

Leaf morphology shift linked to climate change

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Climate change is driving adaptive shifts within species, but research on plants has focused on phenology. Leaf morphology has demonstrated links with climate and varies within species along climate gradients. We predicted that, given within-species variation along a climate gradient, a morphological shift should have occurred over time due to climate change. We tested this prediction, taking advantage of latitudinal and altitudinal variation within the Adelaide Geosyncline region, South Australia, historical herbarium specimens ($n = 255$) and field sampling ($n = 274$). Leaf width in the study taxon, *Dodonaea viscosa* subsp. *angustissima*, was negatively correlated with latitude regionally, and leaf area was negatively correlated with altitude locally. Analysis of herbarium specimens revealed a 2 mm decrease in leaf width (total range 1-9 mm) over 127 years across the region. The results are consistent with a morphological response to contemporary climate change. We conclude that leaf width is linked to maximum temperature regionally (latitude gradient) and leaf area to minimum temperature locally (altitude gradient). These data indicate a morphological shift consistent with a direct response to climate change and could inform provenance selection for restoration with further investigation of the genetic basis and adaptive significance of observed variation.

Keywords: climate change; leaf morphology; adaptive shifts; latitude gradient, altitude gradient; *Dodonaea viscosa*

1. INTRODUCTION

Climate change is expected to drive adaptive shifts within species but work to date on plants has focused almost exclusively on phenology [1]. A body of evidence suggests leaf morphology has adaptive significance linked with climate. Fossil leaf assemblages are used to infer paeleoclimate, particularly temperature [2]. Indeed leaf morphology has been demonstrated to vary within species along spatial climate (latitude and altitude) gradients [3], and broader leaves are more susceptible to extremes of temperature [4]. In previous studies, leaf size within species decreased spatially with increasing mean temperature, decreasing rainfall or increasing altitude [3, 5-8].

Analysis of morphological and genetic variation in animals has demonstrated correlation, adaptation or plasticity along climate gradients and shifts along gradients related to climate change [9-13]. Previous studies of leaf morphology within plant species along climate gradients have focused on localized altitude gradients [3,7,14], microhabitats [4], or changes along larger scale gradients [5,6,8,15,16].

Between 1950-2005, mean maximum temperatures in South Australia rose 1.2°C, while mean rainfall changed little in the study region [17]. Accordingly, we predicted that leaf width should have decreased temporally within some species. Morphological shifts linked to contemporary climate change have been reported sparsely in animals [11] but not plants. We used herbarium and field-collected specimens to investigate change in leaf morphology of *Dodonaea viscosa* subsp. *angustissima* (DC.) J.G.West in the Adelaide Geosyncline region of South Australia over ~120 years in the context of a 5° latitude gradient (herbarium specimens) and a localized 500 m altitude gradient (field samples). We tested the hypothesis that leaf morphology is spatially structured along latitude and altitude gradients and that contemporary climate change has driven a narrowing of leaf width regionally due to

increased summer maximum temperatures.

2. MATERIAL AND METHODS

The study area was the Adelaide Geosyncline region, South Australia, bound by latitude -30 to -35°N and longitude 137 to 139°E. The region is dominated by north-south orientated ranges and experiences a Mediterranean climate. Mean maximum summer temperatures are most strongly correlated with latitude, mean minimum winter temperatures (negatively) with altitude and mean annual rainfall (negatively) with latitude (Fig. 1).

Dodoniaea viscosa (L.) Jacq. is a variable species with subspecies distributed across six continents [18-20]. Variation in leaf morphology within the species is putatively linked to climate [19]. *Dodoniaea viscosa* subsp. *angustissima* has linear to narrowly oblong leaves, with length-to-width ratio typically > 7.5.

Collections with sufficient data ($n = 255$) of *Dodoniaea viscosa* subsp. *angustissima* held at the State Herbarium of South Australia were examined for herbarium regions FR (Flinders Ranges), NL (Northern Lofty) and SL (Southern Lofty). Scaled photographs of collections were taken with a standard digital camera for digital measurement.

Field population samples of *Dodoniaea viscosa* subsp. *angustissima* were taken over an altitude gradient in the Heysen Range (G.R.Guerin 1196 & D.I.Jardine; -31.31455°, 138.56702°). Branchlets were taken from five individuals at 11 x 50 m altitude intervals estimated with a GPS between 300-800 m. Five (/four) mature leaves per branchlet were sampled ($n = 274$). Leaf samples were fully dried before scanning for measurement.

Herbarium collection data were sourced, including date and latitude. Leaf width (at widest point), length and area were measured (Table 1). Pearson correlation coefficients (Pearson's r) were calculated, comparing leaf parameters, latitude, altitude and year. Statistically significant coefficients (adjusted p -values using Holm's method) were used to select response and explanatory variables for modelling. Fit and significance of models was evaluated with p and r^2 values and visual evaluation of residuals plots for trends suggesting significant outliers or non-normality. Coefficients were bootstrapped with 1,000 replicates and 95% confidence intervals calculated. Statistical analyses were conducted in R. Data are available in the ESM.

3. RESULTS

Leaf width was negatively correlated with latitude regionally and leaf area was negatively correlated with altitude locally (Table 2, Fig. 2). A temporal shift towards narrower leaves was confirmed. Leaves have become narrower by 2 mm, equivalent to a 3° northward latitude shift. Variation was a linear function of latitude and year ($r^2 = 0.33400$; $p < 0.0001$) plus within-population variance \pm local altitudinal variation (sampled population: $cv = 0.27$, width of widest leaves 3.5x narrowest, range covers variation in herbarium samples at most latitudes). Temporal variation was not confounded by correlation between latitude and year of collection ($p = 0.539$). Ninety-five percent confidence intervals obtained from bootstrapping of coefficients in the bivariate model (latitude and year) confirmed the relationships (i.e. slopes remained negative within confidence intervals).

4. DISCUSSION

Morphological variation within species along gradients suggests adaptation which may allow local persistence and migration of adaptive potential [21], or at least response linked to climate. As such, spatial gradients are surrogates for temporal change and can link temporal changes to climate. Temporal change predicted by a latitudinal gradient in leaf width in the study taxon was confirmed through analysis of historical collections. We conclude that leaf width is closely linked to maximum temperature at a regional level (latitude gradient) and leaf area to minimum temperature locally (altitude gradient).

There was no correlation between latitude and year of collection that might generate bias. The influence of latitude across the temporal dataset was accounted for by including latitude as a covariate with year. The width of leaves from the earliest collections was not inflated by a southerly bias in latitude of those collections, in fact many were collected at more northern

latitudes.

The relative influence of genetic and plastic response in this dataset is unknown but could be tested formally, for example through common garden experiments. The adaptive significance of observed spatial and temporal shifts could be tested in terms of the physiology or fitness of individuals with different morphologies.

Within-population variation measured from field altitude sampling was significant. Observed spatial, temporal and population variation suggests there is potential for further shifts in leaf morphology to occur within populations. Greater shifts could potentially occur through gene flow, the potential for which is currently unknown.

Restoration practices are needed that pre-empt environmental change and choose species and propagule sources to ensure sufficient adaptive potential [22,23]. The study taxon has potential for morphological shifts in response to climate and may be suitable for restoration in a changing climate. If sufficiently sampled, within-population variation and/or plasticity should allow such shifts. At exposed sites, consideration could be given to sourcing seed from further north where individuals may be pre-adapted to warmer temperatures.

This study was only possible with herbarium collections throughout the region spanning three centuries and their institutional maintenance. Biological collections have proven useful in tracking changes in the distribution, phenology and morphology of species due to climate change [24]. They have also been used in studies of morphological variation along spatial gradients [9], although less frequently than field sampling. Although not systematically sampled, such collections allow wider spatial and temporal sampling than possible with *de novo* field sampling and one can supplement them with field sampling of populations. Datasets with less spatial and temporal coverage have less potential for detecting temporal shifts.

This study adds to a growing number that not only predict temporal shifts in morphology within species through spatial gradient analysis [5-9,11,12,14-16] but attest to real, recent, temporal change [11,25].

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Table 1. Leaf morphology statistics for samples of *Dodonaea viscosa* subsp. *angustissima* from the Adelaide Geosyncline region, South Australia.

Samples	<i>n</i>	Leaf width (mm) [†]	Leaf length (mm) [†]	Leaf area (mm ²) [†]	Leaf length-to-width ratio [†]
Herbarium samples (regional latitude gradient)	255	3.2 ± 1.5 [0.46] (0.7– 8.8)	59.8 ± 12.6 [0.21] (29.9–103.2)	121.4 ± 59.2 [0.49] (28.4–356.8)	23.3 ± 14.0 [0.60] (6.4–129.4)
Field samples (Heysen Range altitude gradient)	274	1.9 ± 0.5 [0.27] (1.0– 3.5)	57.1 ± 11.2 [0.19] (18.7–90.8)	77.7 ± 23.5 [0.30] (29.4–171.6)	31.3 ± 8.4 [0.27] (12.4–58.8)

[†]mean ± standard deviation [coefficient of variation] (range)

Table 2. Statistics for leaf width and area in terms of explanatory variables for *Dodonaea viscosa* subsp. *angustissima*.

Explanatory variable	slope	intercept	Adjusted r^2	p -value	Pearson correlation coefficient (adjusted p -value)
Herbarium samples (leaf width)					
Latitude	-0.66753	-18.11617	0.28740	< 0.0001	-0.54 (< 0.0001)
Year	-0.01756	37.72309	0.05723	< 0.0001	-0.25 (0.0017)
Latitude and year covariates	see below	13.94	0.33400	< 0.0001	-
Latitude (covariate with year)	-0.65535	-	-	< 0.0001	-
Year (covariate with latitude)	-0.01609	-	-	< 0.0001	-
Field samples (leaf area)					
Altitude	-0.067684	114.765793	0.2025	< 0.0001	-0.45 (< 0.0001)

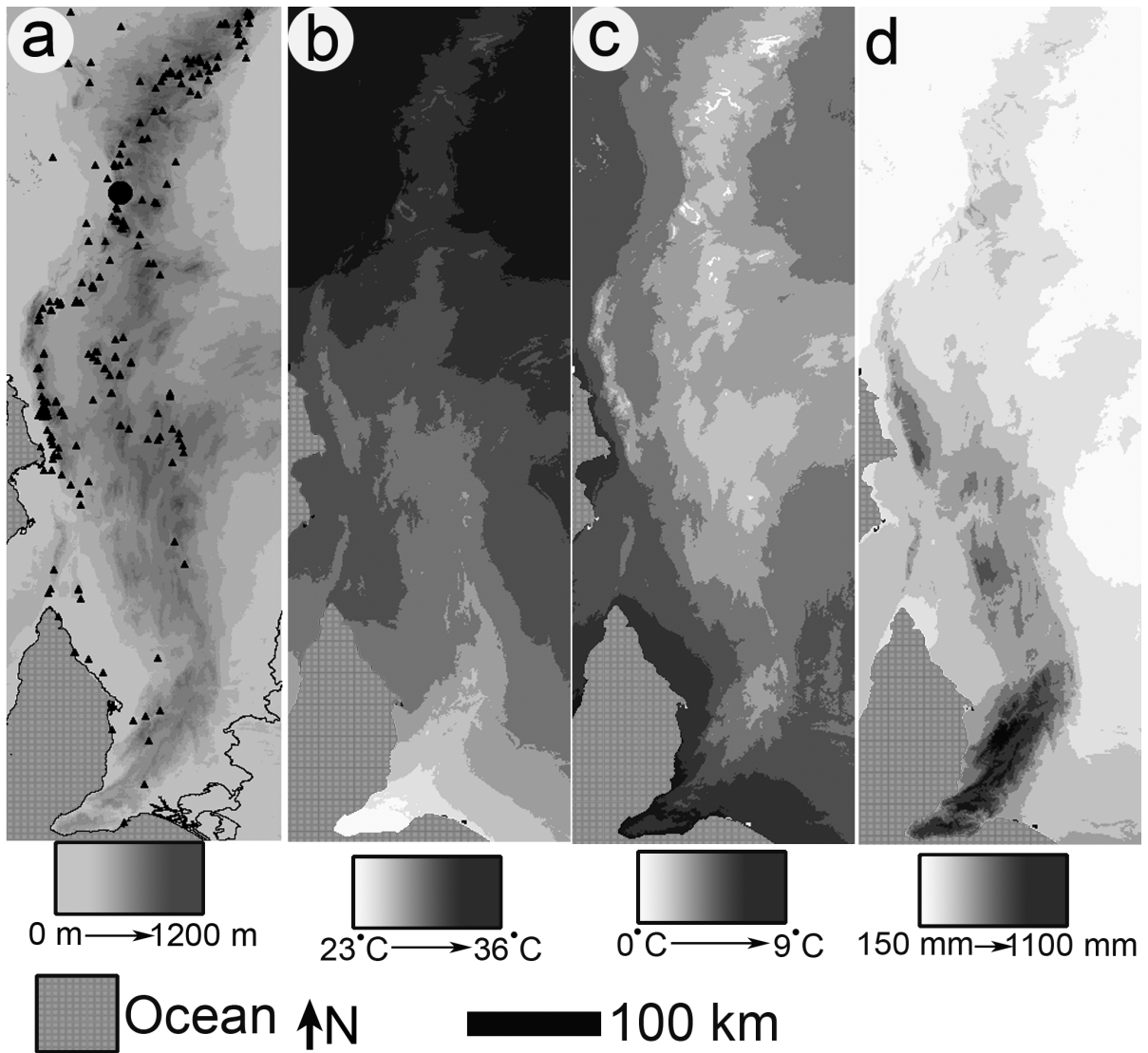


Figure 1. Maps of study region (Adelaide Geosyncline) and key climate gradients. (a) field altitude sampling site (large circle) and collection locations of historical herbarium specimens of *Dodonaea viscosa* subsp. *angustissima* used in the study (triangles) over altitude base map; (b) mean maximum temperature of warmest month; (c) mean minimum temperature of coldest month; (d) mean annual rainfall.

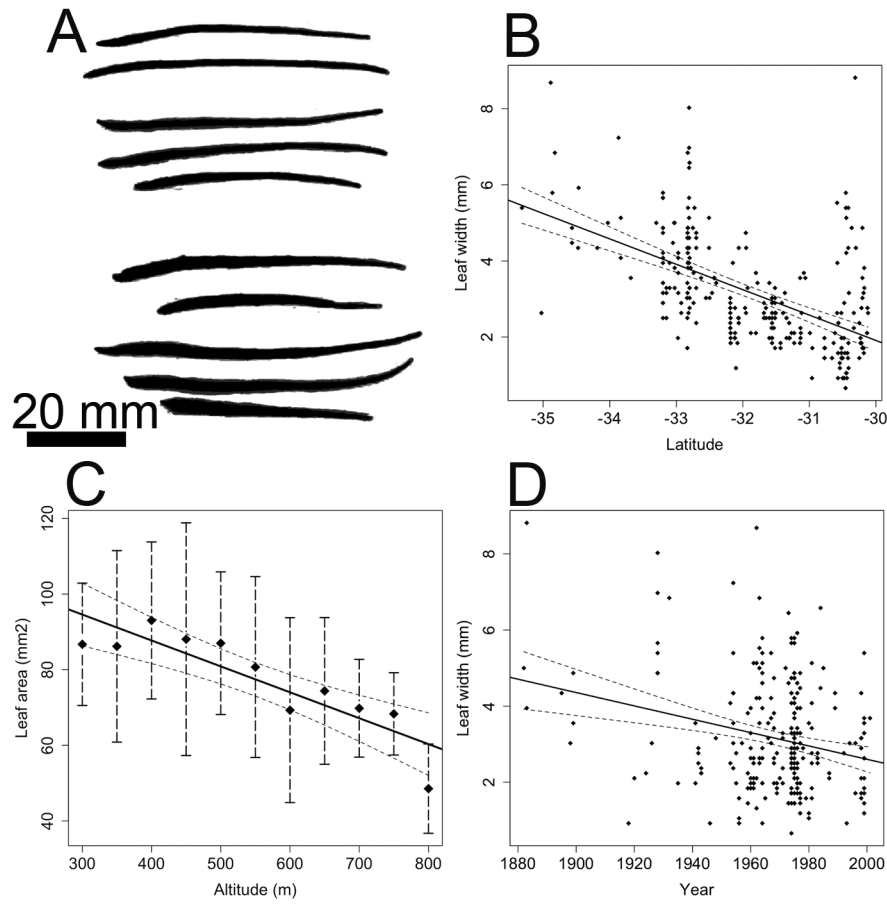


Figure 2. Variation in leaf parameters in *Dodonaea viscosa* subsp. *angustissima*. (a) Scanned leaf examples (two individuals from altitude gradient). (b) Leaf width vs latitude (herbarium collections). (c) Leaf area vs altitude (field samples). (d) Leaf width vs year (herbarium collections). Raw data (points), linear models (solid lines), 95% confidence (dashed lines), one standard deviation (bars).