Determinants of growth of the flammable grass, *Triodia scariosa*: Consequences for fuel dynamics under climate change in the Mediterranean region of South Eastern Australia

REBECCA K. GIBSON,[1]* ROSS A. BRADSTOCK,[1] TRENT PENMAN,[1]
DAVID A. KEITH[2,3,4] AND DON A. DRISCOLL[5,6]

[1]*Centre for Environmental Risk Management of Bushfires, Institute for Conservation Biology and Environmental Management, University of Wollongong, Wollongong (Email: gibson.rebecca@gmail.com),* [2]*NSW Office of Environment and Heritage, Hurstville,* [3]*Australian Wetlands, Rivers and Landscapes Centre, University of New South Wales, Sydney, New South Wales, Australia,* [4]*Long Term Ecological Research Network, Terrestrial Ecosystem Research Network, Australia,* [5]*ARC Centre of Excellence for Environmental Decisions, the NERP Environmental Decisions Hub, Fenner School of Environment and Society and* [6]*Fenner School of Environment and Society, Australian National University, Canberra, Australian Capital Territory, Australia*

Abstract   Environmental conditions may influence the presence and strength of competitive interactions between different life forms, thereby shaping community composition and structure, and corresponding fuel dynamics. Woodland and shrubland communities of the Mediterranean climate region of South Eastern Australia contain a varied mixture of herbaceous and woody plants. The ratio of herbaceous to woody plants changes along gradients of temperature, moisture and soil fertility. This study aimed to experimentally examine the relative importance of, and interactions between environmental controls (moisture and soil fertility) on the balance of dominant herbaceous (*Triodia scariosa*) and woody plants (e.g. *Acacia ligulata* and *Leptospermum coriaceum*) and their ultimate effects on fuel and fire regimes. The results suggest that environmental determinants of the growth of *T. scariosa* are likely to be more important than interactions with shrubs in controlling the distribution of *T. scariosa*. The growth of *T. scariosa* was consistently higher under hot temperatures and on the less fertile yellow sands, which dominate the south of the region. The results suggest that there is strong potential for the distribution and abundance of *T. scariosa* to be altered in the future with changes in temperature associated with climate change. The distribution of soil types across the Mediterranean climate region of South Eastern Australia may be predisposed to favour the southerly expansion of *T. scariosa*-dominated communities in the future under a warmer climate.

Key words: climate change, fuel dynamics, grasses, woody plants.

INTRODUCTION

Productivity influences fire activity via effects on the amount, structure and connectivity of fuels and their availability to burn (i.e. the productivity-fire frequency model; Bond & Keeley 2005; Bradstock 2010; Krawchuk & Moritz 2011; O'Connor *et al.* 2011; Pausas & Paula 2012). The response of fuel to moisture will also be affected by the composition of vegetation communities (Pausas & Paula 2012). Herbaceous (i.e. grasses, forbs) and woody plants (i.e. trees, shrubs) represent fuel types with contrasting properties associated with patterns of growth, fuel accumulation, drying and flammability (Walker 1981; O'Connor *et al.* 2011;

Sullivan *et al.* 2012; Murphy *et al.* 2013). The patterns of growth and flammability in response to moisture will differ fundamentally between these different life forms (Walker 1981; O'Connor *et al.* 2011). Soil fertility may also influence the balance between herbaceous and woody plants (Carrera *et al.* 2000; Lehmann *et al.* 2011; Mills *et al.* 2012; Gibson *et al.* 2014a) and corresponding effects on fire regimes (Gibson *et al.* 2014b).

Relative differences in suitability of environmental conditions for different life forms may influence the presence and strength of competitive interactions, and hence fuels, by shaping community composition and structure (Briones *et al.* 1998; Maestre *et al.* 2003; Eggemeyer *et al.* 2009; Throop *et al.* 2012). Disentangling the relative influences of moisture, soil fertility and species interactions on the cover of herbaceous and woody plants will provide insight into potential effects of climate change on community

composition and structure, which, in turn, may alter fire regimes in the future.

Woodland and shrubland communities of the Mediterranean climate region of South Eastern Australia contain a varied mixture of herbaceous and woody plants. The ratio of herbaceous to woody plants changes along gradients of moisture and soil fertility within the region. Mean annual rainfall is highest in the south and lowest in the north, while soils of relatively low fertility are common in southern parts of the region. As a result of these influences, grass cover is lower and shrub cover is higher towards the south of the region (Pausas & Bradstock 2007; Gibson *et al.* 2014a). This system provides an opportunity to examine the relative importance of shrub–grass interactions and other environmental controls on the balance of herbaceous and woody plants. An understanding of the strength of these determinants will provide insight into the way in which fuels and fire regimes are determined by community composition (Bowman *et al.* 2014).

While previous research in the Mediterranean climate region of South Eastern Australia found evidence of intraspecific competition (between *Triodia scariosa* individuals and between shrub individuals), there was no evidence of competitive interactions between grasses and shrubs (Gibson *et al.* 2014a). However, patterns of total rainfall, temperature, seasonality of rainfall and soils are partly confounded across the region, making it difficult to disentangle their respective effects in these observational field studies. Thus, manipulative experiments are required to separate the potential influence of each of these factors on the presence and strength of interactions between hummock grasses and shrubs, two important fuel components of the woodland and shrubland ecosystems.

In this study, we experimentally examined the influence of temperature, moisture and soil type on the potential for two commonly co-occurring woody shrub species: *Acacia ligulata* and *Leptospermum coriaceum* to suppress the growth of *T. scariosa*. Shrubs were anticipated to diminish the potential growth of *T. scariosa* because of their dominance in above- and below-ground structure of biomass (Eggemeyer *et al.* 2009; Throop *et al.* 2012).

Given the contrasting photosynthetic pathways utilized by *T. scariosa* (C_4) and the shrubs (C_3), temperature was predicted to influence relative growth in contrasting ways. The C_4 photosynthetic pathway allows for greater water use efficiency and higher growth rates at warmer temperatures (Sage *et al.* 1999; Osborne & Freckleton 2009). As such, water availability during the warmer months when C_4 plants are actively growing is expected to support higher growth rates of *T. scariosa*. By contrast, the active growing season of C_3 shrubs is during the cooler months, and winter rainfall regimes are expected to present more favourable conditions for

C_3 plants (Sage *et al.* 1999; Hughes 2003; Murphy & Bowman 2007). Therefore, cooler temperatures were predicted to favour the competitive suppression of *T. scariosa* by shrubs.

Characteristics of different soil types, such as fertility and water holding capacity, may provide a relative advantage to one life form over the other (Knoop & Walker 1985; Ogle & Reynolds 2004; Wills & Clarke 2008). For example, fast water percolation in coarse-textured soils favours woody plants over grasses because of their relatively deeper root systems (Walter 1971; Martin & Cable 1974). In addition, shrubs generally have lower nitrogen requirements compared with perennial grasses (Carrera *et al.* 2000), which may provide an advantage to shrubs over grasses on less fertile soils. Therefore, the relatively less fertile and coarse-textured yellow sands were also predicted to favour the diminution of *T. scariosa* in the presence of shrubs.

MATERIALS AND METHODS

Experimental design

Experimental treatments were selected to simulate the moisture, temperature and soil conditions that occur in the field across the Mediterranean climate landscape of South Eastern Australia. The reference region that was used to develop the experimental design encompasses much of the Murray Lowlands from south-west New South Wales, to central-west Victoria (Fig. 1), which is dominated by semi-arid mallee woodlands ('mallee'). The region spans a rainfall gradient from approximately 200 mm annually in the north to 400 mm annually in the south. This increase in total rainfall corresponds with a decline in mean temperature and a change in rainfall seasonality whereby rainfall becomes increasingly winter-dominated.

Mallee occurs on undulating dune fields of aeolian sands that are either red or yellow in colour (NRIC 1991). Red sands (dd1, dd2, dd3, dd7, aa1, aa2, aa3, NRIC 1991), derived from alluvial and subsequent Aeolian origins, are prevalent in the north, whereas yellow sands, formed by marine processes, are common across the south. Yellow sands (ca2, ya9, ya11, yb1, x4, NRIC 1991) are relatively less fertile than the red sands because of a relatively more acidic pH, and lower clay content, which reduces nutrient availability for plant growth (Blackburn & Wright 1989; Wasson 1989). In addition, the yellow sands are relatively coarser in texture compared with the red sands and are therefore likely to have higher infiltration rates and lower water holding capacity. Coarse-textured soils generally have relatively lower soil water content (Gurevitch *et al.* 2002) and retain water at greater depths compared with fine-textured soils (Sala *et al.* 1997). Eucalypts with the multi-stemmed mallee growth habit are the dominant life form in this community, while the understory contains the C_4 perennial hummock grass, *T. scariosa*, and a diversity of
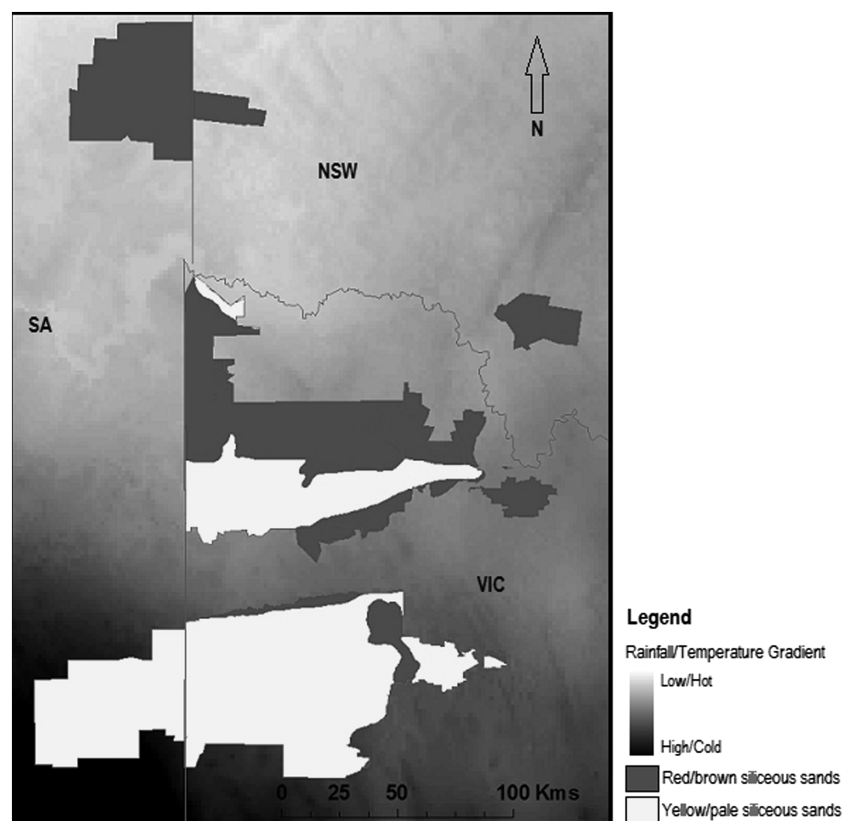
Fig. 1. Location of the reference region in South Eastern Australia that was used to develop the experimental design, demonstrating the confounded nature of rainfall, temperature and soils across the region. Sand types are shown within the boundaries of National Parks and Nature Reserves.

woody shrub species. The relative cover of grasses and shrubs changes across the region; grass cover declines and shrub cover increases in a southward direction. Three species were selected for use in this study, *T. scariosa*, and two common woody shrub species: *L. coriaceum* and *A. ligulata*. These shrub species were selected because they commonly co-occur with *T. scariosa* throughout the mallee region (AVH 2010; Matt White, pers. comm. 2010). Samples of red and yellow sands were collected each from a single representative location within the study area, to ensure that spatial variation in soil properties was minimized.

Two temperature treatments were simulated in four, large, controlled environment chambers at the Australian National University Controlled Environment Facility. These treatments were selected to represent the average annual diurnal cycle of maximum and minimum temperatures that occur in the hot north and cool south of the reference region. Two chambers were allocated to each temperature treatment, with a fixed diurnal cycle of 12 h each of light and dark. Two watering treatment levels were used to represent the average annual precipitation levels that occur in the dry north and wet south. All combinations of temperature and water levels and sand types were examined in the experiment (Table 1).

Preparation and data collection

Seeds of each species were purchased from a commercial native seed supplier (Tony Langdon, Mildura Native Nursery) and sown in trays of each sand type (i.e. red 'fertile' and yellow 'infertile' sands) in greenhouses with water provided daily. Although seedlings of each species varied in their time to emergence, once all seedlings were between 3 and 6 months old, a single seedling of *T. scariosa* was transplanted into each pot (150-mm diameter by 400-mm deep polyvinyl chloride pipe with mesh bottom) containing the same sand type from which the seed had been raised. Next to each *T. scariosa* seedling, a neighbour seedling of either *T. scariosa*, *L. coriaceum* or *A. ligulata* was planted.

The pairing of *T. scariosa* seedlings controlled for a potentially confounding effect of density that may have been implicit within responses of shrub and *T. scariosa* pairs. Thus, effects of shrub seedlings on *T. scariosa* performance were assessed relative to the effect of a conspecific neighbour. This design therefore specifically addressed the potentially suppressive effects of shrubs on relatively closely spaced populations of *T. scariosa*. Such relatively dense stands of *Triodia* species are known to form highly flammable fuel arrays (Bradstock &

Table 1. Treatment combinations of temperature, water and sand type that were used to investigate competitive interactions between shrubs and *Triodia scariosa*

Temperature (°C)			Water		Sand type
Type	Day	Night	Type	mm week^{-1}	
High	25	15	Low	4.5	Red
High	25	15	Low	4.5	Yellow
High	25	15	High	13	Red
High	25	15	High	13	Yellow
Low	20	10	Low	4.5	Red
Low	20	10	Low	4.5	Yellow
Low	20	10	High	13	Red
Low	20	10	High	13	Yellow

Day and night temperatures represent the average annual maximum and minimum temperatures that occur in the 'hot' north and 'cold' south of the reference region. The maximum (day) and minimum (night) temperatures were applied with the chamber lights on and off, respectively. Low and high water levels represent the average weekly rainfall (mm) that occurs in the north and south of the reference region.

Gill 1993; Allan & Southgate 2002), and swards of high-density *Triodia* spp. are known to provide a highly flammable fuel matrix in mallee communities (Bradstock & Cohn 2002). In particular, if the experiments produced a significant diminution of growth of *T. scariosa* seedling in the presence of shrub neighbours, compared with *T. scariosa* neighbours, this would indicate the potential for shrubs to alter the continuity and potential flammability of dense *T. scariosa* populations.

A number of plant deaths occurred in the first week of the experiment, probably because of the stress of transplantation. The number of replicates was therefore reduced and was variable among treatments (Table 2).

Pots were watered on the same day each week and were randomly re-assigned to new positions within each chamber every 4 weeks, to eliminate any potential effects of position within the chamber on temperature or light conditions. The height, diameter and leaf number of *T. scariosa* plants were measured at the start and at the end of the experiment, which ran without interruption for 12 weeks. In the paired *T. scariosa* treatment, measurements were repeatedly performed on one targeted individual only. Volume was calculated (hemispherical) based on height measurements. These measures of plant dimensions were explored as indicators of interactions between individuals. They also may be surrogates for biomass (White & Harper 1970; Idso & Kimball 1997; Niklas & Enquist 2001).

Statistical analyses

Because of limited replication, differentiating the potential interactive effects of individual shrub species *A. ligulata* and

L. coriaceum on *T. scariosa* was not possible. Therefore, data for the shrub species were combined for the analysis. Plant sizes were measured prior to commencement of the experiment to ensure no bias in starting size occurred among the treatments (Table 2). Nonetheless, a relative measure of growth corrected for starting values was estimated for each response variable ('rHeight', 'rDiameter', 'rVolume' and 'rLeaf'), which allowed a standardized comparison of effects based on initial plant size. This estimate was defined as the increase in biomass per unit plant biomass present at the commencement of the study (Poorter 1993) and was calculated using the following formula:

$$rX = \frac{X \text{ at } t_1 - X \text{ at } t_0}{X \text{ at } t_0}$$

where X represented the growth response variable and t_0 and t_1 represented the start and end of the experiment, respectively. All factors were analysed as categorical variables.

For each response variable, model-subset selection using Akaike's information criterion corrected for small sample size (AIC_c) was employed to identify the best model from a set of candidate generalized linear models (GLMs) with a normal (Gaussian) distribution (Burnham & Anderson 2002). The candidate GLMs analysed all combinations of single factors and two-way interactions. Higher order interactions were not included because of sample size and unbalanced designed (i.e. because of mortality). We followed the recommendations of Harrell *et al.* (1996), requiring ten sample points per predictor degree of freedom. The model with the smallest AIC_c value (the top model) and any model within two AIC_c points of the top model were considered to have strong support (Burnham & Anderson 2002). For each growth response variable, a preferred model was selected from the best set of models that included only predictors that were significant (i.e. $P < 0.05$). Shapiro–Wilks tests on the residuals of the GLMs were performed to check that the residuals were normally distributed. Each response variable required a log transformation to achieve normality on the residuals. All analyses were performed using R, v.2.13.1 R Development Core Team (2011).

RESULTS

The best set of models (i.e. the top model with the smallest AIC_c and all models within 2 $dAIC_c$ points) for all of the growth response variables included various combinations of sand, temperature and water, but none included the response variable of shrub neighbour (Table 3).

For raw height, temperature was included as a significant predictor in the best set of models ($t = 3.89$, $P = 0.0003$, Table 4), while sand and water had non-significant effects. Height was significantly larger under high compared with low temperatures (Fig. 2a). For

Table 2.   Dimensions of *Triodia scariosa* seedlings (i.e. means and standard errors (SE) of the height, diameter, volume and leaf count) in the presence of shrub species neighbours, at the commencement of experimental treatments comprised of regimes of contrasting temperature and moisture

Treatment combinations					Start height (mm)		Start diameter (mm)		Start volume (cm³)		Start leaf count	
Sand	Water	Temp.	Neighbour species	n	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Red	High	Low	*T. scariosa*	3	26.6	25.6	33.3	48.4	121.8	196.4	7	4.5
			A. ligulata	2	25	14.1	22.5	10.6	48.4	58.5	3	0.6
			L. coriaceum	1	20	0	15	0	16.7	0	2	0
			Shrub group	3	23.3	10.4	20	8.6	37.8	45.2	2.5	0.3
Red	High	High	*T. scariosa*	0	—	—	—	—	—	—	—	—
			A. ligulata	2	28	16.9	27.5	17.6	71.3	88.7	5	1
			L. coriaceum	2	35	21.2	35	28.3	139.3	173.3	3	0
			Shrub group	4	31.5	16.2	31.2	19.7	105.3	119	4	1.4
Red	Low	Low	*T. scariosa*	2	17	4.2	10	7	11.2	7.8	2	0
			A. ligulata	2	37.5	10.6	30	28.2	123.7	94.9	6.6	4.6
			L. coriaceum	1	13	0	20	0	4.6	0	2	0
			Shrub Group	3	29.3	16	26.6	20.8	84	96.1	4.3	3.2
Red	Low	High	*T. scariosa*	2	31.5	9.2	30	7.1	73.8	58.1	3.5	0.5
			A. ligulata	0	—	—	—	—	—	—	—	—
			L. coriaceum	1	43	0	50	0	166.5	0	8	0
			Shrub group	1	43	0	50	0	166.5	0	8	0
Yellow	High	Low	*T. scariosa*	2	30.6	29.5	30	26	188.9	311.9	4.3	1.6
			A. ligulata	3	26.3	14	28.3	16.1	60.5	73.9	4.8	2.7
			L. coriaceum	3	25	8.6	25	8.6	41.1	42.2	6	2.1
			Shrub group	6	25.6	10.5	26.6	11.7	50.8	54.8	5.3	1.4
Yellow	High	High	*T. scariosa*	2	54	22.6	56.5	26.2	416.6	426.7	4	1
			A. ligulata	2	40.5	7.8	35.5	13.4	146.8	80.6	4.3	1.3
			L. coriaceum	1	22	0	26	0	22.3	0	3	0
			Shrub group	3	34.3	12	32.3	10.9	105.3	91.8	4	0.8
Yellow	Low	Low	*T. scariosa*	2	22.5	3.5	25	0	24.7	11.3	3.5	1.2
			A. ligulata	2	29	5.6	32.5	3.5	53.9	30.1	3.8	0.8
			L. coriaceum	3	24.3	9.3	23.6	14	39.5	43.5	3.3	0.9
			Shrub group	5	26.2	7.6	27.2	11.2	45.3	35.2	3.6	0.6
Yellow	Low	High	*T. scariosa*	3	33	24	25	14.1	135.2	179.1	3.3	0.88
			A. ligulata	3	22.3	6.6	27.6	14.2	27.3	19.5	5.6	2.7
			L. coriaceum	2	23.3	2.9	21.3	5.7	27.4	9.2	12	1
			Shrub group	4	22.8	4.6	24.5	10.3	27.3	13.6	8.2	2.2

n, the number of replicates under each treatment combination.

raw diameter response, there were significant effects of sand ($t = 3.94$, $P = 0.0003$, Table 4) and temperature ($t = 2.43$, $P = 0.019$, Table 4) plus a non-significant effect of water in the best set of models. Diameter was significant larger under high compared with low temperatures (Fig. 2b) and on yellow compared with red sand (Fig. 2c). For raw volume, temperature was included as a significant predictor in the best set of models ($t = 3.82$, $P = 0.0004$, Table 4), while sand and water had non-significant effects. Volume was significantly greater under high compared with low temperatures (Fig. 2d). For raw leaf count, temperature was included as a significant predictor in the best set of models ($t = 2.495$, $P = 0.016$, Table 4), while sand and water had non-significant effects. Leaf count was higher under high compared with low temperatures (Fig. 2e).

For the relative change in height, there were significant effects of sand ($t = 3.27$, $P = 0.002$, Table 5) and temperature ($t = 2.79$, $P = 0.008$, Table 5), plus a non-significant interaction of sand and temperature, in the best set of models. The relative change in height was greater under high compared with low temperatures (Fig. 2f) and on yellow compared with red sand (Fig. 2g). For the relative change in diameter, there were significant effects of sand ($t = 4.38$, $P < 0.0001$, Table 5) and temperature ($t = 2.80$, $P = 0.008$, Table 5), plus a non-significant interaction of sand and temperature, in the best set of models. The relative change in diameter was greater under high compared with low temperatures (Fig. 2h) and on yellow compared with red sand (Fig. 2i). For the relative change in volume, there were significant effects of sand ($t = 3.42$, $P = 0.001$, Table 5)

Table 3.   Summary of effects of neighbour, temperature and moisture on morphological responses of *T. scariosa* seedlings as indicated by results of model-subset of generalized linear models (GLMs), using the deviance in Akaike's information criterion corrected for small sample size (dAIC$_c$) values

	Raw growth response variables			Relative growth response variables		
Response	Model	dAIC$_c$		Response	Model	dAIC$_c$
Height	Temp.	0.00		rHeight	Sand + temp.	0.00
	Sand + temp.	0.23			Sand × temp.	1.25
	Temp. + water	0.94				
	Sand + temp. + water	0.95				
Diameter	Sand + temp. + water	0.00		rDiameter	Sand + temp.	0.00
	Sand + temp.	0.03			Sand × temp.	0.02
	Sand + temp. × water	1.08				
	Sand × temp.	1.71				
Volume	Temp.	0.00		rVolume	Sand + temp.	0.00
	Sand + temp.	0.51			Sand × temp.	0.69
	Temp. + water	0.76				
	Sand + temp. + water	1.06				
	Sand + temp. × water	1.72				
Leaf count	Sand + temp. × water	0.00		rLeaf	Temp. × water	0.00
	Temp.	0.05			Sand + temp. × water	1.25
	Sand + temp. + water	0.16				
	Sand + temp.	0.52				
	Temp. × water	1.74				

The best set of models are shown for each raw and relative growth response variable: height, diameter, volume, leaf count, relative change in height (rHeight), relative change in diameter (rDiameter), relative change in volume (rVolume) and relative change in leaf count (rLeaf).

Table 4.   Parameter estimate (est.), standard error (SE) and significance values for each of the predictor variables contained within the best set of models from the model-subset selection (Table 4) for raw growth for each morphological response: height, diameter, volume and leaf count

Coefficient	Height				Diameter				Volume				Leaf			
	est.	SE	*t* value	*P* value	est.	SE	*t* value	*P* value	est.	SE	*t* value	*P* value	est.	SE	*t* value	*P* value
Sand (yellow)	0.16	0.11	1.44	0.15	0.30	0.13	2.43	**0.019**	0.19	0.12	1.58	0.12	0.03	0.02	1.484	0.14
Temp (high)	0.42	0.11	3.89	**0.0003**	0.49	0.12	3.94	**0.0003**	0.64	0.17	3.82	**0.0004**	0.05	0.02	2.495	**0.016**
Water (low)	−0.13	0.11	−1.18	0.25	−0.19	0.12	−1.54	0.13	−0.02	0.15	−0.16	0.87	−0.03	0.02	−1.646	0.11
Sand (yellow) × temp (high)	—	—	—	—	−0.22	0.26	−0.87	0.39	—	—	—	—	—	—	—	—
Temp (hot) × water (low)	—	—	—	—	−0.29	0.25	−1.19	0.24	−0.32	0.24	−1.343	0.18	−0.04	0.04	−0.842	0.4045

Bold values indicate significance at the *P* = 0.05 level.

and temperature (*t* = 2.86, *P* = 0.007, Table 5), plus a non-significant interaction of sand and temperature, in the best set of models. The relative change in volume was greater under high compared with low temperatures (Fig. 2j) and on yellow compared with red sand (Fig. 2k). For the relative change in leaf count, there was a significant interaction of temperature and water (*t* = −3.09, *P* = 0.003, Table 5), plus a non-significant effect of sand type in the best set of models. The relative change in leaf count was significantly higher under high temperatures and high water compared with all other combinations of temperature and water (Fig. 2l).

DISCUSSION

Our results suggest that environmental determinants of the growth of *T. scariosa* are likely to be more important than interactions with shrubs in controlling the distribution of *T. scariosa* and the switch in fuel systems that occurs across the Mediterranean woodlands of South Eastern Australia. Temperature and sand type had the strongest influence on the growth of *T. scariosa*, whereby growth was consistently higher under high compared with low temperatures and on yellow compared with red sands (Fig. 2, Tables 4 and 5). The results were consistent with a previous field study that found no evidence
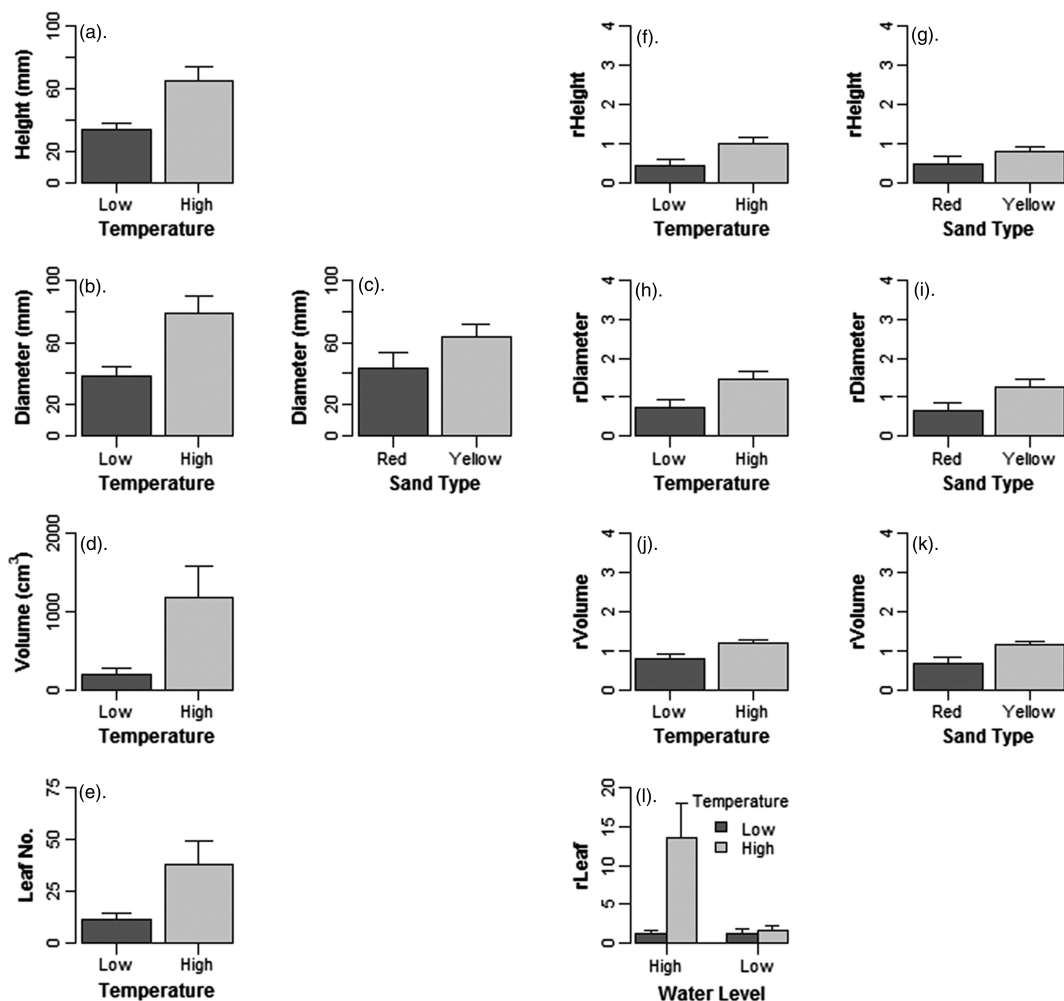
Fig. 2. Effects of experimentally imposed regimes of temperature, moisture and soil type on the growth of *Triodia scariosa* seedlings. Effects of significant predictors contained within the preferred model for the mean and standard error of each growth response are illustrated, including (a) the effect of temperature on height, (b) the effect of temperature on diameter, (c) the effect of sand on diameter, (d) the effect of temperature on volume, (e) the effect of temperature on leaf count, (f) the effect of temperature on the relative change in height (rHeight), (g) the effect of sand type on the relative change in height (rHeight), (h) the effect of temperature on the relative change in diameter (rDiameter), (i) the effect of sand type on the relative change in diameter (rDiameter), (j) the effect of temperature on the relative change in volume (rVolume), (k) the effect of sand type on the relative change in volume (rVolume) and (l) the interaction of temperature and water on the relative change in leaf count (rLeaf).

Table 5. Parameter estimate (est.), standard error (SE) and significance values for each of the predictor variables contained within the best set of models from the model-subset selection (Table 4) for each relative growth for each morphological response: relative change in height (rHeight), relative change in diameter (rDiameter), relative change in volume (rVolume) and relative change in leaf count (rLeaf)

Coefficient	rHeight				rDiameter				rVolume				rLeaf			
	est.	SE	t value	P value	est.	SE	t value	P value	est.	SE	t value	P value	est.	SE	t value	P value
Sand (yellow)	0.46	0.14	3.27	**0.002**	0.62	0.14	4.38	**<0.0001**	0.62	0.18	3.42	**0.001**	0.14	0.12	1.12	0.27
Temp (high)	0.47	0.16	2.79	**0.008**	0.46	0.16	2.80	**0.008**	0.61	0.21	2.86	**0.007**	—	—	—	—
Water (low)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sand (yellow) × temp (high)	−0.23	0.21	−1.10	0.27	−0.33	0.21	−1.55	0.13	−0.36	0.27	−1.32	0.19	—	—	—	—
Temp (hot) × water (low)	—	—	—	—	—	—	—	—	—	—	—	—	−0.74	0.24	−3.09	**0.003**

Bold values indicate significance at the $P = 0.05$ level.

of competitive suppression of *T. scariosa* by shrubs across the rainfall and soil fertility gradients of this region (Gibson *et al.* 2014a) and support the notion that resource partitioning may occur between *T. scariosa* and shrubs (Aerts *et al.* 1991; Schenk & Jackson 2002; February *et al.* 2011; Throop *et al.* 2012).

Environmental determinants of *T. scariosa* growth

The results indicate that temperature plays a strong role in controlling the growth of *T. scariosa*. There was consistency across all growth response variables, whereby high temperatures improved the growth of *T. scariosa*. *Triodia scariosa* utilizes the C_4 photosynthetic pathway, which enhances photosynthesis and water use efficiency under warmer temperatures (Ehleringer & Monsons 1993; Sage *et al.* 1999; Osborne & Freckleton 2009). Given that *T. scariosa* cover is high in the hot, north of the region and declines as temperatures decrease towards the south (Gibson *et al.* 2014a), the effect of temperature on *T. scariosa* growth is likely to be a key determinant of its present-day distribution.

While temperature was a significant predictor of *T. scariosa* growth across all response variables, the effect of sand type was generally only significant for the relative measures of growth and not the raw measures (e.g. rHeight *vs.* height), with the exception of diameter. The large variation in starting values for height, diameter, volume and leaf count (Table 2) may have influenced the results of the raw growth response measures. Therefore, the relative measure of change in growth may provide a more accurate measure of *T. scariosa* growth responses.

The higher growth of *T. scariosa* on the less fertile yellow sands was an unexpected result, as the relatively low fertility of these soils, compared with the red sands, was expected to diminish productivity. Organic matter content of soils can vary widely between soil types and may influence available water content (Oades 1988; Hudson 1994). However, further research exploring potential differences in organic soil properties between the sand types would be required to confirm this as a causal mechanism of higher growth rates on the yellow sands. While the mechanism driving the effect of soils on *T. scariosa* growth may be unclear, the results suggest that the distribution of soil types across the Mediterranean region of South Eastern Australia is unlikely to control the distribution and cover of *T. scariosa*. *Triodia scariosa* is a dominant feature of the understory across the red sands in the north of the region but occurs in low abundance (although notably still present; CHAH 2013) across the yellow sands in the shrub-dominated heath communities across south of the region. Given that the distribution of yellow sands coincides with cooler temperatures across the landscape, but the growth of *T. scariosa* is enhanced by yellow sands, the results suggest that the present-day distribution and abundance of *T. scariosa* is determined by temperature rather than soils.

The experimental design posed several important limitations that may have influenced the results. The use of mean annual maximum and minimum temperatures represents a more narrow range of temperatures than would occur in field situations. For example, summer maximum temperatures at soil levels are likely to be considerably higher (e.g. >55°C; Andersen 1983), and responses may differ under such conditions. Water may also be more limiting under field conditions, given the potential for higher temperatures and desiccation rates. In addition, the regular weekly delivery of pro-rata average annual rainfall (for practical reasons) does not simulate the sporadic nature of natural rainfall that occurs in the field. This study assessed possible effects of environmental determinants and shrubs on *T. scariosa* during a relatively small phase of the life cycle. The lack of any observed suppressive effects of shrubs on *T. scariosa* was consistent with correlative field evidence (Gibson *et al.* 2014a). Potential suppression of shrubs by *T. scariosa*, or potential effects of climatic conditions and competition at different stages in the life cycle (e.g. reproduction and recruitment), remains to be determined experimentally. Furthermore, below-ground growth responses were not examined. Nonetheless, the results provide important insight into the environmental determinants of the growth of *T. scariosa*.

Implications of climate change on fuel dynamics

The results suggest that there is strong potential for the distribution and abundance of *T. scariosa* to be altered in the future with changes in temperature associated with climate change. Across the study region, an increase in mean annual temperature by 4–5°C is within the range projected to occur by 2070 (Suppiah *et al.* 2007). Given that *T. scariosa* is present, albeit in very low abundance, within the shrub-dominated heath communities on yellow sands across the south of the region, such an increase in temperature may promote growth and abundance of *T. scariosa* across the yellow sands. As yellow sands significantly enhanced the growth of *T. scariosa* compared with red sands, the distribution of soil types across this region may be predisposed to favour the southerly expansion of *T. scariosa*-dominated mallee communities in the future under a warmer climate, as hypothesized by Keeley *et al.* (2012).

However, future changes in community states in this region may ultimately depend on the relative response of shrubs compared with grasses to future changes in temperature, moisture and CO_2. For example, given that C_3 shrubs are more likely to occur under winter rainfall regimes, warmer, drier conditions in the future

may be expected to negatively affect shrubs across the yellow sands towards the south of the Mediterranean region of South Eastern Australia. This may allow *T. scariosa* to rapidly increase in abundance and result in a shift in community states from high diversity heath communities with relatively short fire intervals influenced by a fire probability that increases as a function of time since fire (i.e. fuel age dependent), to *T. scariosa*-dominated mallee with longer fire intervals and fire probability independent of fuel age (Gibson *et al.* 2014b). However, elevated CO_2 is expected to provide a relatively greater benefit to C_3 shrubs than C_4 grasses (Bond & Midgley 2012; Wang *et al.* 2012; Tooth & Leishman 2013). Therefore, quantification of the relative responses of *T. scariosa* and shrubs to CO_2 in association with moisture, temperature and soils will help to predict the potential for community composition change and corresponding influences on fire regimes that may occur in this region in the future.

ACKNOWLEDGEMENTS

REFERENCES

Aerts R., Boot R. G. A. & van der Aart P. J. M. (1991) The relation between above and belowground biomass allocation patterns and competitive ability. *Oecologia* **87**, 551–9.

Allan G. E. & Southgate R. I. (2002) Fire regimes in spinifex landscapes. In: *Flammable Australia* (eds R. A. Bradstock, J. E. Williams & A. M. Gill) pp. 145–76. Cambridge University Press, Cambridge.

Andersen A. N. (1983) Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. *Aust. J. Ecol.* **8**, 127–37.

AVH. (2010) Australia's Virtual Herbarium; Atlas of Living Australia.

Blackburn G. & Wright M. J. (1989) Soils. In: *Mediterranean landscapes in Australia: mallee ecosystems and their management* (eds N. I.R & R. A. Bradstock) pp. 35–53. CSIRO Australia, Melbourne.

Bond W. & Keeley J. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* **20**, 387–94.

Bond W. J. & Midgley G. F. (2012) Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society B* **367**, 601–12.

Bowman D. M. J. S., MacDermott H. J., Nichols S. C. & Murphy B. P. (2014) A grass-fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecol. Evol.* **4**, 4185–94.

Bradstock R. (2010) A biogeographic model of fire regimes in Australia: contemporary and future implications. *Glob. Ecol. Biogeogr.* **19**, 145–58.

Bradstock R. A. & Cohn J. S. (2002) Fire regimes and biodiversity in semi-arid mallee ecosystems. In: *Flammable Australia* (eds R. A. Bradstock, J. E. Williams & A. M. Gill) pp. 238–58. Cambridge University Press, Cambridge.

Bradstock R. A. & Gill A. M. (1993) Fire in semi-arid, mallee shrublands: size of flames from discrete fuel arrays and their role in the spread of fire. *International Journal of Wildland Fire* **3**, 3–12.

Briones O., Montana C. & Ezcurra Z. (1998) Competition intensity as a function of resource availability in semi-arid ecosystems. *Oecologia* **116**, 365–72.

Burnham K. & Anderson D. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York.

Carrera A. L., Sain C. L. & Bertiller M. B. (2000) Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. *Plant and Soil* **224**, 185–93.

CHAH. (2013) Australia's virtual herbarium. The Council of Heads of Australasian Herbaria.

Eggemeyer K. D., Awada T., Harvey F. E., Wedin D. A., Zhou X. & Zanner C. W. (2009) Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C4 grasses in a semiarid grassland. *Tree Physiol.* **29**, 157–69.

Ehleringer J. R. & Monsons R. K. (1993) Evolutionary and ecological aspects of photosynthetic pathway variation. *Annu. Rev. Ecol. Systemat.* **24**, 411–39.

February E. C., Allsopp N., Shabane T. & Hattas D. (2011) Coexistence of a C4 grass and a leaf succulent shrub in an arid ecosystem. The relationship between rooting depth, water and nitrogen. *Plant and Soil* **349**, 253–60.

Gibson R. K., Bradstock R. A., Penman T., Keith D. A. & Driscoll D. A. (2014a) Changing dominance of key plant species across a Mediterranean climate region: implications for fuel types and future fire regimes. *Plant Ecol.* **215**, 83–95.

Gibson R. K., Bradstock R. A., Penman T., Keith D. A. & Driscoll D. A. (2014b) Climatic, vegetation and edaphic influences on the probability of fire across mediterranean woodlands of south-eastern Australia *Journal of Biogeography* **42**(9), 1750–1760.

Gurevith J. Scheiner S. M. & Fox G. A. (2002) The ecology of plants. Sunderland, Massachusetts.

Harrell F. E., Lee K. L. & Mark D. B. (1996) Tutorial in biostatistics multivariable prognostic models: issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. *Stat. Med.* **15**, 361–87.

Hudson B. D. (1994) Soil organic matter and available water capacity. *J Soil Water Conservat.* **49**, 189–94.

Hughes L. (2003) Climate change and Australia: trends, projections and impacts. *Ecology* **28**, 423–43.

Idso S. B. & Kimball B. A. (1997) Effects of long-term atmospheric CO_2 enrichment on the growth and fruit production of sour orange trees. *Glob. Chang. Biol.* **3**, 89–96.

Keeley J. E., Bond W. J., Bradstock R. A., Pausas J. G. & Rundel P. W. (2012) *Fire in Mediterranean Ecosystems; Ecology, Evolution and Management*. Cambridge University Press, Cambridge.

Knoop W. T. & Walker B. H. (1985) Interactions of woody and herbaceous vegetation in a southern African savanna. *J. Ecol.* **73**, 235–53.

Krawchuk M. & Moritz M. (2011) Constraints on global fire activity vary across a resource gradient. *Ecology* **92**, 121–32.

Lehmann C. E. R., Archibald S. A., Hoffmann W. A. & Bond W. J. (2011) Deciphering the distribution of the savanna biome. *New Phytologist* **191**, 197–209.

Maestre F. T., Bautista S. & Cortina J. (2003) Positive, negative and net effects in grass-shru interactions in Mediterranean semiarid grasslands. *Ecology* **84**, 3186–97.

Martin S. C. & Cable D. R. (1974) *Managing semidesert grass-shrub ranges: vegetation responses to precipitation, grazing, soil texture and mesquite control*. USDA Forest Service, Washington, DC.

Mills A. J., Milewski A. V., Fey M. V., Grongroft A., Peterson A. & Sirami C. (2012) Constraint on woody cover in relation to nutrient content of soils in western southern Africa. *OIKOS* **122**, 136–48.

Murphy B. P. & Bowman D. M. J. S. (2007) Seasonal water availability predicts the relative abundance of C3 and C4 grasses in Australia. *Glob. Ecol. Biogeogr.* **16**, 160–9.

Murphy B. P., Bradstock R. A., Boer M. M., *et al.* (2013) Fire regimes of Australia: a pyrogeographic model system. *J. Biogeogr.* **40**, 1048–58.

Niklas K. J. & Enquist B. J. (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc. Natl. Acad. Sci. U. S. A.* **98**, 2922–7.

NRIC (1991) Australian digital soils atlas. In: *Australian Soils* (ed N. R. I. Centre) . Bureau of Rural Sciences.

O'Connor T. G., Mulqueeny C. M. & Goodman P. S. (2011) Determinants of spatial variation in fire return period in a semiarid African savanna. *International Journal of Wildland Fire* **20**, 540–9.

Oades J. M. (1988) The retention of organic matter in soils. *Biogeochemistry* **5**, 35–70.

Ogle K. & Reynolds J. F. (2004) Plant responses to precipitation in desert ecosystems: integrating funcitonal types, pulses, thresholds and delays. *Oecologia* **141**, 282–94.

Osborne C. P. & Freckleton R. P. (2009) Ecological selection pressures for C4 photosynthesis in the grasses. *Proceedings of the Royal Society Biological Sciences* **276**, 1753–60.

Pausas J. & Bradstock R. (2007) Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-east Australia. *Glob. Ecol. Biogeogr.* **16**, 330–40.

Pausas J. & Paula S. (2012) Fuel shapes the fire-climate relationship: evidence from Mediterranean ecosystems. *Glob. Ecol. Biogeogr.* **21**, 1074–82.

Poorter H. (1993) Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetatio* **104**, 77–97.

Sage R. F., Wedin D. A. & Li M. (1999) The Biogeography of C4 photosynthesis: patterns and controlling factors. In: *C4 Plant Biology* (eds R. F. Rowan & R. K. Monson) pp. 313–89. Academic Press, San Diego, California.

Schenk H. J. & Jackson R. B. (2002) Rooting depths, lateral root spread and below-ground/above-ground allometries of plants in water-limited ecosystems. *J. Ecol.* **90**, 480–94.

Sala O. E. Lauenroth W. K. & Golluscio R. A. (1997) Plant functional types in temperate semi-arid regions. In plant functional types (eds) Smith, T.M., Shugart, H.H. & Woodward, F.I., cambridge university, Press cambridge, 217–233.

Sullivan A., McCaw L., Cruz M., Matthews S. & Ellis P. F. (2012) Fuel, fire weather and fire behaviour in Australian ecosystems. In: *Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World* (eds R. A. Bradstock, A. M. Gill & R. J. Williams) pp. 51–78. CSIRO, Collingwood, Victoria.

Suppiah R., Hennessy K. J., Whetton P. H., *et al.* (2007) Australian climate change projections derived from simulations performed for the IPCC 4th Assessment Report. *Aust. Meteorol. Mag.* **56**, 131–52.

Team R.-D. C (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Throop H. L., Reichmann L. G., Sala O. E. & Archer S. R. (2012) Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert Grassland. *Oecologia* **169**, 373–83.

Tooth I. M. & Leishman M. R. (2013) Post-fire resprouting responses of native and exotic grasses from Cumberland Plain Woodland (Sydney, Australia) under elevated carbon dioxide. *Austral Ecol.* **38**, 1–10.

Walker J. (1981) Fuel Dynamics in Australian Vegetation. In: *Fire and the Australian Biota* (eds A. M. Gill, R. H. Groves & I. R. Noble) . Australian Academy of Science, Canberra.

Walter H. (1971) *Ecology of tropical and subtropical vegetation*. Oliver and Boyd, Edinburgh.

Wang S., Heckathorn S. A., Wang X. & Philpott S. M. (2012) A meta-analysis of plant physiological and growth responses to temperature and elevated CO_2. *Oecologia* **169**, 1–13.

Wasson R. J. (1989) Landforms. In: *Mediterranean landscapes in Australia: mallee ecosystems and their management*, Vol. **13-34**, (eds N. I.R & R. A. Bradstock) . CSIRO Australia, Melbourne.

White J. & Harper J. L. (1970) Correlated changes in plant size and number in plant populations. *J. Ecol.* **58**, 467–85.

Wills K. E. & Clarke P. J. (2008) Plant trait-environmental linkages among contrasting landscapes and climate regimes in temperate eucalypt woodlands. *Aust. J Bot.* **56**, 422–32.