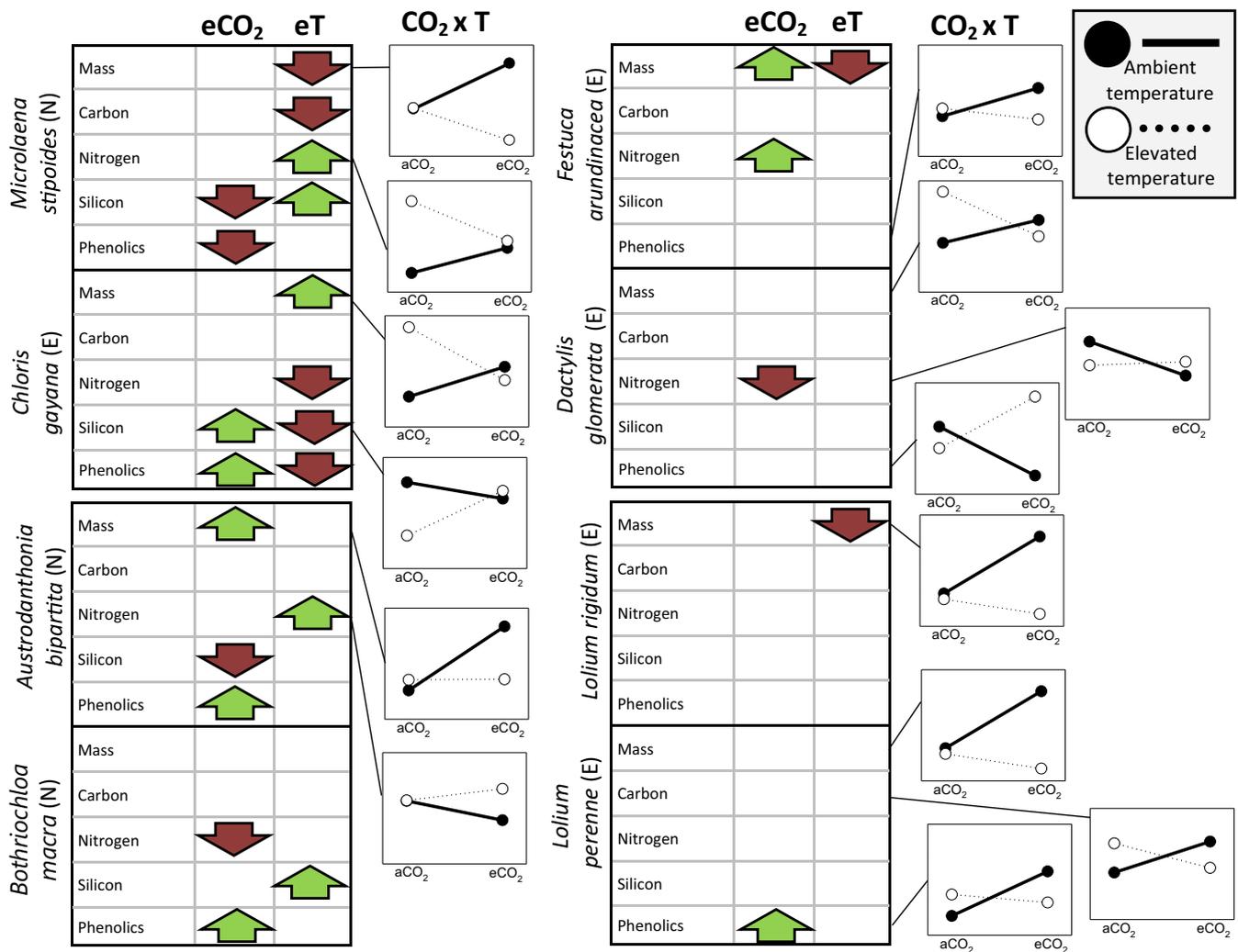


FIGURE 4 Summary of impacts of $e\text{CO}_2$ and $e\text{T}$ on grass traits. Native (N) and exotic (E) species indicated. Downward arrows indicate significant declines and upward arrows indicate increases. Significant interactions between factors shown in scaled illustrated panels [Colour figure can be viewed at wileyonlinelibrary.com]

Coleoptera (including many herbivores), whereas phenolics and tannins were unrelated to insect abundance. While we focused on foliar defences in the present study, phenolic defences are often ineffective against root herbivores (see examples in Johnson & Nielsen, 2012). Canegrub performance was even positively correlated with phenolic concentrations in sugarcane because of the trade-off with the more effective silicon defences (Frew et al., 2016). There are potential examples of grass phenolics being effective against both foliar and root herbivores (Moore & Johnson, 2017; Vicari & Bazely, 1993), however, so increases in phenolics might compensate for any overall decreases in silicon uptake. We also found negative correlations between plant dry mass (and implicitly growth rates) and both defences. This is at least compatible with a growth-defence trade-off in plants; defence acquisition comes at the cost of plant growth. Interestingly, silicon accumulation would appear to be the less costly defence since it was acquired at almost four times the rate as phenolic biosynthesis per unit of dry mass decrease.

5 | CONCLUSION

$e\text{CO}_2$ was a stronger driver of silicon uptake than $e\text{T}$ although temperature did affect some species either increasing or decreasing silicon uptake. Given the importance that silicon plays in the Poaceae, particularly in terms of stress mitigation, we suggest silicon should be included in the suite of chemical responses that experimenters measure when assessing the potential impacts of global change on plant communities. Here, we provide empirical support for this suggestion and our findings demonstrate that diminished silicon accumulation in a high CO_2 world could leave some grass species more susceptible to herbivores and potentially other forms of plant stress.

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