RESEARCH ARTICLE



Morphological, physiological and biochemical responses of two Australian biotypes of *Parthenium hysterophorus* to different soil moisture regimes

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Abstract Parthenium weed is a problematic invasive species in several countries around the world. Although it is considered to be a highly invasive species within Australia, not all biotypes of parthenium weed exhibit the same ability in regard to aggressive colonization and distribution. Differences among biotypes, particularly in regard to environmental ranges as a possible basis for this variation, have not always been elucidated. To determine whether drought tolerance could be a factor in biotype demographics, we quantified the biological responses of two Australian parthenium weed biotypes known to differ in invasive ability Clermont ("high") and Toogoolawah ("low") to 100, 75 and 50% of soil water holding capacity (WHC). The Clermont biotype had greater vegetative growth, seed production and chlorophyll content than Toogoolawah, across all moisture levels. Net photosynthesis, stomatal conductance, internal CO2 concentration, seed production per plant, 1000 seed weight and subsequent germination percentage were also higher for Clermont than for Toogoolawah and were maximum at 75% WHC. Clermont plants also had higher total soluble sugar, phenolics and free proline content than Toogoolawah, and a significant increase in the levels of all of these biochemicals was observed at 50% WHC. In conclusion, Clermont grew and reproduced better than Toogoolawah across all moisture regimes consistent of

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² The Centre for Plant Science, Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, Gatton, Queensland 4343, Australia enhanced invasive ability of this biotype. Overall, the ability of parthenium weed to maintain good growth, physiology and seed production under moisture stress may enable it to colonize a wide range of Australian environments.

Keywords Parthenium weed \cdot Biological invasion \cdot Weed physiology \cdot Drought

Introduction

Parthenium weed (Parthenium hysterophorus L.) has been introduced to more than 40 countries around the world (Bajwa et al. 2016) and is considered as one of the world's most invasive weeds (Kohli et al. 2006). Parthenium weed is characterized by considerable genetic and phenotypic diversity (Hanif et al. 2012; Bajwa et al. 2016). Such diversity may allow this weed to adapt to a wide range of biotic and abiotic conditions. Parthenium weed causes decline in crop yields, pasture and livestock productivity, native biodiversity and agricultural land value in several countries across the world (Bajwa et al. 2016). It is also a 'Weed of National Significance' in Australia, infesting millions of hectares of land (Adkins and Shabbir 2014; Bajwa et al. 2016). It is associated with economic losses to livestock and crop production and reduced plant biodiversity; in addition, the weed can also cause severe allergies and contact dermatitis to livestock and people (Navie et al. 1996; Adkins and Shabbir 2014). In Australia, parthenium weed has been introduced on two separate occasions, once at Toogoolawah and once near Clermont. Based on their colonization ability and demographic spread, these different introductions represent different biotypes and are known to differ significantly in their invasive ability (Hanif et al. 2012; Adkins and Shabbir 2014). The Clermont biotype is highly invasive and is spreading in eastern Australia while the Toogoolawah biotype has, for the last 60 years, remained near its site of introduction (Navie et al. 1996; Hanif et al. 2012).

Environmental conditions play an important role in weed invasion by affecting the weed ecology and weed physiology (Bajwa et al. 2015). Is the basis for the differences in invasive potential between these biotypes related to a greater ability to survive a wider range of environmental conditions? Intuitively, the ability of parthenium weed to establish itself in a wide range of environmental conditions in a large number of countries is endemic to its successful establishment and proliferation (Adkins and Shabbir 2014; Bajwa et al. 2016). However, the interactions between parthenium weed and certain environmental factors have not always been quantified. Only a few studies have indicated that parthenium weed can tolerate different types of environmental stresses, including heat and salinity (Hegde and Patil 1982; Kohli et al. 2006; Sharma et al. 2014; Nguyen et al. 2017a). Yet, such knowledge would be essential to understanding its potential spread and any subsequent management. Among environmental factors of significance, climate modeling has shown that rainfall events will decline as temperatures rise in eastern Australia and droughts increase in frequency (DEE 2016). Soil moisture is one of the most important factors determining the establishment and subsequent spread of invasive weed species (Chauhan and Johnson 2010). Different weed species respond differently to soil moisture stress; however, some invasive weeds have been reported to complete their life cycle, maintain good growth and produce sizable amounts of seeds even under drought conditions (Chauhan and Johnson 2010; Kaur et al. 2016). Therefore, it will be crucial to investigate the impact of different soil moisture regimes on parthenium weed growth, its reproductive capacity and the quality of seed produced. Such parameters could also be used to evaluate and differentiate the invasive capacity of Clermont and Toogoolawah with future drought conditions.

The present study was conducted to evaluate and quantify the biochemical, morphophysiological and reproductive response of Clermont and Toogoolawah to three different soil moisture levels. The objectives were (a) to evaluate the growth and reproductive abilities of parthenium weed to moisture stress per se; and (b) to distinguish whether these parthenium weed biotypes differ in their response to moisture stress and whether this difference was associated with the potential for greater establishment and spread under future drought conditions.

Materials and methods

Experimental design

A study was carried out in a completely randomized design with a factorial arrangement in a temperature-controlled glasshouse (28/22 \pm 2 °C, day/night) at the University of Queensland, Gatton Campus, Australia, during the summer of 2015. Two Australian biotypes of parthenium weed (Toogoolawah and Clermont) were grown at three different soil moisture levels, as determined by soil water holding capacity (WHC), 100 (control), 75 and 50%. Each treatment had four replicates. Seeds of both biotypes were germinated on a 1% water agar medium (w/v) in Petri dishes placed in an incubator set at a 25/15 °C day/night thermoperiod and a 12/12 h photoperiod. Seeds were sorted for uniformity and viability and transplanted to soil-filled (15 kg of air-dry soil) plastic pots (30 by 30 cm, diameter by height). Initially, three seedlings per pot were established, later seedlings were thinned to a single, vigorous plant 3-4 days after transplanting. The different soil moisture levels were maintained throughout the study period. The soil was collected from the University of Queensland, Gatton Research Farm and was a heavy clay loam having a pH of 6.7, an electrical conductivity of 0.14 dS m^{-1} and an organic matter content of 2.8%. The N, P and K rates were 62, 87 and 412 kg ha^{-1} , respectively.

The WHC was determined using a modified method of Chauhan and Johnson (2010) and Nguyen (2011). Briefly, ca. 10 kg of the soil was placed into three pots and saturated with tap water, the pot surface was covered with black plastic and the pots allowed to drain for 48 h. After this time, the plastic sheet was removed and three soil samples (each ca. 300 g) were taken from the mid position of each pot. These samples were weighed (wet weight of soil, A) before being oven dried (90 °C for 72 h) and reweighed (dry weight of soil, B). The WHC was then calculated by the formula $(A - B) \times 100/B$. The 75 and 50% WHC were determined based on that fraction of the WHC. To reestablish the WHC in the pots during the study, each pot was weighed every 2 to 3 days and an appropriate amount of tap water was sprinkled over the surface of the soil. To account for the weight of the growing plants, extra plants were grown to record their weight in the three treatments and at different stages of growth and used to determine plant weight in the treatments. The experiment ran for 85 days until the plants were fully mature and seed production had ceased.

Growth, gaseous exchange and seed parameters

The number of leaves and branches produced and leaf chlorophyll contents were determined 40 days after transplanting, when the plants were at their peak vegetative growth. For the chlorophyll measurements, a SPAD-502 Plus chlorophyll meter (Konica Minolta, Tokyo, Japan) was used to take readings from five fresh, fully expanded, healthy and lush green leaves from each plant. The SPAD units were then averaged to produce a single comparative estimation of chlorophyll content. The selected gaseous exchange parameters were measured 42 days after transplanting between 10:00 am and 12:00 pm, on healthy, fully expanded and undamaged penultimate leaves using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) with an air molar flow per unit leaf area of 390 mmol mol^{-1} m⁻² s⁻¹, with a water vapor pressure into the leaf chamber of 158 Pa, a photosynthetically active radiation greater than 1000 mol m^{-2} s⁻¹, a leaf temperature of 29 to 31 °C, an ambient temperature of 31 °C and a relative humidity of 47%. Net photosynthesis, stomatal conductance, internal CO₂ concentration and transpiration rates were measured directly on fully expanded leaves for all experimental treatments. The number of days after transplanting to the initiation of the first flower was also recorded for each plant.

At harvest, the shoot and root lengths and whole plant fresh and dry biomass (90 °C for 72 h) were recorded. Physiologically mature seeds were collected regularly from plants and individually kept in paper bags with silica gel beads at 15 °C. After drying and cleaning, 25 seeds were taken from pooled seed samples from each replication and treatment and were placed on a 1% (w/v) agar medium (10 mL) in Petri dishes in a germination incubator (set at a 25/15 °C day/night thermoperiod with a 12/12 h photoperiod) and germination was quantified. Final germination percentages were assessed after 15 days of incubation. The total number of seeds produced per plant was determined after cleaning, and randomly collected subsamples of 1000 seeds were taken to determine 1000 seed weight for each treatment.

Biochemical analysis

Fresh, healthy and undamaged penultimate leaves (ca. 3 g) from each plant were collected 45 days after transplanting. The samples were preserved in zipped lock plastic bags and stored at 4 °C until used for analysis ca. 5 days later. From these leaves, the soluble phenolics were determined by the Folin-Ciocalteu reagent method as described by Julkenen-Titto (1985). Briefly, a 0.5 g sample of freshly ground leaf material was extracted in 80% acetone (ν/ν), centrifuged and mixed with 0.5 mL Folin-Ciocalteu's phenol reagent (Sigma Chemical). The absorbance of this solution was then determined at 750 nm using a spectrophotometer and used to determine the total soluble phenolics

Fig. 1 Effect of three different soil moisture levels on a number of branches, **b** number of leaves, **c** shoot length and **d** root length of two Australian biotypes of parthenium weed \pm S.E. WHC50, WHC75 and WHC100 represent 50, 75 and 100% moisture of soil water holding capacity, respectively. Different capital and small letters represent significant differences among biotypes and moisture levels, respectively at $p \leq 0.05$



against a standard curve prepared by using gallic acid samples.

The total soluble sugar content of each sample was determined by the phenol sulphuric method of Dubios et al. (1956) and improved by Lee and Kim (2000). Briefly, each leaf sample was extracted in boiling water for 1 h, filtered and made up to 50 mL with distilled water. Anthrone reagent (5.0 mL; Sigma Chemical) was then added to 1 mL of extract and the solution vortexed in a test tube for 1 min, then heated (95 °C) in a water bath for 20 min. After cooling, the absorbance of the solution was determined at 620 nm using a spectrophotometer and the total soluble sugar content determined from a standard curve prepared with glucose.

Free leaf proline content was measured using the method described by Bates et al. (1973). Briefly, a 0.5 g leaf sample was homogenized in 10 mL of a 3% sulphosalicylic acid (ν/ν) solution. Then, 2 mL of acid ninhydrin and 2 mL of glacial acetic acid were added to 2 mL of filtered extract and heated at 100 °C in a water bath for 1 h. The reaction was terminated by placing the sample in an ice bath and 4 mL toluene was then added and vigorously shaken for 15 to 20 s. The chromophore containing the free proline was aspirated in another test tube, absorbance was taken at 520 nm using a spectrophotometer and free proline contents were calculated using a standard curve prepared by proline.

Statistical analysis

Graphs were prepared by using the Microsoft Excel Program, with the main bars representing the mean values and with errors bars showing the two standard errors of those means. The effects of treatments on the variables were also statistically analyzed by an analysis of variance (ANOVA) using the computer software Statistix 8.1. Comparisons among treatment means were made using Tukey's honest significant difference test calculated at

Fig. 2 Effect of three different soil moisture levels on **a** root to shoot length ratio, **b** fresh weight, **c** biomass and **d** days taken to start flowering of two Australian biotypes of parthenium weed \pm S.E. WHC50, WHC75 and WHC100 represent 50, 75 and 100% moisture of soil water holding capacity, respectively. Different capital and small letters represent significant differences among biotypes and moisture levels, respectively at $p \le 0.05$



 $p \le 0.05$. The letters on top of the bars in graphs and along with means in tables show the significant differences $(p \le 0.05)$ due to treatment factors and their interactions.

Results

Morphological and growth parameters

A greater number of branches, leaves and shoot length were produced on plants growing at 75% relative to 100% WHC (Fig. 1a-c). At 50% WHC, significant reductions in branch and leaf numbers were observed relative to100% WHC; however, maximum root length and root to shoot ratio was observed at 50% WHC (Figs. 1d and 2a). The plants growing at 50% WHC started flowering earlier (at 36 days) than those growing at 100% (40 days) and 75% WHC (44 days). With regard to biotype, the growth parameters for Clermont were significantly higher than Toogoolawah at all soil moisture levels ($p \le 0.05$) with the exception of root to shoot length ratio which did not differ (p = 0.625). No significant interactions between biotype and moisture level were observed. However, Toogoolawah took significantly less time (38 days) to initiate flowering as compared to Clermont (42 days; Fig. 2d).

Seed and reproductive traits

Soil moisture stress negatively affected seed production and related traits in both biotypes (Fig. 3). The 50% WHC reduced seed production by 50% compared to 100% WHC (Fig. 3a) but did not differ between the 75 and 100% WHC. Similarly, the 1000 seed weight was significantly less at 50% WHC relative to 100% WHC, but did not differ between 75 and 100% WHC (Fig. 3b). Maximum germination was observed from seeds produced on plants growing at 75% WHC (91%), followed by 50% WHC (81%), whereas, the germination was the lowest from seeds produced at 100% WHC (72%; Fig. 3c).

For biotypes, Clermont produced significantly more seeds (8268 per plant) than Toogoolawah (6440 seeds per plant; $p \le 0.05$). The 1000 seed weight was the same for both biotypes (p = 0.152). The germination of freshly harvested seed from Clermont plants was significantly higher (86%) than for Toogoolawah seed (77% Fig. 3c). The interaction between biotype and moisture level was not significant (p = 0.740) for seed production, seed weight or germination percentage.

Gas exchange parameters

Soil moisture significantly affected gas exchange and photosynthetic functions in both biotypes ($p \le 0.05$) with maximum values observed at 75% WHC (Table 1). Net photosynthesis and stomatal conductance were significantly higher for





Fig. 3 Effect of three different soil moisture levels on **a** seed production, **b** 1000 seed weight and **c** germination ability of the harvested seeds of two Australian biotypes of parthenium weed \pm S.E. *WHC50*, *WHC75* and *WHC100* represent 50, 75 and 100% moisture of soil water holding capacity, respectively. Different capital and small letters represent significant differences among biotypes and moisture levels, respectively at $p \le 0.05$

Clermont than for Toogoolawah at all soil moisture levels (Table 1). A significant interaction between biotype and soil moisture level was observed for all gas exchange parameters Table 1 Effect of different soil moisture levels on gaseous exchange parameters of two Australian biotypes of parthenium weed

Moisture level	Toogoolawah	Clermont	Mean (moisture level)			
	Net photosynthes	sis (mol m ^{-2} s ^{-1})				
WHC50	17.3f	21.8e	19.5C			
WHC75	30.8b	35.2a	33.0A			
WHC100	25.0d	27.2c	26.1B			
Mean (biotype)	24.4A	28.1B				
HSD ($p \le 0.05$)	Biotype = 0.68; moisture level = 1.03 ; biotype × moisture level = 1.81					
	Stomatal conducta	nce (mol $m^{-2} s^{-1}$)				
WHC50	0.3d	0.7 cd	0.5C			
WHC75	1.6b	3.4a	2.5A			
WHC100	0.9c	1.2bc	1.0B			
Mean (biotype)	0.9B	1.7A				
HSD ($p \le 0.05$)	Biotype = 0.19; moisture level = 0.28; biotype \times moisture level = 0.50					
Internal CO_2 concentration (µmol mol ⁻¹)						
WHC50	263e	300d	282C			
WHC75	320ab	328a	324A			
WHC100	309c	316bc	312B			
Mean (biotype)	297B	315A				
HSD ($p \le 0.05$)	Biotype = 3.10; moisture level = 4.49; biotype \times moisture level = 7.94					
	Transpiration (mmol $m^{-2} s^{-1}$)				
WHC50	6.1	7.2	6.7C			
WHC75	10.6	11.2	10.9A			
WHC100	8.5	9.2	8.9B			
Mean (biotype)	8.4	9.2				

WHC50, WHC75 and WHC100 represent 50, 75 and 100% moisture of soil water holding capacity, respectively. Interaction and main effect mean sharing the same case letter for any parameter that does not differ significantly $(p \le 0.05)$ by Tukey's Honest Significant Difference (HSD) test

Biotype = ns; moisture level = 1.70; biotype × moisture level = ns

measured. Maximum net photosynthesis, stomatal conductance and internal CO₂ concentration were observed in Clermont plants growing at 75% WHC, while minimum values were observed for Toogoolawah plants growing at 50% WHC (Table 1).

HSD ($p \le 0.05$)

Biochemical attributes

Soil moisture level had a significant effect on leaf biochemistry (Table 2). Chlorophyll content was maximum at 75% and minimum at 50% relative to 100% WHC. At 50% relative to 100% WHC, a 41% increase in total soluble sugar was observed. The amount of total soluble phenolics and free proline increased by 51 and 74%, respectively, at 50% WHC as compared to 100% WHC (Table 2). Soluble sugars, phenolics and free proline content were also significantly higher at 75% relative to 100% WHC.

Chlorophyll content and total soluble sugars were significantly more in Clermont relative to Toogoolawah (Table 2). Clermont had 16% more total soluble sugar than Toogoolawah (Table 2). Maximum total soluble phenolics (32.4 mg g^{-1} of fresh weight) and free proline (0.089 mg g^{-1} of fresh weight) were recorded for Clermont when grown at 50% WHC, whereas, minimum amounts of these biochemicals were recorded from Toogoolawah when grown at 100% WHC (Table 2). Clermont had 18.5 and 19.6% more total soluble phenolics and free proline, respectively, as compared to Toogoolawah. Interactions between biotype and soil moisture content were significant only for total soluble phenolics and free proline content ($p \le 0.05$).

Discussion

Projected changes in soil moisture, especially those associated with projected climate, may mean increasing drought (frequency and severity) for Australia (DEE 2016). How invasive species respond to these changing conditions remains an environmental and economic priority. In the current study, parthenium weed had its most vigorous growth (Fig. 1) and its highest reproductive output (Fig. 3) at a relatively low soil moisture level (75% WHC). This feature is similar to some, but not all, invasive weeds (Bajwa et al. 2016). For example, giant ragweed (Ambrosia trifida L.), a close relative of parthenium weed, also showed optimal vegetative growth and seed production at 75%

Table 2 Effect of different soilmoisture levels on biochemicalattributes of two Australianbiotypes of parthenium weed

Moisture level	Toogoolawah	Clermont	Mean (moisture level)			
Chlorophyll content (SPAD value)						
WHC50	36.7	39.4	38.1C			
WHC75	42.4	47.1	44.7A			
WHC100	40.4	44.9	42.7B			
Mean (biotype)	39.8B	43.8A				
HSD ($p \le 0.05$)	Biotype = 1.04; moisture level = 1.56; biotype \times moisture level = ns					
Total soluble sugars (mg g^{-1} of fresh weight)						
WHC50	35.5	39.9	37.7A			
WHC75	21.9	28.3	25.1B			
WHC100	20.4	23.9	22.1C			
Mean (biotype)	25.9B	30.7A				
HSD ($p \le 0.05$)	Biotype = 1.58 ; moisture level = 2.36 ; biotype × moisture level = ns					
	Total soluble phenolics (mg g^{-1} of fresh weight)					
WHC50	25.8b	32.4a	29.1A			
WHC75	21.7c	24.3bc	23.0B			
WHC100	12.0e	16.3d	14.2C			
Mean (biotype)	19.8B	24.3A				
HSD ($p \le 0.05$)	Biotype = 0.99; moisture level = 1.48 ; biotype × moisture level = 2.63					
Free proline (mg g^{-1} of fresh weight)						
WHC50	0.082b	0.096a	0.089A			
WHC75	0.033d	0.046c	0.039B			
WHC100	0.021e	0.025de	0.023C			
Mean (biotype)	0.045B	0.056A				
HSD ($p \le 0.05$)	Biotype = 3.20×10^{-3} ; moisture level = 4.78×10^{-3} ; biotype × moisture level = 8.45×10^{-3}					

WHC50, WHC75 and WHC100 represent 50, 75 and 100% moisture of soil water holding capacity, respectively. Interaction and main effect mean sharing the same case letter for any parameter that does not differ significantly ($p \le 0.05$) by Tukey's Honest Significant Difference (HSD) test

WHC (Kaur et al. 2016). In addition, parthenium weed was also able to grow and produce significant seed even at 50% WHC, consistent with drought conditions.

A significant increase in soluble sugars, soluble phenolics and free proline content was associated with parthenium weed's ability to tolerate soil moisture stress and to successfully complete its life cycle. The elevated production of these biochemicals has been seen before in several plant species in response to multiple abiotic stresses (Anjum et al. 2011; Bajwa and Farooq 2016). These biochemicals ameliorate the damaging effects of reactive oxygen species produced under moisture stress and, therefore, help plants regulate physiological function (Bajwa and Farooq 2016). Previous studies have also shown that parthenium weed tolerates biological predation, moisture and salt stresses by effectively modifying its photosynthesis and enzymatic regulation (Florentine et al. 2005; Hegde and Patil 1982). Moreover, different soluble phenolics produced by parthenium weed have been reported to have an allelopathic potential (Kanchan and Jayachandra 1980; Bajwa et al. 2016). So, enhanced synthesis of phenolics under drought conditions may provide parthenium weed not only with a defense mechanism against that stress but also with a competitive advantage over neighboring plant species.

Parthenium weed has been reported to be adaptable to a range of soil types (Annapurna and Singh 2003). In high clay content soils (having a high WHC), parthenium weed prolonged its life in the rosette stage of growth and eventually produced plants with superior shoot, as compared to root, growth (Annapurna and Singh 2003). This could be one reason for the observed greater shoot growth and vegetative biomass production at the two higher soil WHC treatments while increasing the root length under the lowest WHC (Fig. 1). Increasing root length in dry soils would help plants extract water efficiently. Similarly, the higher root to shoot length ratios observed under low soil WHC may be another key feature of tolerance to soil moisture deficiency. In contrast, Sarangi et al. (2016) reported a significant reduction in root length and root to shoot length ratio in response to water stress in common water hemp (Amaranthus rudis Sauer).

Sustaining growth through morphological adaptation and physiological regulation even at very low soil WHC provides parthenium weed with an excellent mechanism to reproduce and spread effectively (Nguyen 2011). More branching, leaf production and tall stature ensures vigorous growth and greater physiological activity (Fig. 1). Nguyen (2011) also reported that parthenium weed could tolerate reduced soil moisture level while increasing its growth by 20%; but also reported a 43% reduction in parthenium weed life span under drought conditions. This is in contrast to the current result which shows that water stress initiated early flowering but did not affect total life span. It is important to note that a drought after weed emergence has been reported to induce tolerance in other weeds and to speed up the flowering process (Chauhan and Johnson 2010).

High seed production is a biological feature of parthenium weed that makes it highly invasive (Bajwa et al. 2016; Nguyen et al. 2017a). Parthenium weed seed banks are very difficult to deplete even with continuous integrated management (Nguyen et al. 2017b). In the current study, 50% WHC halved seed production; however, more than 4400 seeds (Fig. 3) per plant indicate that sufficient seed under drought conditions would allow for further spread. Interestingly, parthenium weed seeds produced under moisture stress had higher germination percentage than those produced under 100% WHC consistent with previous reports from Nguyen (2011). Bench-Arnold et al. (1992) reported that moisture stress during seed development also reduced the dormancy in Johnson grass (Sorghum halepense (L.) Pers). These observable changes in parthenium weed suggest that seed production and dormancy could be adaptable to future drought conditions (Bajwa et al. 2016).

An assessment of growth and reproductive characteristics may also provide clues as to biogeographic changes in the differential spread of Toogoolawah or Clermont biotypes in response to drought (Bajwa et al. 2016). The present study indicates that Toogoolawah and Clermont vary significantly in their growth and fecundity in response to soil moisture. The Clermont biotype, generally considered to be the more aggressive in terms of colonization and spread (Hanif et al. 2012; Adkins and Shabbir 2014), had greater growth, physiological activity, biomass production and reproductive output over all the WHC treatments relative to Toogoolawah. This could be a key factor in the successful and remarkable invasion ability of the Clermont biotype and may provide a partial explanation for their contrasting invasion records.

The basis for the greater adaptability of Clermont relative to Toogoolawah is unclear. Hanif et al. (2012) reported a significant difference in the level of genetic variations seen in these two biotypes; suggesting that differences seen in growth, seed production and biochemical attributes, under the various soil moisture levels, could be a result of the greater genetic variation in Clermont as compared to Toogoolawah. Such extensive genetic variation within a species may contribute to invasive potential and management efficacy.

Conclusions

The current study indicates that parthenium weed can survive low WHC, down to 50%, while maintaining significant levels of seed production. The basis for this adaptation is reflective of morphophysiological changes in leaf chemistry, gas exchange, growth and fecundity. In the wake of a drier climate, parthenium weed may expand its range due to its moisture stress tolerance ability. However, the current study also suggests that projected changes in drought stress may differentially affect parthenium weed biotypes, with Clermont having a greater adaptive capacity to soil moisture stress, relative to Toogoolawah. Overall, this information, while incomplete, may provide an initial basis for quantifying future parthenium weed spread and improving management of this invasive species.

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References

- Adkins S, Shabbir A (2014) Biology, ecology and management of the invasive parthenium weed (*Parthenium hysterophorus* L.) Pest Manag Sci 70:1023–1029. doi:10.1002/ps.3708
- Anjum SA, Wang L, Farooq M, Xue L, Ali S (2011) Fulvic acid application improves the maize performance under well-watered and drought conditions. J Agron Crop Sci 197:409–417. doi:10.1111/j. 1439-037X.2011.00483.x
- Annapurna C, Singh JS (2003) Variation of *Parthenium hysterophorus* in response to soil quality: implications for invasiveness. Weed Res 43: 190–198. doi:10.1046/j.1365-3180.2003.00332.x
- Bajwa AA, Chauhan BS, Farooq M, Shabbir A, Adkins SW (2016) What do we really know about alien plant invasion? A review of the invasion mechanism of one of the world's worst weeds. Planta 244:39–57. doi:10.1007/s00425-016-2510-x
- Bajwa AA, Farooq M (2016) Seed priming with sorghum water extract and benzyl amino purine along with surfactant improves germination metabolism and early seedling growth of wheat. Arch Agron Soil Sci 63:319–329. doi:10.1080/03650340.2016.1211268
- Bajwa AA, Mahajan G, Chauhan BS (2015) Nonconventional weed management strategies for modern agriculture. Weed Sci 63: 723–747. doi: http://dx.doi.org/10.1614/WS-D-15-00064.1
- Bates LS, Waldren RP, Teare ID (1973) Rapid determination of free proline for water stress studies. Plant Soil 39:205–207. doi:10. 1007/BF00018060
- Bench-Arnold R, Fenner M, Edwards PJ (1992) Changes in dormancy level in Sorghum halepense seeds induced by water stress during seed development. Funct Ecol 6:596–605. doi:10.2307/2390058
- Chauhan BS, Johnson DE (2010) Growth and reproduction of junglerice (*Echinochloa colona*) in response to water stress. Weed Sci 58: 132– 135. doi: http://dx.doi.org/10.1614/WS-D-09-00016.1

- DEE (2016) Department of the environment and energy, Australian Government. Available at https://www.environment.gov.au/ climate-change/climate-science/impacts/qld [Verified 18 December 2016]
- Dubios M, Giles KA, Hamilton JK, Roberes P, Smith F (1956) Colorometric method for determination of sugars and related substances. Anal Chem 28:350–356. doi:10.1021/ac60111a017
- Florentine SK, Raman A, Dhileepan K (2005) Effects of gall induction by *Epiblema strenuana* on gas exchange, nutrients, and energetics in *Parthenium hysterophorus*. BioControl 50:787–801. doi:10.1007/ s10526-004-5525-3
- Hanif Z, Adkins SW, Prentis PJ, Navie SC, O'Donnell C (2012) Characterization of the reproductive behavior and invasive potential of parthenium weed in Australia. Pak J Weed Sci Res 18:767–774
- Hegde BA, Patil TM (1982) Effect of salt stress on the structure and carbon flow mechanism in a noxious weed *Parthenium hysterophorus* L. Weed Res 22:51–56. doi:10.1111/j.1365-3180. 1982.tb00143.x
- Julkenen-Titto R (1985) Phenolic constituents in the leaves of northern willows: methods for the analysis of certain phenolics. J Agric Food Chem 33:213–217. doi:10.1021/jf00062a013
- Kanchan SD, Jayachandra (1980) Allelopathic effects of *Parthenium hysterophorus* L. Plant Soil 55:67–75. doi:10.1007/BF02149710
- Kaur S, Aulakh J, Jhala AJ (2016) Growth and seed production of glyphosate-resistant giant ragweed (*Ambrosia trifida* L.) in response to water stress. Can J Plant Sci 96:828–836. doi:10.1139/cjps-2015-0309
- Kohli RK, Batish DR, Singh HP, Dogra KS (2006) Status, invasiveness and environmental threats of three tropical American invasive weeds (*Parthenium hysterophorus L., Ageratum conyzoides L., Lantana*

camara L.) in India. Biol Invas 8:1501–1510. doi:10.1007/s10530-005-5842-1

- Lee SS, Kim JH (2000) Total sugars, $\alpha\text{-amylase}$ activity and emergence after priming of normal and aged rice seeds. Kor J Crop Sci 45:108–111
- Navie SC, McFadyen RE, Panetta FD, Adkins SW (1996) The biology of Australian weeds. 27. Parthenium hysterophorus L. Plant Prot Q 11: 76–88
- Nguyen TL, Bajwa AA, Navie SC, O'Donnell C, Adkins SW (2017a) Parthenium weed (*Parthenium hysterophorus* L.) and climate change: the effect of CO2 concentration, temperature, and water deficit on growth and reproduction of two biotypes. Environ Sci Pollut Res 24:10727–10739. doi:10.1007/s11356-017-8737-7
- Nguyen TL, Bajwa AA, Navie SC, O'Donnell C, Adkins SW (2017b) The soil seedbank of pasture communities in central Queensland invaded by *Parthenium hysterophorus* L. Range Ecol Manage 70: 244–254. doi: http://dx.doi.org/10.1016/j.rama.2016.07.010
- Nguyen TLT (2011) The invasive potential of parthenium weed (*Parthenium hysterophorus* L.) in Australia. PhD Thesis, School of Agriculture and Food Sciences, The University of Queensland, Australia.
- Sarangi D, Irmak S, Lindquist JL, Knezevic SZ, Jhala AJ (2016) Effect of water stress on the growth and fecundity of common waterhemp (*Amaranthus rudis*). Weed Sci 64: 42–52. doi: http://dx.doi.org/10. 1614/WS-D-15-00052.1
- Sharma AD, Bhullar A, Rakhra G, Mamik S (2014) Analysis of hydrophilic antioxidant enzymes in invasive alien species *Parthenium hysterophorus* under high temperature abiotic stress like conditions. J Stress Physiol Biochem 10:228–237