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Evaluation of the growth response of arid zone invasive species *Salvia verbenaca* cultivars to atmospheric carbon dioxide and soil moisture

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Abstract. Although climate change is expected to affect the ecology of many weed species, the nature and scale of these responses is presently not well defined. This presages a suite of potential problems for the agricultural industries. Consequently, we investigated the effects of anticipated climate change on biomass and seed production, for two varieties of wild sage, *Salvia verbenaca* L. var. *verbenaca* and *Salvia verbenaca* var. *vernalis* Bioss. For the investigation, ambient (400 ppm) and elevated (700 ppm) carbon dioxide conditions, in combination with well-watered (100% field capacity) and drought conditions (60% field capacity), were selected to represent alternative climate scenarios. The alteration in biomass production was represented by a combined measurement of nine variables; plant height, stem diameter, number of leaves, number of branches, leaf area, leaf thickness, shoot biomass, root biomass and dry leaf weight, and fecundity was measured via two variables; 100 seed weight and number of seeds per plant. All biomass measurements were reduced in a drought situation compared with well-watered conditions in ambient carbon dioxide (400 ppm), and each corresponding measurement was greater under elevated carbon dioxide (700 ppm) regardless of water treatment. In contrast, this was not observed for 100 seed weight or number of seeds per plant. Although a similar profile of a reduction in fecundity parameters was observed under drought conditions compared with well-watered conditions in ambient carbon dioxide, there was an increase in seed mass only for var. *verbenaca* under elevated carbon dioxide in both water treatments. In addition, there was a very small increase in the number of seeds in this species under drought conditions in elevated carbon dioxide, with neither increase in seed mass or seed number being observed in var. *vernalis*. These results suggest that although future climate change may result in increased competition of both these varieties with desirable plants, their management strategies will need to focus on effects of increased size of the weeds, rather than only attempting to reduce the seed bank holdings.

Additional keywords: elevated CO_2, fecundity weed, plant growth, wild sage.

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Introduction

Climate change is emerging as one of the most serious threats to grazing and agricultural stability, partly through the likelihood of increased periods of more intense drought (IPCC 2018). However, the possibility of reduced soil moisture will not act in isolation on plant growth and productivity, since simultaneous changes to atmospheric carbon dioxide levels are likely to complicate the responses of individual plant species to drought events (Dukes 2000; Ziska 2010; Manea and Leishman 2011; Singh *et al*. 2011; Oliveira and Marenco 2019).

In this respect, carbon dioxide is known to be essential for plant growth, and decades of research into the phenomenon of increased availability of this essential input has concluded that it has the capacity to significantly increase plant biomass. This effect has been observed in crop species (Wong 1979; Baker *et al*. 1990; Thomas and Strain 1991; De Luis *et al*. 1999; Ottman *et al*. 2001; Centritto *et al*. 2002; Qaderi *et al*. 2006; De Souza *et al*. 2008; Högy *et al*. 2009; Vu and Allen 2009; Kumar *et al*. 2017), native species (Owensby *et al*. 1993; Mortensen 1995; Picon *et al*. 1996; Polley *et al*. 1999) and weeds (Ziska 2003; Singh *et al*. 2011; Jabran and Dogan 2018; Prince *et al*. 2018). With the increasing onset of weather events linked to climate change, the effect of concomitant moisture stress on plant biomass is of interest to researchers, since is it expected that more regular patterns of drought will alternate with above average rainfall (IPCC 2018). Of itself, drought typically reduces plant biomass (De Luis *et al*. 1999; Ottman *et al*. 2001; Centritto *et al*. 2002; Qaderi *et al*. 2006), but there are indications that when combined with elevated carbon dioxide, the effect of drought may be overcome by some type of compensatory mechanism, at least in some species. For example, in rice, oak trees, alfalfa, honey mesquite, sorghum, peach seedlings, canola and sugarcane, a higher biomass was recorded in plants exposed to drought and elevated carbon dioxide compared with plants exposed to drought under ambient carbon dioxide conditions (Baker *et al*. 1990; Picon *et al*. 1996; De Luis *et al*. 1999; Polley *et al*. 1999; Ottman *et al*. 2001; Centritto *et al*. 2002; Qaderi *et al*. 2006; De Souza *et al*. 2008; Vu and Allen 2009).

Although previous research has been thorough, there is still a lack of information regarding the combined effects of elevated atmospheric carbon dioxide and drought on weed species. In the extant research, the effects of increased atmospheric carbon dioxide and coincident drought on the growth of economically important crop plants appears to have been somewhat prioritised over that of weeds. However, since weed infestation also presents a significant impediment to crop and pasture productivity, it is equally important to focus on the effect that alterations to external conditions, due to climate change, will have on weed species. To this end, a continuation of our research into the seed ecology of an important agricultural weed in Australia, *Salvia verbenaca*, has been undertaken. In addition to investigations of *Salvia verbenaca* as a significant weed of rangelands in New South Wales (Robards and Michalk 1979; Fisher *et al.* 2016), where it competes with native fodder species through more rapid germination following significant rainfall events, previous work has examined the effect of various environmental factors on seed germination ecology of two cultivars of *S. verbenaca* (*verbenaca* and *vernalis*), including seasonal temperature ranges, light regime, the effects of variations in soil pH, salinity, moisture availability, as well as seed burial depth (Javaid *et al*. 2018). Therefore, this work extends the initial investigation of the basic biology of this weed into the effects of elevated carbon dioxide and drought on the biomass of this species, subsequent to successful germination. The specific parameters examined are plant height, stem diameter, number of leaves, number of branches, leaf area, leaf thickness, shoot biomass, root biomass, leaf dry weight, 100 seed weight, and number of seeds produced per plant. It is expected that the results of this work will provide information on the potential growth patterns of this weed in agricultural, rangeland grazing and conservation settings.

Materials and methods

Experimental design and data collection

This experiment was conducted using randomised block design in the two Eurotherm 3504 environmental chambers (length 2.1 m × height 2.0 m × width 2.1 m) (Steridium Pty Ltd, Brendale, Qld, Australia) each of which set to the relevant carbon dioxide level, either ambient or elevated. Given that this species germinates during September (Spring), the average day/night temperature and humidity of the chambers was maintained throughout the experiment at 24°C day time and 16°C during night time and 45–65% respectively.

The seeds used were from the same sources as for Javaid *et al.* (2018). The *S. verbenaca* var. *verbenaca* seeds were sourced from Birchip in north-western Victoria (35°58.59.94°S, 142°54.52.41°E) and the var. *vernalis* seeds were sourced from Nanya, Federation University Australia's research station in central western New South Wales (33.12.33°S, 141.19.09°E). In Nanya station, this species infests areas around ground water tanks and drainages, which are grazed by native and feral animals, as well as along the roadsides. A total of 40 plastic pots (25 cm height × 20 cm diameter; 20 pots each for *S. verbenaca* var. *verbenaca* and *S. verbenaca* var. *vernalis*) were filled with 750 g of a 2 : 1 mixture of garden soil and potting mix. There were two carbon dioxide and two soil moisture treatments. Of these 40 pots, 20 pots were placed in the 400 ppm (ambient) and other 20 in the 700 ppm (elevated) environmental chambers. To minimise the disturbance of seeds in the potting medium during germination, the pots were placed into large plastic trays to which water was added. Pots were corded with numbered plastic tags. After two days, five seeds were selected randomly from each variety and planted into each pot. The plants were watered every second day. After 12 days, plants were thinned by removing the three smallest individuals from each pot, leaving only the two largest plants. Following thinning, watering was continued until the plants had grown to sufficient size, when they had approximately eight leaves per plant. From this point onwards, the differential water treatments (60 or 100% field capacity) commenced. Water holding capacity of the soil used in this experiment was established based on the work by Bajwa *et al.* (2017). Within each carbon dioxide treatment, half of the pots were well watered (100% field capacity) and the remainder subjected to drought conditions (60% field capacity). To maintain each condition accurately, pots were weighed before water was added. For both cultivars, each combination of the carbon dioxide and water treatments was replicated five times. Each replicate consisted of a single pot containing two plants, to allow for measurement of total leaf area separately from the remainder of the biomass and fecundity parameters (see below).

The experimental measurements were carried out 65 days after the commencement of the growing period. Plants were removed from pots for the measurement of the nine biomass parameters: plant height, stem diameter, number of leaves, number of branches, leaf thickness, total leaf area per plant, shoot dry matter weight, root dry matter weight and biomass as leaf dry weight and the two reproductive parameters: 100 seed weight and fecundity, as measured by number of seeds produced per plant. Leaf area was measured (Leaf area was measured separately for each plant using a Planimeter (Paton Electronic Planimeter developed in conjunction with CSIRO. Serial number 711–14-531/21) from one of the two plants in each pot while the remaining biomass and fecundity parameters were measured from the other. Plant shoot and root (washed) were removed from the pots and placed in labelled paper bags. Roots were washed in a running water, dried using paper towel and placed in labelled paper bags. These samples were dried in the oven at 70°C for 48 h to obtain dry biomass.

Statistical analyses

The data were analysed using the ANOVA test within SPSS to determine whether drought or elevated carbon dioxide significantly affected the growth and seed production compared with well-watered and ambient conditions for these two cultivars. Residual plots of each ANOVA were obtained to examine homogeneity of the variance.

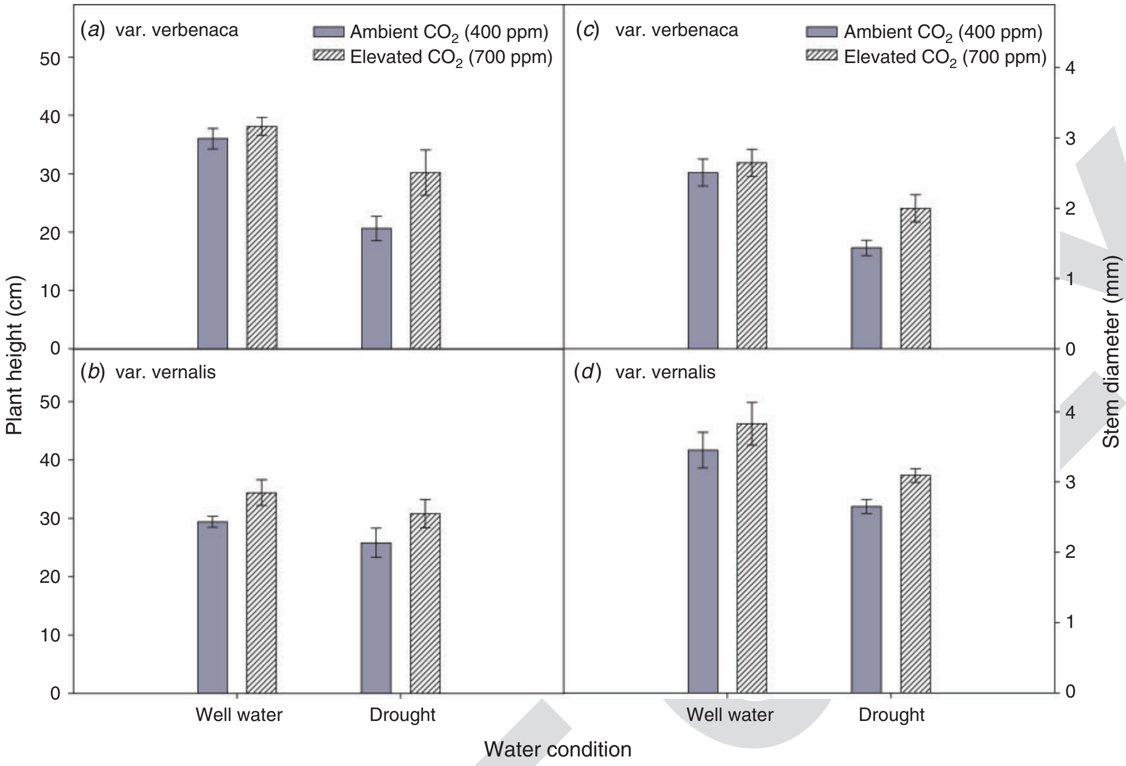

Fig. 1. (*a–d*) Mean plant height (cm) and stem diameter (mm) of *Salvia verbenaca* var. *verbenaca* (*a*, *c*) and *Salvia verbenaca* var. *vernalis* (*b*, *d*).

Results

Biomass measures

Plant height

Under well-watered conditions in ambient carbon dioxide, var. *verbenaca* plants were taller than var. *vernalis* (Fig. 1*a, b*). However, in the same carbon dioxide treatment, plant height was reduced significantly by drought for var. *verbenaca* ($P < 0.001$) but not with var. *vernalis* ($P = 0.109$). Elevated carbon dioxide increased plant height in both species, whether they were drought stressed or not (var. *verbenaca* $P = 0.033$, var. *vernalis* $P = 0.031$), with a larger relative increase being observed in var. *verbenaca* than in var. *vernalis*.

Stem diameter

Overall, stem diameter was larger in var. *vernalis* than var. *verbenaca* in both soil moisture and carbon dioxide treatments (Fig. 1*c, d*). The stem diameter of both species was significantly reduced with drought in ambient carbon dioxide (var. *verbenaca* $P = 0.002$ and var. *vernalis* $P = 0.012$), but with elevated carbon dioxide in both soil moisture treatments, results were not statistically significant (var. *verbenaca* $P = 0.156$; var. *vernalis* $P = 0.150$).

Number of leaves per plant

Fewer leaves were produced by both species in ambient carbon dioxide under drought conditions compared with well-watered samples (Fig. 2*a, b*) and this reduction was seen to be significant ($P < 0.001$) for both species. There was an increase in number of leaves in elevated carbon dioxide which was significant in both species under well-watered conditions ($P < 0.001$), being more pronounced in var. *vernalis* than in var. *verbenaca* (Fig. 2*b*).

Number of branches per plant

Both species produced fewer branches under drought conditions compared with those in well-watered conditions ($P < 0.001$ for both species) (Fig. 2*c, d*). Elevated carbon dioxide increased the number of branches produced, but this was significant only for var. *vernalis* ($P = 0.005$) in the well-watered treatment (Fig. 2*d*). There was no significant increase in number of branches per plant in var. *verbenaca*, with elevated carbon dioxide ($P = 0.093$).

Leaf thickness

Leaf thickness was significantly reduced under drought, compared with well-watered conditions (var. *verbenaca* $P < 0.001$, var. *vernalis* $P = 0.002$) (Fig. 3*a, b*). Elevated carbon dioxide significantly increased leaf thickness of var. *verbenaca* under well-watered conditions ($P = 0.002$) and under drought (Fig. 3*a*). In contrast, elevated carbon dioxide did not significantly increase leaf thickness in var. *vernalis* ($P = 0.688$) (Fig. 3*b*).

Leaf area per plant

Drought significantly reduced total leaf area per plant ($P < 0.000$ for both species) (Fig. 3*c, d*), the trend being stronger

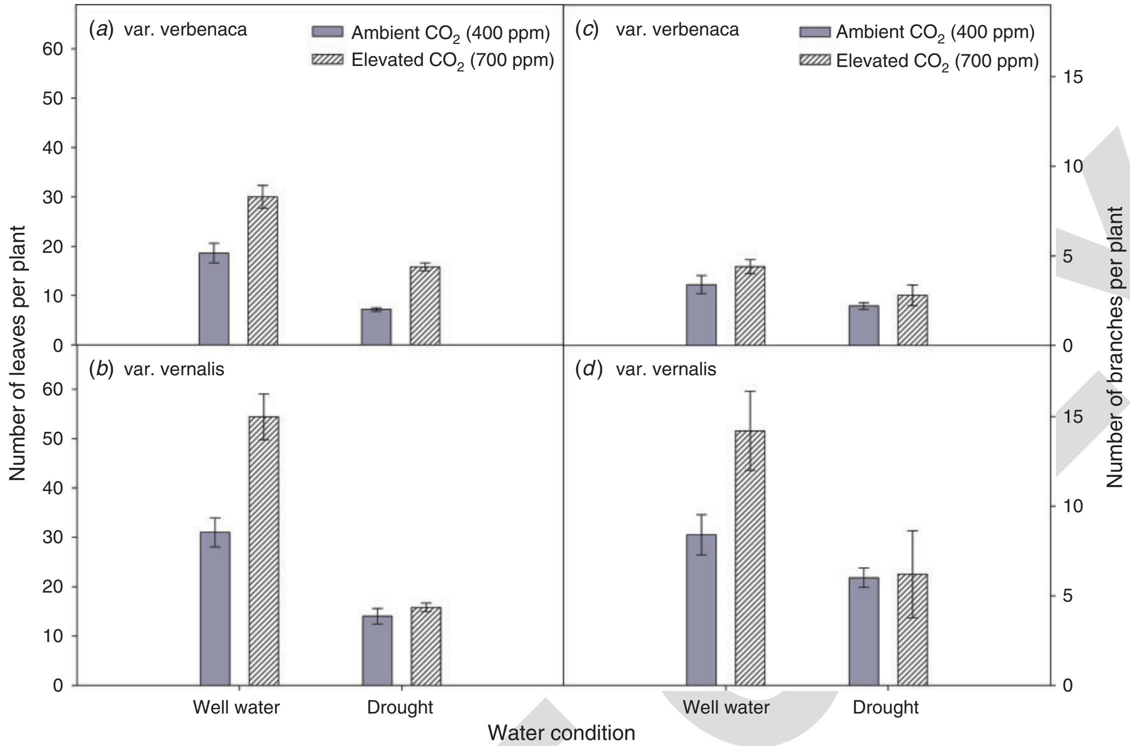

Fig. 2. (*a–d*) Mean number of leaves and branches per plant of *Salvia verbenaca* var. *verbenaca* (*a*, *c*) and *Salvia verbenaca* var. *vernalis* (*b*, *d*).

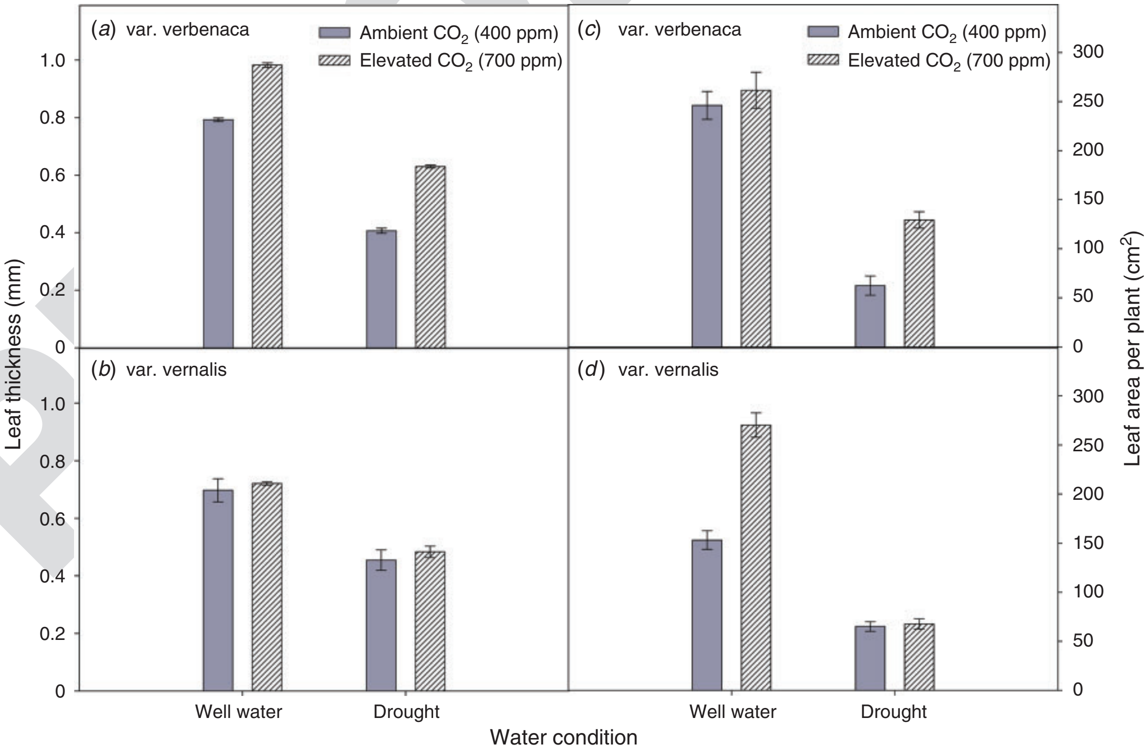

Fig. 3. (*a–d*) Mean leaf thickness (mm) and leaf area (cm^2) per plant of *Salvia verbenaca* var. *verbenaca* (*a*, *c*) and *Salvia verbenaca* var. *vernalis* (*b*, *d*).

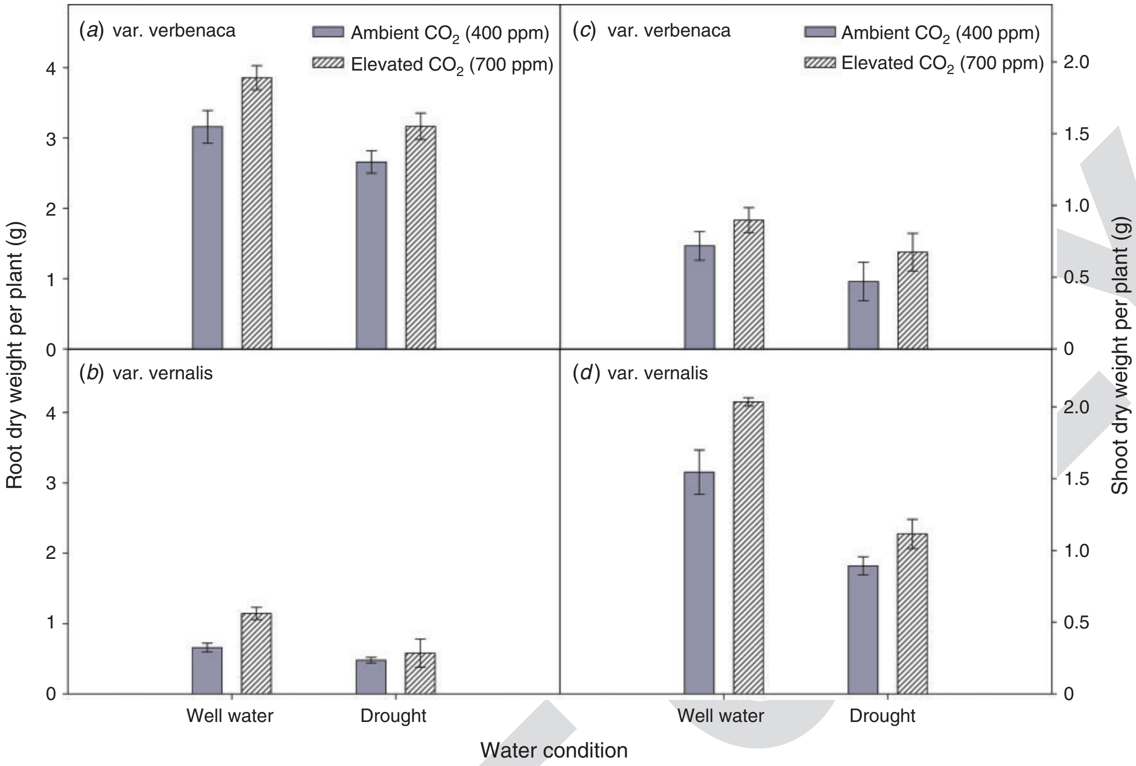

Fig. 4. (*a–d*) Mean root and shoot dry weight per plant (g) of *Salvia verbenaca* var. *verbenaca* (*a*, *c*) and *Salvia verbenaca* var. *vernalis* (*b*, *d*).

in var. *verbenaca* than var. *vernalis*. Under elevated carbon dioxide and in well-watered conditions, the leaf area of var. *verbenaca* was not significantly increased ($P = 0.080$), which contrasted with var. *vernalis* ($P < 0.000$). However, under drought conditions, carbon dioxide influenced a considerable difference in leaf area; ver. *verbenaca* increased significantly (Fig. 3*c*), whereas there was almost no change in var. *vernalis* (Fig. 3*d*).

Root dry matter

Overall, significantly less root dry matter was produced by var. *vernalis*, compared with var. *verbenaca*, under all conditions (Fig. 4*a*, *b*). In ambient carbon dioxide, the reduction in the amount of root dry matter due to drought was not significant for var. *verbenaca* ($P = 0.160$), but it was for var. *vernalis* ($P = 0.003$). Under elevated carbon dioxide and in both soil moisture treatments, more root matter was produced by both species. This increase was not statistically significant for var. *verbenaca* ($P = 0.155$), but was for var. *vernalis* ($P < 0.001$).

Shoot dry matter

In contrast to root dry matter, significantly more shoot dry matter was produced by var. *vernalis* than var. *verbenaca* under all conditions (Fig. 4*c*, *d*). In ambient carbon dioxide conditions, there was a stronger trend of reduced biomass production in response to drought for var. *vernalis* compared with var. *verbenaca*, being significant for both species ($P < 0.000$). Both species were significantly more productive under elevated carbon dioxide in each of the soil moisture treatments (var. *verbenaca* $P < 0.001$; var. *vernalis* $P = 0.002$). The increase in shoot dry matter was relatively larger in var. *vernalis* compared with var. *verbenaca*, under well-watered conditions.

Dry weight of leaves per plant

There was a significant reduction in leaf dry matter under drought conditions compared with those which were well watered under ambient carbon dioxide (var. *verbenaca* $P = 0.000$; var. *vernalis* $P = 0.004$), with the effect being relatively larger for var. *verbenaca* than var. *vernalis* (Fig. 5*a*, *b*). Under elevated carbon dioxide, there was a significant increase in leaf dry matter, which contrasted between soil moisture treatments for each species (var. *verbenaca* $P = 0.009$, var. *vernalis* $P = 0.048$). In var. *verbenaca*, there was a relatively larger increase under drought and elevated carbon dioxide conditions compared with var. *vernalis*, where the increase was more modest. By contrast, under well-watered conditions, var. *vernalis* responded more strongly to an increase in carbon dioxide availability.

Fecundity

Each variety contrasted significantly for the weight and number of seeds produced, with var. *verbenaca* producing fewer, but heavier, seeds than var. *vernalis*. The changes in each factor according to drought and carbon dioxide also contrasted significantly between varieties.

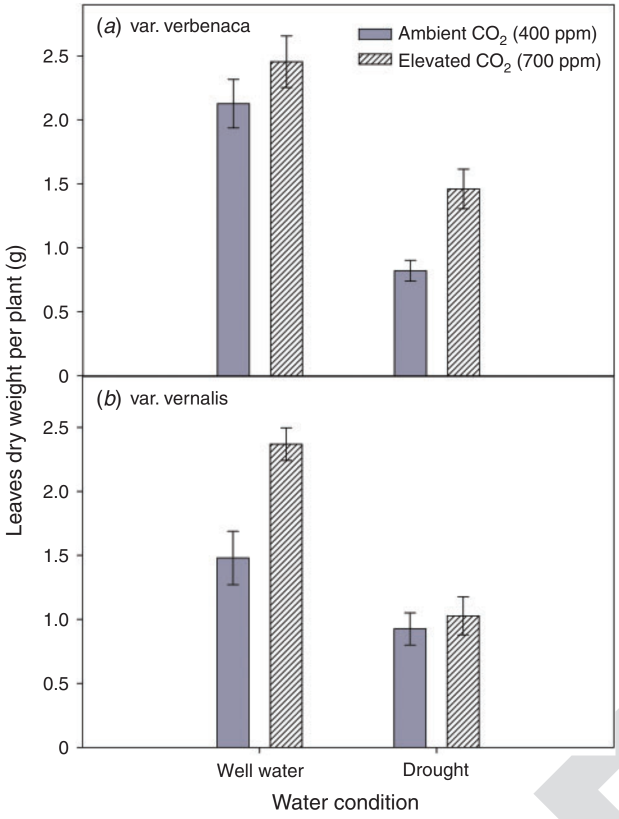

Fig. 5. (*a–d*) Mean dry weight of leaves per plant of *Salvia verbenaca* var. *verbenaca* (*a*) and *Salvia verbenaca* var. *vernalis* (*b*).

Seed weight

There was a reduction in 100 seed weight for both species in ambient carbon dioxide under drought conditions, the reduction being larger for var. *verbenaca* when compared with var. *vernalis* (Fig. 6*a*, *b*). This reduction was significant for var. *verbenaca* ($P < 0.001$) but was borderline for var. *vernalis* ($P = 0.050$). In the elevated carbon dioxide treatment, the trend for seed weight contrasted sharply between species. There was a significant increase in 100 seed weight in var. *verbenaca* ($P < 0.001$) and a small, but significant, reduction in var. *vernalis* ($P = 0.008$).

Number of seeds per plant

Significantly fewer seeds were produced overall by var. *verbenaca* compared with var. *vernalis* (Fig. 6*c*, *d*). Also, the numbers of seed produced by both species were significantly reduced by drought (var. *verbenaca* $P = 0.004$; var. *vernalis* $P = 0.002$). In contrast to the trends observed for other biomass indicators, changes in seed production was not significant for either species (var. *verbenaca* $P = 0.706$; var. *vernalis* $P = 0.775$).

Discussion

Although overall biomass consistently decreased in both varieties under drought conditions, reductions in biomass were at least partially offset by elevated carbon dioxide in nearly all cases. The individual responses of each variety to drought and elevated carbon dioxide, as observed from nine biomass variables (plant height, stem diameter, number of leaves, number of branches, leaf thickness, leaf area per plant, root dry weight, shoot dry weight and leaf dry weight) and two fecundity

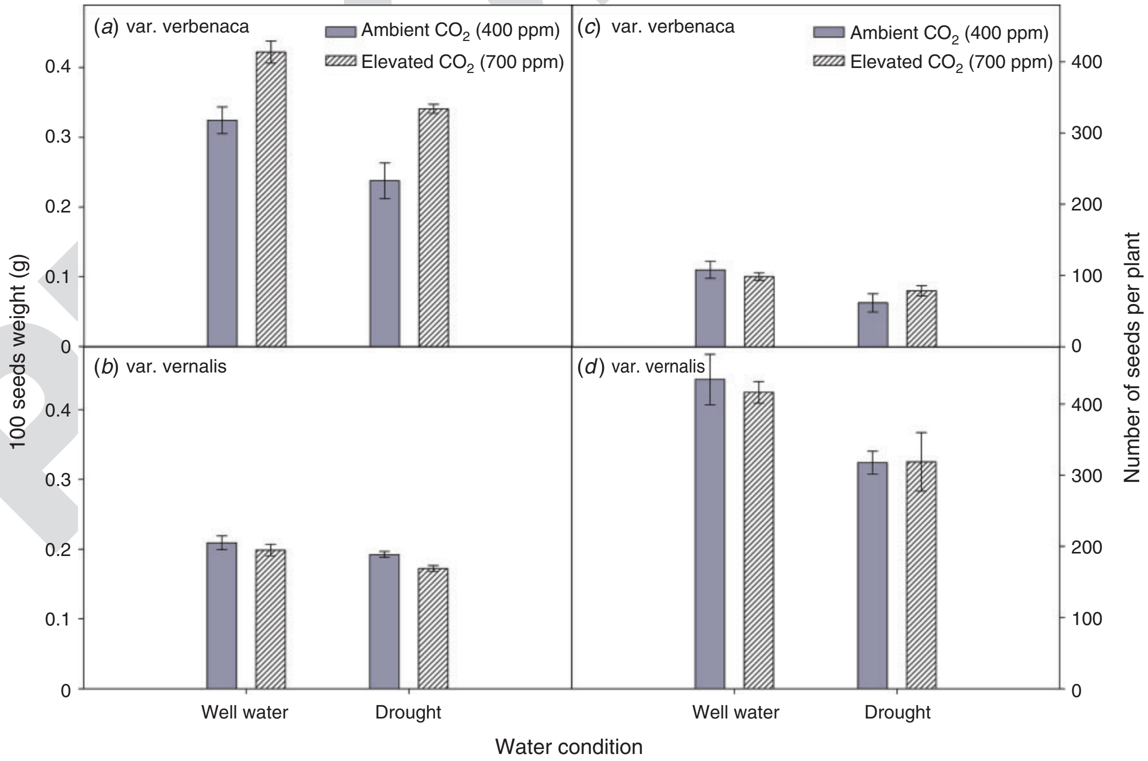

Fig. 6. (*a–d*) Mean 100 seed weight and number of seeds per plant of *Salvia verbenaca* var. *verbenaca* (*a*, *c*) and *Salvia verbenaca* var. *vernalis* (*b*, *d*).

variables (100 seed weight and total seeds per plant), showed that each appears to adapt to these environmental factors in unique ways. For example, although var. *verbenaca* was relatively more affected by drought compared with var. *vernalis*, it also appeared to gain relatively more benefit from exposure to elevated carbon dioxide, under drought conditions in particular. Other species have demonstrated apparently similar trends of elevated carbon dioxide overcoming reductions in plant biomass that might be expected under drought conditions (Ziska and George 2004; Xu *et al*. 2013; Sicher and Bunce 2015). However, these changes are not uniform across all species, which indicates a large degree of uncertainty for future responses of all plant species under conditions of further increased atmospheric carbon dioxide.

These changes in biomass for the two cultivars of *S. verbenaca* in response to drought and elevated carbon dioxide are not entirely unexpected, since they are fairly typical responses of species that possess a C_3 metabolic pathway (Ziska and Dukes 2010). Although direct confirmation of these varieties of these plants as C_3 metabolites was not able to be obtained from the literature, a related species in the same family (Lamiaceae), *Plectranthus parvifloris*, has been definitely identified as being in this class (Manea and Leishman 2011). This suggests that their responses to elevated carbon dioxide and water restriction can be reasonably investigated for similarities and differences compared with other C_3 species.

Additionally, a medicinal species *Salvia sclarea* (Kumar *et al*. 2017) has been investigated for the effect of elevated carbon dioxide on growth and development, with a finding that increased total plant biomass resulted from exposure to elevated (520–580 ppm) carbon dioxide concentration compared with ambient carbon dioxide (390 ppm). This increase resulted mainly from increases in plant height, root length and volume, rather than an increase in the number or size of leaves, since the number of leaves per plant was less in elevated than in ambient carbon dioxide (Kumar *et al*. 2017). The responses of vars. *verbenaca* and *vernalis* are quite similar to *S. sclarea*, which is not unexpected given their family relationship.

The two remaining variables, 100 seed weight and numbers of seeds produce per plant, are measures of a species' fecundity. In the cases of var. *verbenaca* and var. *vernalis*, these two variables showed the least variation for each variety across all treatment factors. The var. *verbenaca* plants consistently produced the heaviest seeds, whereas the var. *vernalis* consistently produced the greatest number of seeds. However, within these variables there was a pattern of difference according to soil moisture and carbon dioxide treatment. For 100 seed weight, the mass of seeds in var. *verbenaca* was reduced under drought, but increased in response to elevated carbon dioxide. However, the opposite trend was observed in var. *vernalis*, since drought-induced reductions in seed mass were not offset by elevated carbon dioxide. This means that under future elevated carbon dioxide conditions, var. *verbenaca* plants may be at an advantage over var. *vernalis*, since heavier seeds are more likely to survive for longer times in soil seed banks and are also more likely to germinate from greater burial depths than smaller seeds (Baskin and Baskin 2014). Of some concern was that previous research on these two varieties appears to contradict this possibility for this species, since the seeds of var. *vernalis*, although much smaller than var. *verbenaca*, were able to emerge from a slightly deeper burial depth (Javaid *et al*. 2018).

With respect to variable fecundity, it is evident that variation in the number of seeds produced may increase the potential for population dominance of one plant species over another. Since var. *vernalis* consistently produced more seed than var. *verbenaca*, there is a possibility that even though the latter produces larger seeds than the former, sheer numbers produced by the smaller-seeded species may be of greater concern to weed managers than a species having the advantage of larger seeds. Seed bank manipulation will therefore depend on the particular species infesting a given situation, and this may lead to such strategies as alternative tilling regimes. In rangelands, stimulation of weed growth and increased seedbank input may occur under future conditions of elevated atmospheric carbon dioxide and large rainfall events. Water availability is a significant factor for promoting germination of both cultivars (Javaid *et al*. 2018). Subsequently, there is a risk of reduction in carrying capacity, due to germination and growth resulting in increased competition with the native plants usually grazed by livestock, and particularly where grazing pressure is increased (Robards and Michalk 1979), which may occur when feral animals are present (e.g. goats). Further studies into future management approaches will be both necessary and instructive in this respect. We have consistently argued that an important agricultural issue is to investigate the nature of weeds which invade crops or pastures and reduce yields to determine whether elevated carbon dioxide will have any effects on the weeds themselves. This current study has shown that future atmospheric carbon dioxide increases will likely lead to increases in above ground biomass in var. *vernalis* and below ground biomass in var. *verbenaca*.

Conclusion

The implication here is that each weed will affect surrounding plants in different ways. Under conditions of elevated carbon dioxide, var. *vernalis* may produce more shade, thereby potentially supressing the growth of nearby plants, whereas the var. *verbenaca* will likely out-compete surrounding plants for the available soil moisture and nutrients. Therefore, where these two species are known to be invasive of crops or pastures, the implications are that future levels of carbon dioxide will be likely to increasingly suppress the growth of cropping plants in their vicinity due to their increased virility. Thus, as a consequence of these findings suggesting general increases in biomass for both of these weed varieties under increasing carbon dioxide levels, we anticipate that they will continue to be a problem for land managers in the future. However, it is noted that the effects of biomass increase are yet to be rigorously tested. It is also unknown at this stage whether the current status of these species for herbicide susceptibility, as well as what possible changes to this susceptibility status might occur in these species under drought and increased atmospheric carbon dioxide. Given that other species have also begun to undergo mutational changes in degrees of resistance to commonly used herbicides, the added uncertainty to their response under climate change, which includes increases in atmospheric carbon dioxide, any neglect of this issue must be prevented.

Conflicts of interest

The authors declare no conflicts of interest.

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