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Leaf trait associations with environmental variation in the wide-ranging shrub *Dodonaea viscosa* subsp. *angustissima* (Sapindaceae)

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Abstract Intra-species variation in specific leaf area (SLA) and leaf area (LA) provides mechanistic insight into the persistence and function of plants, including their likely success under climate change and their suitability for revegetation. We measured SLA and LA in 101 Australian populations of the perennial shrub *Dodonaea viscosa* (L.) Jacq. subsp. *angustissima* (narrow-leaf hop-bush) (Sapindaceae). Populations were located across about a 1000 km north–south gradient, with climate grading from arid desert to mesic Mediterranean. We also measured leaves from 11 populations across an elevational gradient (300–800 m asl), where aridity and temperature decrease with elevation. We used regression and principal component analyses to relate leaf traits to the abiotic environment. SLA displayed clinal variation, increasing from north to south and correlated with latitude and the first principal component of joint environmental variables. Both SLA and LA correlated positively with most climatic and edaphic variables. Across latitude, LA showed more variability than SLA. Changes in leaf density and thickness may have caused the relative stability of SLA. Only LA decreased with elevation. The absence of a SLA response to elevation could be a consequence of abiotic conditions that favour low SLA at both ends of the elevational gradient. We demonstrated that the widely distributed narrow-leaf hop-bush shows considerable variability in LA and SLA, which allows it to persist in a broad environmental envelope. As this shrub is widely used for revegetation in Australia, South America and the Asia-Pacific region, our results are consistent with the notion that seed used to revegetate mesic environments could be sourced from more arid areas to increase seed suitability to future climate change.

Key words: *Dodonaea viscosa* subsp. *angustissima*, elevational gradient, intra-specific trait variation, latitudinal gradient, leaf area, specific leaf area.

INTRODUCTION

Variability in functional traits within and among populations allows plants to persist across a broad range of environmental conditions. By virtue of expanding niche breadth, intra-specific functional trait variation, caused by local adaptation and plasticity, is assumed to result in wider species distributions (Ramirez-Valiente *et al.* 2010; Bolnick *et al.* 2011). Consequently, intra-specific functional trait variation influences the assembly, dynamics and function of local communities (Cornwell & Ackerly 2009; Violle *et al.* 2012; Kunstler *et al.* 2015; Siefert *et al.* 2015; Escudero & Valladares 2016; Funk *et al.* 2017). The assessment of functional traits across environmental clines provides insight into the mechanisms and

drivers of trait variation, as well as into the persistence and function of widespread species (Hulshof *et al.* 2013; Carlson *et al.* 2016). Inference can be made of the likely success of those species under future climate change and their suitability for revegetation projects (Laughlin 2014). However, most studies explore trait variation in few populations, along short geographic and environmental distances, and often with many co-varying environmental parameters (e.g. spatial, edaphic and climatic variation). Limited sampling and co-varying environmental parameters make it difficult to determine the specific abiotic driver(s) of trait variation and limit the utility of those studies.

Specific leaf area (SLA, equivalent to leaf area per unit mass) and leaf area (LA) are traits known to vary in response to plant habitat as these traits influence heat and gas exchange with the atmosphere (Westoby *et al.* 2002; Díaz *et al.* 2016). Functionally, SLA indicates how much leaf surface is produced by one unit of

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leaf biomass, which closely correlates with photosynthetic and growth rates, resource use efficiency, leaf life span and cost of construction (Wright *et al.* 2004; Poorter *et al.* 2009; Kunstler *et al.* 2015). The impact of intra-specific variation in SLA expands to ecosystem function by influencing productivity, litter breakdown and nutrient recycling (de Bello *et al.* 2010). The multiple roles of SLA, its ease of measurement and the availability of a large worldwide database (Kattge *et al.* 2011) make it a preferred trait for research in functional ecology. LA influences leaf temperature regulation and transpiration rate through its effect on the boundary layer thickness, and consequently also impacts on leaf heat and water balance (Díaz *et al.* 2016). For numerous species with contrasting life forms and from different biomes, SLA and LA correlate well with abiotic stresses such as drought, nutrient availability and insolation (Poorter *et al.* 2009).

Australia's wide variation in aridity and substrates, coupled with the presence of common species whose natural distribution spans these gradients, makes the continent an excellent natural laboratory in which to test the processes influencing intra-specific plant trait variation. The perennial shrub *Dodonaea viscosa* (L.) Jacq. subsp. *angustissima*. (DC.) JG West (West 1984) (Sapindaceae) (hereafter *Dodonaea*) is appropriate for our study because it is distributed from the hot, arid centre of the continent to the temperate Mediterranean zone on the southern coast, and also at all elevations of the Flinders and Mt Lofty Ranges in South Australia. This wide distribution suggests *Dodonaea* should have substantial variability in SLA and LA, which is supported by accounts of phenotypic clines in leaf width (Guerin *et al.* 2012), stomatal density (Hill *et al.* 2014) and allele frequencies of genes associated with water use efficiency (Christmas 2015; Christmas *et al.* 2016) in this species. It is possible that *Dodonaea* is now being pushed to adapt to climate change at a rate that may exceed its adaptive potential. Despite this threat, its extensive range, apparent plasticity and ability to pioneer degraded sites suggest that it may have more capacity to adapt to changing environmental conditions than other native shrubs (Booth *et al.* 1996). *Dodonaea* is a ruderal species able to grow on disturbed or eroded soils, and is often employed for restoration and soil stabilization in Australia (Monie *et al.* 2013; Pickup *et al.* 2013) and overseas (Groenendijk *et al.* 2005; Bonfil & Trejo 2010; Ammond *et al.* 2013; Yelenik *et al.* 2015). As such, intra-specific trait variation could be a useful basis on which to decide on seed sources for restoration by increasing the likelihood of planting success and resilience under climate change (Laughlin 2014). Here, we intensively sample *Dodonaea* across a broad environmental and spatial range to identify the likely drivers of two important leaf traits. We couple this analysis with leaf trait analysis of populations distributed over altitudinal

gradients, representing a short linear distance but with steep environmental variation, effectively decoupling geographic distance from environmental distance. We aim to answer the following questions: (i) what is the range of *Dodonaea*'s SLA and LA responses to its environment? (ii) which abiotic variables associate with these leaf traits? and (iii) do latitude and elevation have similar effects on SLA and LA?

METHODS

Study species and populations

Dodonaea (narrow-leaf hop-bush) is a 1–4 m tall woody shrub, with upright, narrow, tough and sticky leaves covered by reflective wax. It is widely distributed throughout the southern half of Australia, predominantly on well-drained soils. Locally, it forms sparse-to-dense cover in shrublands and in open woodlands as a recognizable shrub layer (Hyde & Playfair 1997; Foulkes & Gillen 2000; Lang *et al.* 2003; Brandle 2010).

We analysed SLA and LA from two data sets. The first comprised samples from 101 populations across about a 1000-km non-linear latitudinal sequence (23.6–35.9°S), mainly focused in the Northern Territory and South Australia (Fig. 1). Climatic and edaphic variables for each population site include mean annual precipitation, the aridity index ranging from 0 (most arid) to 1 (least arid), air temperature, solar radiation, soil pre-European nitrogen concentration and phosphorous content, clay percentage and bulk density. Environmental data were sourced from the Atlas of Living Australia at 0.01° (~1 km) resolution (<http://www.ala.org.au>; accessed 15 February 2016) (Williams *et al.* 2012). From north to south, there are gradual decreases in solar radiation and temperature with parallel increases in rainfall and soil fertility. The annual mean aridity index (annual rainfall / potential or pan evaporation) integrates water stress condition and decreases southwards. Latitude and discrete abiotic variables such as aridity, rainfall, mean temperature and soil N and P quantities relate linearly from 23°S to about 30°S, but further southwards this relationship becomes exponential (data not shown).

The second data set comprised 11 populations sampled at 50 m elevation intervals between 300 to 800 m asl, in the Heysen Range (31.31° S; 138.57° E; Fig. 1) (Guerin *et al.* 2012). We obtained the low elevation climate records from the Atlas of Living Australia (<http://www.ala.org.au>; accessed 15 February 2016) (Williams *et al.* 2012) (mean air temperature = 16.0°C; mean annual rainfall = 300 mm). Climatic data were unavailable for the highest elevation, but considering the average elevation lapse rate, we estimated mean temperature and mean annual rainfall to be 12.0°C and 500 mm, respectively, with both temperature and aridity decreasing at higher elevations.

Trait measurements

We measured LA and SLA on either recently collected (fresh) or dried, preserved leaves. Samples came from

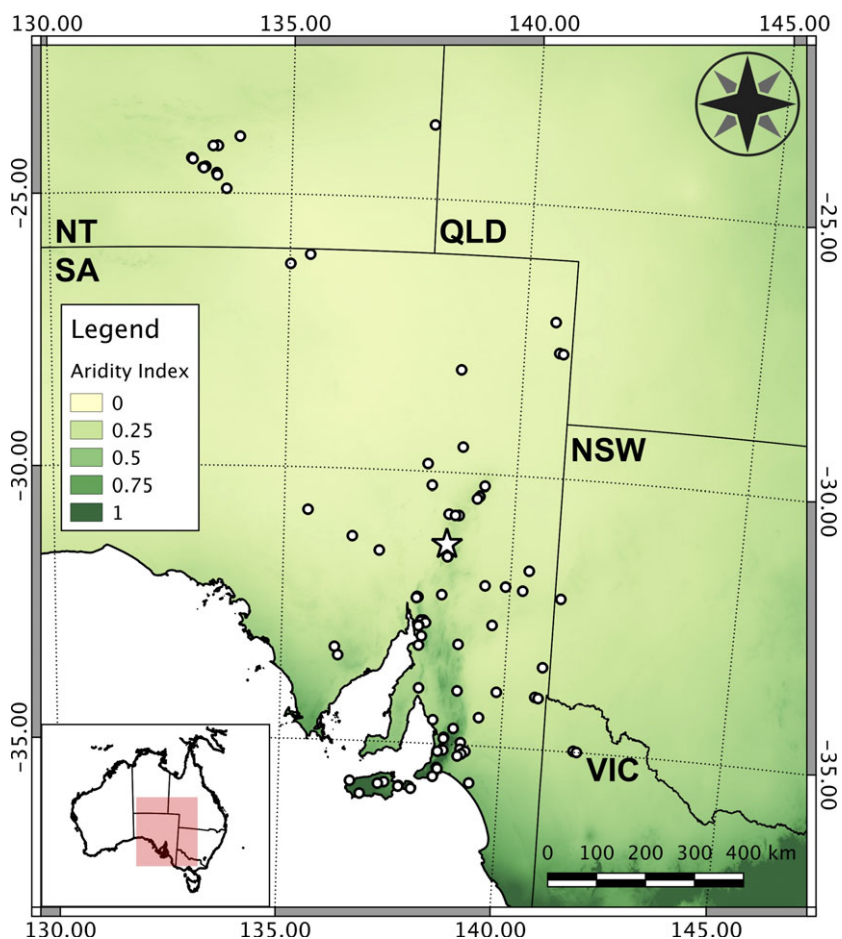


Fig. 1. Location of the sampled populations of *Dodonaea viscosa* subsp. *angustissima*. Colours represent the aridity index (range: 0–1; more to less arid). The star symbol indicates the elevation gradient site. Insolation, temperature range and aridity increase northwards, whereas rainfall and soil N and P amounts increase southwards.

one to five individuals per population and we analysed five undamaged leaves per individual. We followed standard procedures for field sampling and preservation of fresh leaves (Pérez-Harguindeguy *et al.* 2013). We scanned the leaves and measured their area with ImageJ (Rasband 2011), before oven drying at 65°C for 48 h, then weighing and calculating SLA. To account for the area contraction of preserved leaves, which made direct comparison with fresh samples impossible, we calculated a shrinkage factor by measuring fresh and dry LAs from two populations: one from a mesic site (Mt. Bryan 33.33°S; 139.05°E) and the other from an arid site (Andamooka 30.47°S; 137.15°E). Leaves from the northern and more arid site showed less shrinkage ($15.6 \pm 2.4\%$; $n = 20$) than those from the wetter southern site ($23.4 \pm 4.3\%$; $n = 25$) ($F_{(1,42)} = 50.2$; $P < 0.001$). The mean shrinkage ($20.1 \pm 5.3\%$) is consistent with published values (Torrez *et al.* 2013; Queenborough & Porras 2014). Consequently, all LAs were converted into a fresh basis by: Fresh LA = Dry LA / 0.201 before SLA was calculated and used in further analysis. By including preserved leaves, we expanded the data available for this study several fold.

Data analysis

For both data sets, we correlated SLA and LA and each trait with the abiotic variables listed above. In addition, and to obtain an integrated response of leaf traits to multiple physical variables, we employed principal component analysis (PCA) to ordinate the population sites within the environmental space using PC-Ord V6 (McCune & Mefford 2011). We then regressed the coordinates generated by PCA along its main variance axis to latitude, SLA and LA using the lm function in R v. 3.3.1 (R Core Team 2016). Due to a southern bias in our sampling along the latitudinal gradient, we carried out bootstrap resampling with 10 000 iterations using the boot function in the R package v. 1.3-18 (Canty & Ripley 2016) to obtain the confidence intervals for regression coefficients.

RESULTS

SLA significantly increased southwards but LA did not show a significant correlation with latitude

Table 1. Regression coefficients of *Dodonaea viscosa* subsp. *angustissima*-specific leaf area (SLA) and leaf area (LA) against a range of environmental variables as well as coordinates of Axis 1 of a principal component analysis (PC1) ordination of the environmental variables along the latitudinal and elevational clines. *P* values relate to the significance of the slope values and those in bold represent statistically significant relationships. Ninety-five per cent confidence limits (based on 10 000 bootstraps) of intercepts, slopes and r^2 are shown in Appendix S2

Regression	Intercept	Slope	r^2	<i>P</i>
<i>Latitudinal cline</i>				
SLA versus latitude	18.72	-1.51	0.14	<0.001
SLA versus aridity	56.07	34.08	0.35	<0.001
SLA versus precipitation	48.58	0.05	0.36	<0.001
SLA versus insolation	140.23	-3.821	0.23	<0.001
SLA versus mean temp	96.24	-1.72	0.11	<0.001
SLA versus N	35.54	0.57	0.18	<0.001
SLA versus P	56.01	0.02	0.21	<0.001
SLA versus % clay	73.68	-0.24	0.03	0.088
SLA versus bulk density	31.35	24.06	0.05	0.033
LA versus latitude	1.45	-0.01	0.0007	0.790
LA versus aridity	1.23	1.34	0.16	<0.001
LA versus precipitation	0.87	0.002	0.18	<0.001
LA versus insolation	3.17	-0.07	0.02	0.0799
LA versus mean temp	1.26	0.02	0.01	0.500
LA versus N	1.0	0.01	0.02	0.137
LA versus P	1.33	<0.01	0.05	0.024
LA versus % clay	2.27	-0.02	0.06	0.011
LA versus bulk density	0.22	0.97	0.02	0.145
SLA versus LA	52.43	8.45	0.25	<0.001
Latitude versus PC1				
	-22.0	1.04	0.00	0.306
Above -30°				
	-32.41	-0.76	0.68	<0.001
Below -30°				
SLA versus PC1	66.19	-2.41	0.23	<0.001
LA versus PC1	1.63	-0.05	0.03	0.089
<i>Elevational cline</i>				
SLA versus LA (elevation)	44.80	2.23	<0.01	0.466
SLA versus elevation	48.49	<0.01	<0.01	0.454
LA versus elevation	1.07	<0.01	0.17	<0.001

(Table 1; Fig. 2a,b). There was greater variance in LA compared to SLA, particularly at the ends of the latitudinal cline. Both SLA and LA significantly increased with an increase in precipitation and a decrease in aridity (Table 1; Appendix S1a, b). Only SLA correlated significantly with other climatic variables such as insolation and mean air temperature (Table 1; Appendix S1c, d). The relationships of SLA and LA with soil variables were mixed. Both traits correlated significantly with soil P concentration, but only SLA showed a significant correlation with N content (Table 1; Appendix S1e, f). Neither trait demonstrated correlations with the percentage of clay in the soil, but denser soils were associated with higher SLA (Table 1; Appendix S1g, h). The first axis of the PCA explained most of the variation in the ordination of population sites (68.01%) within the environmental space including all climatic variables and soil N and P amounts (Table 2; Fig. 3a). When plotted against latitude, PCA1 showed a clear

discontinuity in population cline at ca. 29–30°S (Table 1; Fig. 3b). SLA correlated significantly with the whole span of integrated environmental variables represented in PCA1 (Table 1; Fig. 3c).

The elevational responses of leaf traits contrasted with the latitudinal responses. SLA did not vary significantly along the entire 500 m elevational gradient, whereas LA did decrease significantly with elevation (Table 1; Fig. 4a,b).

DISCUSSION

Leaf trait variation across latitude

We observed considerable intra-specific variability in SLA and LA, comparable to that reported for other sclerophyllous shrubs (Cornwell & Ackerly 2009; Carlson *et al.* 2016). Only SLA showed positive

clinal variation along the sampled latitudinal gradient, increasing from north to south. The responses of SLA and LA to the abiotic variables across the gradient differed, indicating that the mathematical relationship between SLA and LA did not translate into similar responses. We suggest that these different responses were due to their separate and specific roles in leaf function. Both traits decreased with

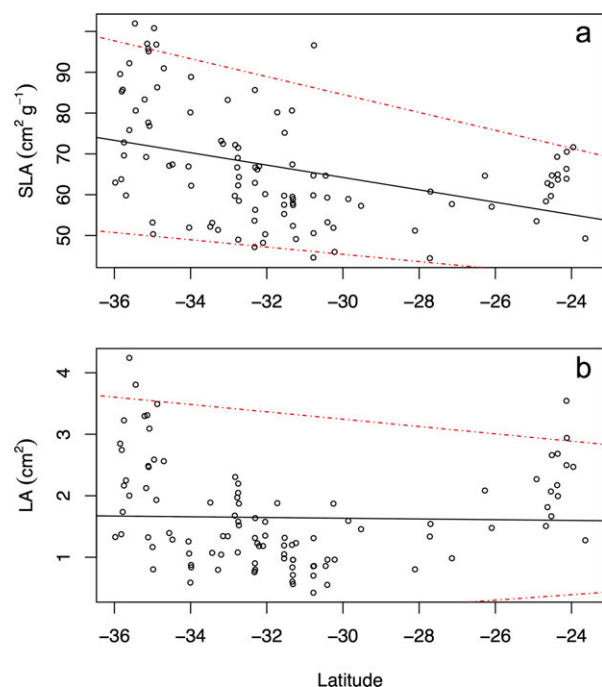


Fig. 2. Leaf trait responses of *Dodonaea viscosa* subsp. *angustissima* to the latitudinal gradient. Linear regressions between (a) SLA and (b) LA and latitude. Coefficients and statistical significance are shown in Table 1. Symbols represent the average for each population. In all panels, broken lines indicate 95% confidence limits.

increasing aridity, but the response of SLA was more pronounced. Furthermore, only SLA responded to air temperature and soil N and P amounts, which are predictable and common responses in sclerophyllous shrubs (Fonseca *et al.* 2000; Ackerly *et al.* 2002; Poorter *et al.* 2009). Soil fertility (as measured by N and P soil amount) was positively associated with SLA, but not with LA. These findings correspond to the tendency that perennial sclerophyllous shrubs growing on oligotrophic soils, such as the northern *Dodonaea* populations with their low SLA, exhibit conservative strategies that minimize nutrient loss by producing more robust, long-lived leaves (Fonseca *et al.* 2000; Wright *et al.* 2004; Ordoñez *et al.* 2009; Poorter *et al.* 2009).

The variability in LA across the latitudinal gradient was higher than SLA, which attests to the higher plasticity of LA reported in other shrubs (Carlson *et al.* 2016). Coordinated changes in leaf tissue anatomy related to leaf density and thickness may have played a role in the relative stability of SLA in *Dodonaea* (Witkowski & Lamont 1991; Poorter *et al.* 2009; Villar *et al.* 2013). In evergreen woody species, SLA is influenced more by leaf density in terms of less intercellular air spaces and smaller cells (Villar *et al.* 2013), but confirmation for *Dodonaea* requires further investigation.

The latitudinal trends of both traits across our sampling area appear to be driven by the main north-south environmental gradients. However, when integrated into a single PCA axis of variation, two patterns stand out. Firstly, the environmental disjunction between northern (23.5–30°S) and southern (30–35°S) sites becomes obvious. We suggest that the change from summer-dominant or non-seasonal rains in the north to a defined winter rain regime in the south, or the putatively high soil salinity near Lake Eyre at the disjunction latitude, may have caused the

Table 2. Pearson correlations with coordinates of Axes 1 and 2 of the PCA ordination of abiotic variables along the latitudinal cline. Regression coefficients in bold represent highly correlated environmental variables. Included is the percentage of the total variance explained by each axis. High correlation coefficients are shown in bold lettering

Axis	PC1		PC2	
	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
Aridity index	-0.92	0.84	0.05	0.00
Annual Mean Rainfall (mm)	-0.93	0.86	0.12	0.02
Solar radiation (MJ m ⁻² day ⁻¹)	0.95	0.91	0.12	0.02
Temperature (mean) (°C)	0.88	0.77	-0.01	0.00
Temperature (range) (°C)	0.94	0.89	0.07	0.00
Soil nitrogen concentration (mg kg H ₂ O ⁻¹)	-0.87	0.75	0.11	0.01
Soil phosphorus content (kg ha ⁻¹)	-0.94	0.88	0.07	0.00
Clay (%)	0.22	0.05	-0.88	0.77
Soil bulk density (g cm ⁻³)	-0.43	0.18	-0.78	0.61
% Variance explained		68.01		15.89

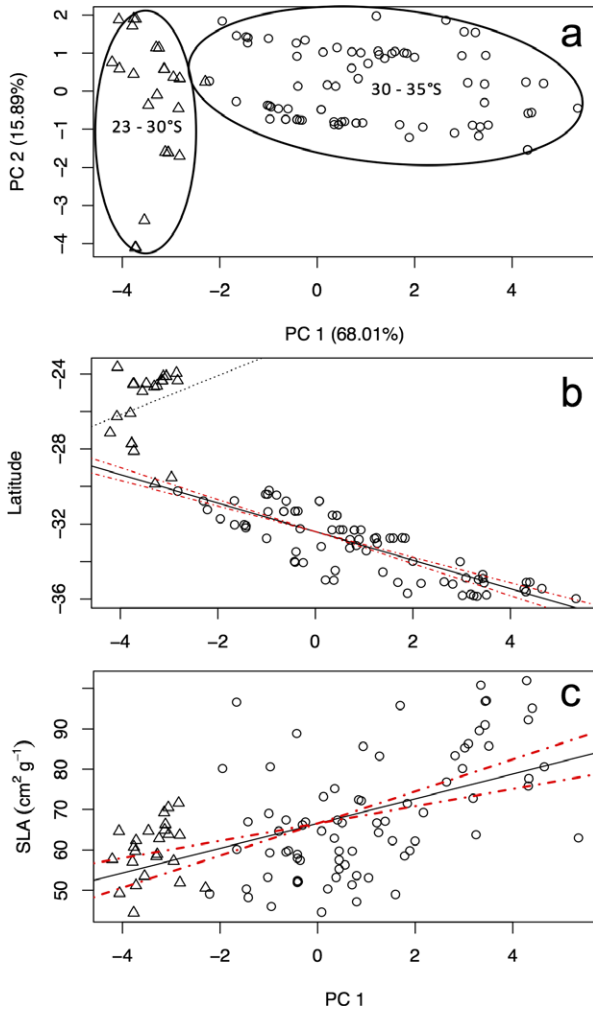


Fig. 3. (a) Principal component analysis (PCA) of the environmental variables shown in Table 2. In parentheses is the percentage of total variation explained by each PC axis. (b) Linear regression between latitude and the coordinates along Axis 1 of PCA. Solid line indicates regression for samples below -30° ; dotted line indicates (insignificant) regression for samples above -30° . (c) Linear regression between *Dodonaea viscosa* subsp. *angustissima* SLAs and the coordinates of PCA along Axis 1. In all panels, circles represent the southern ($30\text{--}35^{\circ}\text{S}$) populations and triangles represent the northern ($23\text{--}29^{\circ}\text{S}$) populations. In panels (b) and (c) the red broken lines indicate 95% confidence limits and the coefficients and statistical significance are shown in Table 1.

observed discontinuity. Secondly, the SLA cline does not show any apparent disjunction, which is more difficult to explain as we would have expected that leaf traits would also respond to the environmental discontinuity. More intensive sampling at the discontinuity latitude may clarify this point.

It is important to note that the approach we have taken here did not allow us to test the responses of SLA and LA to specific abiotic factors. Many of the

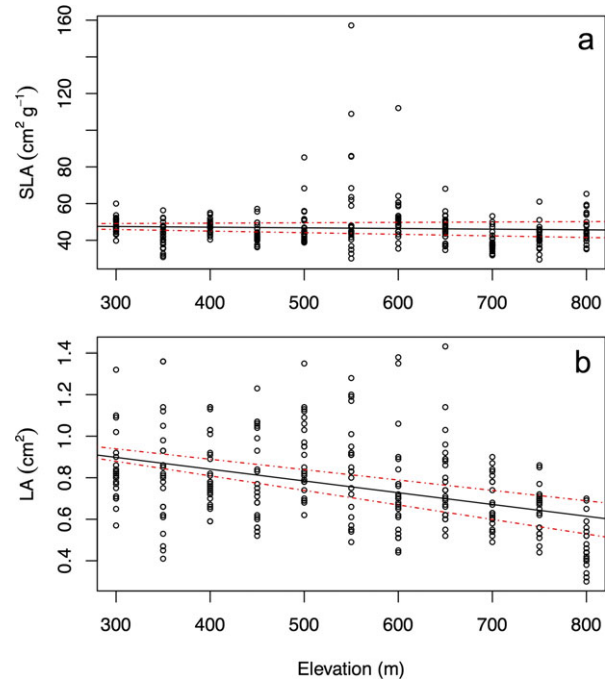


Fig. 4. Linear regression between *Dodonaea viscosa* subsp. *angustissima* (a) SLA and (b) elevation. Symbols represent values for individual leaves. In all panels, the broken lines indicate 95% confidence limits and the coefficients and statistical significance are shown in Table 1.

abiotic variables co-varied along the gradient. We, therefore, cannot disentangle the relative contributions of the specific environmental variables we consider to direct (or indirect) effects on leaf traits. As such, we took a principal component analysis approach to account for these correlations, reducing redundancy in the abiotic data and addressing statistical issues associated with multiple testing. The associations we have identified do hint at causative responses to environment, but further testing (e.g. controlled glasshouse trials) of the effects of specific abiotic factors on leaf traits in *Dodonaea* is required.

Leaf trait variation across elevation

SLA and LA reacted differently to the parallel changes in decreasing temperature and increasing precipitation taking place from low to high elevation. Reduced LA at higher elevations and under lower temperature has been previously shown in *Dodonaea* (Guerin *et al.* 2012) and in other species (Gratani *et al.* 2012; Kichenin *et al.* 2013; Pescador *et al.* 2015). However, the absence of an SLA response is challenging to explain. We suggest that it could have arisen because there are forces that

favour low SLA at both ends of the elevation gradient. At higher elevation, low LA causes low SLA. At low elevation, higher aridity reduces SLA. However, similar conditions prevail along the latitudinal range we sampled, where SLA responded linearly to the complex environmental gradient. To account for this discrepancy, we suggest that the elevational range we sampled (500 m) is too short to generate population differences in SLA due to unimpeded gene flow. Also, the combined effects of increased UV radiation and wind velocity at higher altitude might influence SLA. Again, the mechanism involved in this type of SLA homeostasis likely implicates simultaneous changes in leaf density and thickness. The elevational stability of SLA suggests that maintaining SLA within narrow limits may be critical to the life history of *Dodonaea*. Similar trends were reported for the sclerophyllous shrub *Protea repens* in South Africa and in Mediterranean highlands (Pescador *et al.* 2015; Carlson *et al.* 2016). Common garden trials or growing *Dodonaea* under controlled conditions with simultaneous measurements of leaf thickness and density could reveal the mechanism behind the stability of SLA.

CONCLUSIONS

Dodonaea shows substantial variability in SLA and LA, as a consequence of it responding to a wide variety of environmental demands throughout its extensive range and helping to facilitate its presence in multiple community assemblages. The relative stability of SLA compared to LA is probably the result of trade-offs imposed by the web of close relationships with other important life-history traits. Common garden experiments and growth trials under controlled conditions are needed to understand the effects of abiotic forces on these anatomical and ecophysiological relationships. The covariance of climate and soils with latitude makes it difficult to separate the individual effects of each of these variables on SLA and LA responses. In addition, it is difficult to explain the absence of an SLA response to changes in climate with elevation in contrast to its clear response to changes in climate across latitudes. A combination of inherent SLA stability, small inter-population distances along the slope, increased UV radiation and wind velocity at higher elevations might be responsible for this disparity in SLA response. As *D. viscosa* subspecies are widely employed for revegetation, our results are consistent with the notion that, if differences in leaf traits are genetically based, seed from populations from more arid areas could be used to revegetate mesic environments to increase seed suitability to climate change (Breed *et al.* 2013).

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DATA ARCHIVING

All leaf trait data have been published online via the AEKOS data repository and can be accessed via the following links: Latitudinal data set: <http://www.aekos.org.au/dataset/262394>; DOI: 10.4227/05/57C2343E4E9C2. Altitudinal data set: <http://www.aekos.org.au/dataset/264061>; DOI: 10.4227/05/57C396637EE56

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

- Appendix S1.** Linear regressions of *Dodonaea* leaf traits SLA and LA with eight environmental variables
- Appendix S2.** Regression coefficients of *Dodonaea* specific leaf area (SLA) and leaf area (LA) against a range of environmental variables