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Plastic heteroblasty in beach groundsel (*Senecio lautus*)

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Abstract *Senecio lautus* (Asteraceae) is a heteroblastic herb that produces entire juvenile leaves and lobed adult leaves. Juveniles commonly grow from rock fissures where they are shaded and sheltered from high winds, whereas adult plants are exposed to high light and wind as they outgrow these refuges. Because the duration each plant is sheltered varies with the depth of rock fissures, I hypothesised that heteroblasty in *S. lautus* varies plastically in response to environmental conditions. I tested this hypothesis in a glasshouse experiment, which exposed developing plants to different light and wind conditions. Plants grown in windy conditions showed similar ontogenetic changes in leaf morphology to plants growing in a control treatment. However, the juvenile-adult transition was slowed in shaded conditions, indicating that heteroblasty in *S. lautus* varies plastically in response to light. Results were therefore consistent with the hypothesis that plastic heteroblasty is favoured in species that experience unpredictable environmental gradients during ontogeny.

Keywords experiment; leaf shape; morphology; ontogeny; leaf mass per unit area

INTRODUCTION

Plants that change leaf morphology during ontogeny are termed “heteroblastic” (Goebel 1900). The New Zealand flora is notable for unusually high rates of heteroblasty. There are approximately 200 heteroblastic plant species in New Zealand (Cockayne 1912), in a flora containing approximately 2300 indigenous vascular plant species (Wardle 2002). Thus, nearly 10% of New Zealand’s vascular flora is heteroblastic. Only the Mascarene Islands and New Caledonia are believed to have comparable incidences of heteroblasty (Friedmann & Cadet 1976; K. C. Burns & J. W. Dawson unpubl. data).

It has been postulated that heteroblasty is an adaptation to changing environmental conditions as plants grow. If juvenile and adult leaf morphologies enhance performance under different environmental conditions, and these conditions alternate during development, heteroblasty may help plants cope with environmental heterogeneity (see Dawson & Lucas 2004). For example, light levels typically increase vertically in forests. If juvenile leaves are shade-adapted, and adult leaves are better adapted to high light environments, heteroblasty may help forest plants adjust to changing light conditions as they grow (Gould 1993; Day & Gould 1997; Day et al. 1997). Heteroblasty could also be an adaptation to drought, frost, wind, or herbivores (McGlone & Webb 1981; McGlone & Clarkson 1993; Givnish et al. 1994; Darrow et al. 2001, 2002; Hansen et al. 2003; Eskildsen et al. 2004; Gras et al. 2005).

Heteroblastic changes in leaf morphology could arise from several developmental mechanisms. Heteroblasty could follow a rigid developmental programme, with consistent changes in leaf morphology occurring regardless of the conditions plants experience during development (see Ashby 1948; Wells & Pigliucci 2000). Conversely, heteroblasty could be generated entirely by plastic responses of individual leaves to environmental conditions (Sultan 2000; Zwieniecki et al. 2004). Heteroblasty could also result from a combination of programmed and

plastic developmental changes, whereby the transition from juvenile to adult leaves is either slowed or accelerated under different environmental conditions (Watson et al. 1995; Winn 1996a,b; James & Bell 2001). Winn (1996a) hypothesised that different developmental mechanisms are favoured under different environmental regimes. When the sequence of environmental conditions plants experience during development is predictable, heteroblasty should be rigidly programmed. Conversely, when the sequence of environmental conditions experienced during ontogeny regularly varies among plants, plastic heteroblasty should be favoured.

Beach groundsel (*Senecio lautus* Willd.) is a heteroblastic herb that produces entire juvenile leaves and lobed adult leaves (Fig. 1). In the Wellington region it commonly grows from cracks in rock surfaces at the shoreline. Thus, juvenile plants are sheltered from high winds and direct solar radiation by rock surfaces, while adult plants are exposed to high light and wind as they emerge from rock fissures. The transition from one suite of environmental conditions to the other occurs concomitantly with changes in leaf morphology. Plants growing in rock fissures typically have larger, entire leaves, which provide more photosynthetic surface area per unit construction cost (see Givnish 1986). Plants growing above rock surfaces typically have lobed leaves, which may be more stable when buffeted by high winds and less prone to abrasion damage. However, the length of time plants are exposed to each set of light and wind conditions varies with the depth of rock fissures. Plants growing from deeper cracks are shaded and sheltered for longer periods than plants growing in smaller cracks. Therefore, according to Winn's (1996a) hypothesis, heteroblasty in *S. lautus* should vary plastically in response to variable environmental conditions. I tested Winn's (1996a) prediction by growing plants under different light and wind conditions in a glasshouse experiment. Ontogenetic changes in leaf size and shape were then compared between environmental treatments to test for phenotypic plasticity in heteroblasty.

METHODS

Seeds of *Senecio lautus* were collected from Houghton Bay, Wellington (41°20.5'S, 174°47.1'E). Approximately 10 seeds were collected from each of 10 plants and stored together. Seeds were cleaned of debris, soaked in water for 1 h, and sorted into small pots containing 150 ml of Debco™ sterilised

potting mixture. All seeds were buried approximately 1 mm below the soil surface and placed in full sun in the glasshouse facilities at Victoria University of Wellington.

After germination (i.e., both cotyledons had fully emerged), 20 seeds were randomly assigned to each of three experimental treatments, which ultimately contained 20 plants. All pots were watered once daily to saturation throughout the duration of the experiment. A "wind" treatment was generated by two AZTEC 5240 electric fans placed on the high setting approximately 0.5 m from the pots. Pots were placed in front of fans in fixed positions within a rectangular grid measuring 30×30 cm. Pots were periodically rotated between positions on the grid to ensure that all plants experienced the same conditions throughout the experiment. Measurements of wind speeds with a Kestral 1000 wind meter at the four corners and the centre of the rectangular grid showed that wind conditions were spatially consistent ($2.68 \text{ m s}^{-1} \pm 0.29 \text{ SE}$). Average experimental wind speeds were higher than that observed on typical a summer day (Nov–Mar) along exposed regions of the Wellington coastline ($1.59 \text{ m s}^{-1} \pm 0.18 \text{ SE}$, K. C. Burns unpubl. data). Photon flux densities, measured from the same positions on a clear cloudless day at 12:00 p.m. with a LI-COR LI 1000 light meter, averaged $2009.4 \pm 105.7 \text{ } \mu\text{moles m}^{-2} \text{ s}^{-1}$ at the soil surface. Fans were set on timers so that plants experienced 14 hours of windy conditions and 10 hours of calm conditions daily.

A "shade" treatment was generated by metal screening fastened to a rectangular box constructed from PVC piping placed over seedlings. Pots were again arranged in a 30×30 cm rectangular grid and periodically rotated. In this treatment, photon flux densities averaged $86.6 \pm 6.3 \text{ } \mu\text{moles m}^{-2} \text{ s}^{-1}$ and wind speeds were negligible (0 m s^{-1}).

A "control" treatment was also constructed to evaluate heteroblastic changes in leaf morphology under high light and still wind conditions. Seedlings were arranged and rotated as in the shade and wind treatments. Photon flux densities averaged $2031.9 \pm 96.2 \text{ } \mu\text{moles m}^{-2} \text{ s}^{-1}$, and wind-speeds were negligible (0 m s^{-1}).

A treatment consisting of shaded, windy conditions was not conducted. A fully factorial design was not adopted for two reasons. First, plants rarely encounter high wind, low light conditions in the field, because the same rock surfaces that shade plants also shelter them from high winds. Second, and more importantly, shaded, windy conditions were difficult to generate in the glasshouse. The enclosures used



Fig. 1 Leaves produced by a single plant of *Senecio lautus*, collected from the south coast of Wellington. Leaves are arranged according to their order of production, with the earlier produced leaves (juvenile) positioned farthest right and the last leaf produced (adult) farthest left.

to shade plants interfered with wind flow, making it impossible to standardise wind conditions across treatments.

Plants were harvested after 100 days, because preliminary trials showed that by that time most plants 1) produced at least 10 leaves, 2) were in the early stages of reproduction, signifying they were no longer “juveniles”, and 3) rarely abscise leaves. Plants were cut at their base and the distance between each node and the base of the plant (leaf height) was measured. Each leaf was then separated from its petiole and placed individually on an HP scanjet 5400c computer scanner ($n = 532$). A high resolution, black and white image of each leaf was imported into ImageJ (Abramoff et al. 2004) and the perimeter and total area of each leaf was measured to the nearest centimetre. Leaves were then dried to a constant mass in a drying oven (30°C), and leaf mass was measured to the nearest 0.01 mg with an electronic balance. Four dependent variables, the dissection index (i.e., leaf lobing), leaf heights (cm), leaf mass per unit area (LMA; g m^{-2}), and total leaf area (cm^2), were generated from these measurements to characterise changes in leaf morphology. The dissection index was calculated as the ratio of

leaf perimeter to the square root of leaf area (leaf perimeter $(\sqrt{\text{leaf area}})^{-1}$). This measure is highly correlated with more complex measures, such as fractal dimension (McLellan & Endler 1998).

Results were analysed with ANCOVA, using treatment as a fixed factor, plant as a random factor, and node (i.e., each leaf numbered according to their sequence of production) as a covariate. Two main effects (plant and node) and the interaction between node and treatment were assessed using Type I sums-of-squares, to remove the effect of plant on heteroblastic trends. The main effect of the covariate (node) characterised overall heteroblastic trends. The interaction between node and treatment tested whether ontogenetic trends differed among environmental treatments. Sample sizes varied according to the total number of leaves produced by each plant. Several plants abscised leaves during the course of the experiment, which were subsequently treated as structural zeros and removed from statistical analyses. All dependent variables were log-transformed for assumptions, and separate tests were conducted on each dependent variable. All analyses were conducted using the general linear model procedure in SPSS (Lead Technologies 2002).

RESULTS

Pronounced ontogenetic changes in leaf morphology were observed in *Senecio lautus*. Similar statistical results were obtained in analyses of all four dependent variables (Table 1). Leaf lobing, leaf heights, leaf mass per unit area (LMA), and total leaf area all differed between plants and nodes. The effect of plant indicates that individual plants often showed different responses to environmental conditions. The effect of node illustrates overall heteroblastic trends. Regardless of treatment, younger leaves were entire, smaller, produced closer to the ground, and had lower LMA. Leaves produced later in development were lobed, larger, higher above the ground, and had greater LMA.

Statistical interactions between treatment and node were observed for all four dependent variables, indicating that ontogenetic changes in leaf morphology differed among environmental treatments. However, differences among treatments were generated only by light availability. Shaded plants continued to produce entire leaves with lower LMA later in development than plants in both the wind and control treatments (Fig. 2). Although shaded plants produced leaves which were less lobed than in the other treatments, leaves produced at later nodes by shaded plants were more lobed than those produced at earlier nodes. Conversely, leaf area and

leaf heights increased among nodes more rapidly in the shade treatment relative to both the wind and control treatments (see Fig. 2).

DISCUSSION

Senecio lautus initially produced small, entire leaves with low leaf mass per unit area (LMA). At maturity, however, leaves were larger, lobed, and had higher LMA. Heteroblasty in *S. lautus* is notable for several reasons. First, changes in leaf shape are opposite to most other heteroblastic species in New Zealand. Juvenile leaves are typically lobed, while adult leaves are entire (e.g., *Elaeocarpus hookerianus* Raoul (Elaeocarpaceae), *Pseudopanax edgerleyi* Hook. f. (C.Koch) (Araliaceae)). Second, heteroblasty is most common in long-lived, woody plants in New Zealand, not herbs (cf. Webb 1984). Lastly, *S. lautus* is typically found near the shoreline, a habitat in New Zealand where heteroblasty is uncommon (Day 1998).

Ontogenetic changes in leaf morphology differed among environmental treatments. Shaded plants produced larger, entire leaves with low LMA later in development relative to the control and wind treatments. This result indicates that the expression of heteroblasty in *S. lautus* is influenced by

Table 1 Results of ANCOVA for four measures of leaf morphology in *Senecio lautus*. *, $P < 0.001$.

Parameter	d.f.	MS	F
Leaf lobing			
Plant	59	0.021	25.1*
Node	1	0.474	573.5*
Treatment × Node	2	0.033	39.7*
Error	469	0.001	-
Leaf area			
Plant	59	0.158	8.0*
Node	1	0.694	35.2*
Treatment × Node	2	3.314	168.1*
Error	469	0.020	-
Leaf mass per unit area			
Plant	59	0.238	27.1*
Node	1	5.012	571.0*
Treatment × Node	2	0.435	49.5*
Error	469	0.009	-
Leaf height			
Plant	59	2.341	485.6*
Node	1	6.791	1408.3*
Treatment × Node	2	0.686	142.4*
Error	469	0.005	-

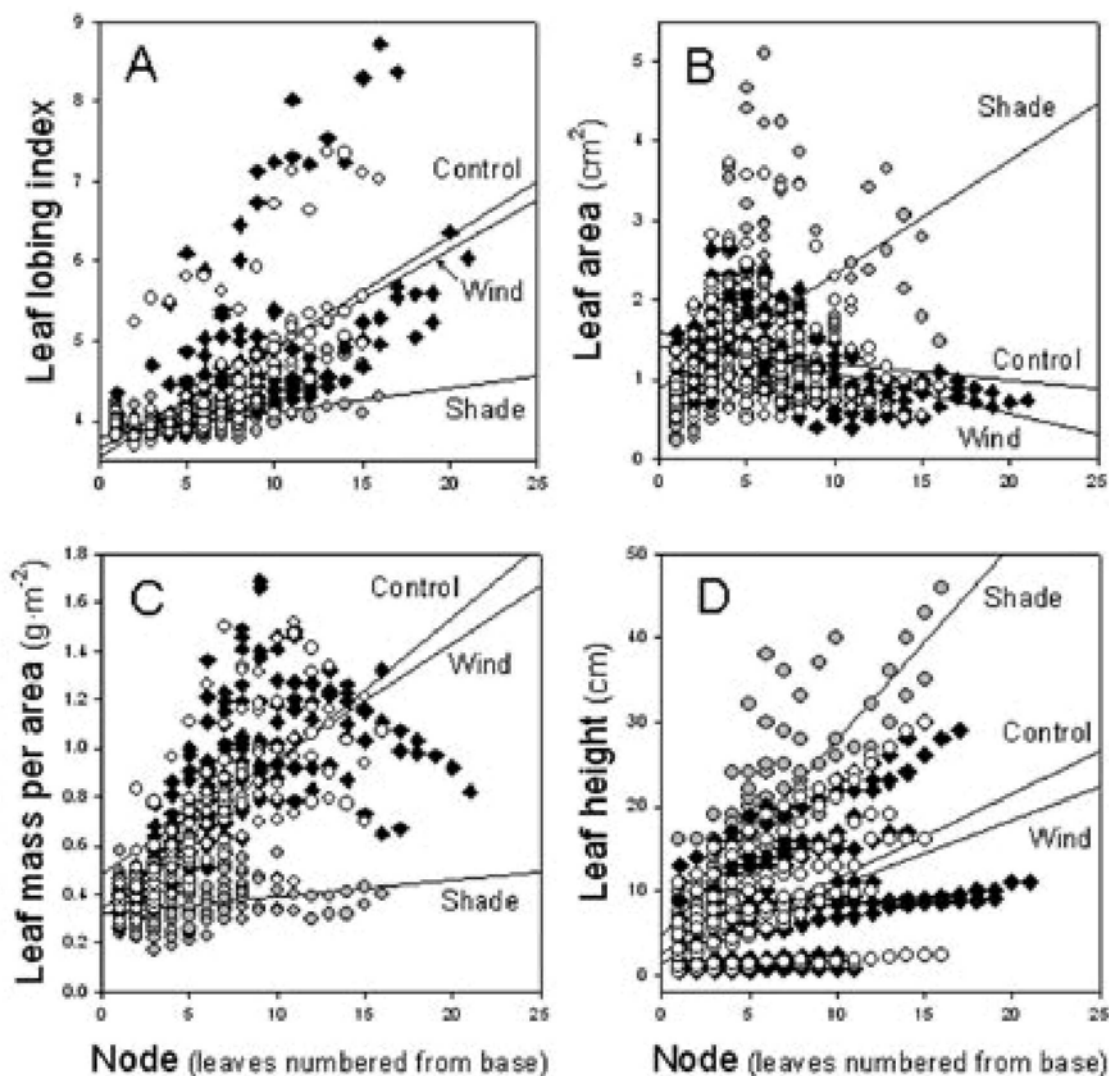


Fig. 2 Relationships between leaf lobing (A, leaf perimeter ($\sqrt{\text{leaf area}}^{-1}$), leaf area (B, cm²), leaf mass per area (C, g m⁻²), leaf height (D, cm) and leaf node, or the sequence of leaves produced through development (1 = the first leaf produced, 22 = the twenty-second leaf produced). Different symbols and separate best fit lines are shown for three experimental treatments. Shaded circles refer to shaded conditions, black diamonds refer to windy conditions, and white circles refer to a control treatment (ambient light and wind conditions).

environmental conditions. However, several lines of evidence suggest that heteroblastic trends also result from programmed developmental changes. First, heteroblastic changes in leaf morphology did eventually occur in the shade, albeit much more slowly. This is illustrated by the gradually sloping best-fit line for leaf lobing in the shade treatment (Fig. 2A). Slower transitions from juvenile to adult leaves in

the shade treatment could have resulted from stunted growth due to insufficient light. However, this explanation seems unlikely, as plants growing in the shade grew much taller than plants in both the wind and control treatments. Second, plants in all three treatments produced morphologically similar leaves at the first few nodes, which were generally smaller and entire. Therefore, results provide evidence for

both programmed and plastic influences on leaf morphology, suggesting that heteroblasty in *S. laetus* results from an interaction between programmed and plastic changes in leaf size and shape.

Heteroblasty has been shown to arise from phenotypic plasticity alone. For example, Zwieniecki et al. (2004) showed that *Quercus rubra* leaves are virtually identical in size and shape at the time of bud break. However, leaf shape varies vertically within plants, with understory leaves being less lobed than those exposed to direct light. Differences in leaf morphology are determined by the environmental conditions that each leaf experiences during development. Therefore, vertical patterns in leaf morphology result from vertical changes in environmental conditions generated by the growing plant. Conversely, some heteroblastic species show consistent heteroblastic changes regardless of the conditions plants experience during development (e.g., *Hedera helix*; see Ashby 1948; Wells & Pigliucci 2000). Results reported here are similar to a larger number of studies illustrating that heteroblasty results from a combination of programmed developmental changes and phenotypic plasticity (Jones 1995; Watson et al. 1995; Winn 1996a,b; James & Bell 2001).

Because all plants produced multiple leaves, self-shading may have influenced trends in leaf morphology. However, this is unlikely for two reasons. First, leaves produced early in development are located at different positions along each plant's vertical axis, which reduces self-shading. Second, plants were harvested prior to the production of leaves on lateral stems. Therefore, all leaves emerged from buds located at the apex of each plant, and were not shaded by previously produced leaves.

Plasticity in heteroblasty could also be investigated by correlating light and wind to naturally occurring plants in the field. This would provide a more direct link between the expression of heteroblasty and the environmental conditions plants typically encounter in the field. However, light and wind are strongly correlated in the field and colinearity between independent variables would hamper efforts to disentangle their effects on leaf morphology. Furthermore, the vertical distance separating leaves is typically smaller than the size of light and wind meters, making it impossible to obtain pair-wise measurements of environmental conditions and leaf morphology. Therefore, I chose to use a manipulative approach.

The observation of plastic heteroblasty in *S. laetus* supports the hypothesis that plastic heteroblasty is favoured when changes in environmental conditions

are unpredictable (Winn 1996a). Because plants grow from fissures in rock surfaces that vary in depth, plasticity likely helps plants cope with spatial variation in environmental gradients. It should be noted, however, that not all plastic phenotypic traits are adaptive (see Padilla & Adolph 1996; Sultan 2000). If the environmental conditions that determine a leaf's morphology suddenly change after it fully develops, phenotypic plasticity would not be adaptive. However, environmental conditions at the rocky shoreline are relatively stable. Rock surfaces typically shift during large earthquakes, which occur infrequently relative to the lifetime of annual plants.

Plastic responses to wind were not observed. This result was somewhat surprising, as other studies have documented plastic morphological responses to wind. For example, Henry & Thomas (2002) found that *Abutilon theophrasti* (Malvaceae) decreased in height and stem diameter in windy conditions. However, results from this study suggest that lobed leaves do not enhance performance in high winds. Another explanation is that lobed leaves are less prone to wind damage, yet *S. laetus* does not use wind as a cue to alter heteroblastic changes in leaf morphology (see Givnish 2002). Finally, although experimental wind speeds were higher than average wind speeds experienced at the coast, even greater wind speeds may be required to induce a change in leaf shape. Instantaneous wind speeds at the coast frequently exceed 100 km hr⁻¹, which is far greater than the wind speeds plants experienced in the glass-house.

Juvenile leaves appear to be advantageous in low light environments. Large, entire leaves with low LMA utilise low light environments more efficiently (see Westoby et al. 2002; McDonald et al. 2003; Burns 2004). The adaptive significance of lobed leaves is less clear. Winn (1999) showed that lobed leaves are better able to tolerate high temperatures and may be an adaptation to reduce temperature stress. In this experiment, the effects of light and temperature were not decoupled and warrant further investigation. Lobed leaves may also reduce self-shading, increase interception of horizontally projected light, or help plants cope with moisture stress (Rich et al. 1995; Sisó et al. 2001). Conversely, leaf lobing could be a selectively neutral trait that evolved under past climates (McGlone & Webb 1981).

Results from this study are consistent with the hypothesis that plastic heteroblasty is favoured in plants that experience unpredictable environmental

gradients during ontogeny. Although heteroblastic trends in the wind treatment were similar to the control treatment, shaded plants produced larger, entire leaves with low LMA later in ontogeny. All plants initially produced similar leaves and shaded plants began to produce lobed leaves later in development. Therefore, a combination of both programmed and environmentally induced changes in leaf morphology occurred during ontogeny. The effects of plastic heteroblasty on plant fitness, and the adaptive significance of the adult leaf form, remain unclear and await future research.

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