



Phenotypic responses of the twining vine *Ipomoea purpurea* (Convolvulaceae) to physical support availability in sun and shade

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Abstract

Vines depend on external support to prevent shading by neighbouring plants. Hence, it is important to determine whether shading enhances the phenotypic responses of vines to support availability. I evaluated the consequences of support availability (a vertical stake) on shoot and leaf traits of the morning glory *Ipomoea purpurea* (Convolvulaceae) under full sunlight and extreme shade. It was hypothesised that phenotypic responses of vines to support availability should be greater in the shade. In addition, to investigate possible constraints to such phenotypic responses, the correlations among phenotypic traits and the plasticity of such correlations were evaluated. The phenotypic variation of the main stem length and of the number of branches was consistent with the hypothesis, i.e. greater responses to support availability in the shade. In contrast, both internode length and leaf area (two traits that showed a significant and positive correlation) decreased in the sun and increased in the shade with support availability. Petiole length decreased with support in the sun but had no response in the shade. On the other hand, the number of significant trait correlations found in plants in the sun and supported plants was higher than those of shade and non-supported plants, respectively. Several of the correlations were significantly sensitive to the environment. Flowering only occurred in the sun treatment. Whereas no shoot or leaf trait was significantly correlated with flower number in supported plants, both petiole length and shoot biomass showed a significant correlation with such estimate of plant fitness in non-supported plants.

Introduction

Since the seminal studies of Darwin on climbing plants (Darwin 1875) the growth habit of vines has received considerable attention from plant physiologists, botanists, and ecologists (French 1977; Peñalosa 1983; Putz 1984; Putz and Chai 1987; Putz and Mooney 1991; Ray 1992). Herbaceous vines depend on external support to position leaves in upper layers to maximise solar radiation capture and hence prevent shading by neighbouring plants. Previous experimental work has described in detail the biomechanics of the process of searching (circumnutation) and twining that allow vines to find and exploit physical support (Peñalosa 1983; Putz and Holbrook 1991; Silk and Hubbard 1991; Matista and Silk 1997; Lar-

son 2000). Likewise, the consequences of finding support on climbing plants morphology and biomass allocation have been described (Puntieri and Pyšek 1993; Klimeš and Klimešová 1994; Den Dubbelden and Oosterbeek 1995; Den Dubbelden et al. 1996; Schweitzer and Larson 1999). The development of a twining habit in otherwise creeping herbaceous plants could be considered an adaptation to shading since it allows them to seek light in upper layers and thereby enhance the harvest of solar radiation and eventually avoid the shade. Therefore, it is of importance to determine whether shading enhances the phenotypic responses of vines to support availability.

The latter also may be viewed within the context of the integration of plastic responses by plants. Thus, the expression of plasticity of plant traits to support

availability and shading may not be independent phenomena. On the other hand, correlations among traits may change with the environment (Lechowicz and Blais 1988; Schlichting 1989; Pigliucci and Schlichting 1995; Gianoli and Hannunen 2000). This plasticity of trait correlations (*sensu* Schlichting (1989)) may have evolutionary implications in the case of selection of plant traits in variable environments (Pigliucci and Schlichting 1996; Schlichting and Pigliucci 1998).

In the present work I evaluated the consequences of support availability on shoot and leaf traits of an herbaceous vine. This was evaluated in a common garden experiment under two contrasting conditions: full sunlight and extreme shade. It was hypothesised that phenotypic responses of vines to support availability will be of greater magnitude in the shade. This hypothesis is based on the assumption that there is a greater adaptive value in reaching upper layers under shade conditions as compared to under full sunlight. In addition, to investigate possible constraints in the pattern of phenotypic responses to support availability in contrasting environments, I evaluated the structure of correlations of phenotypic traits and its plasticity across environments. The morning glory *Ipomoea purpurea* (L.) Roth (Convolvulaceae), a common vine in agricultural fields, was used as a model plant.

Materials and methods

Plant species

Ipomoea purpurea (L.) Roth (Convolvulaceae), the common morning glory, is a self-compatible annual herbaceous vine. The cylindrical stems (0.5–2 m long) are twining when physical support is available. *I. purpurea* is distributed throughout the Americas (Austin and Huamán 1996) and occurs in cultivated fields, orchards, pastures, gardens and forest edges (Matthei 1995).

Experiment

Seeds of *I. purpurea* were collected from several individuals (ca. 20 plants) in the edge of orchards in Central Chile in April 1999 (autumn). Seeds were pooled before sorting them into experimental treatments in order to minimise genotypic effects. This was done because the aim of the study was to detect

general patterns of phenotypic responses across a range of maternal genotypes rather than to isolate genotypic effects from phenotypic effects. Seed scarification consisted of immersion in concentrated sulphuric acid for 5 min followed by washing in running tap water for 5 min. Seeds were germinated in a room at 22 ± 2 °C on wet filter paper in covered plastic boxes and planted in plastic pots (500 ml) filled with potting soil. One week after seedlings attained the second true leaf they were transplanted into plastic pots (5 l) filled with potting soil and transferred to the experimental plot. The plot was located outdoors, in the campus of the Facultad de Ciencias, Universidad de Chile, within an enclosure of wire netting (16 m × 8 m), and was previously weeded and covered with a layer of coarse sand. Experiments were performed during the summer (November 1999–February 2000), at maximum and minimum temperatures of 29 ± 3 °C and 12 ± 3 °C, respectively, and a day length of 15 h.

Four experimental treatments (N = 14 plants per treatment) arose after an array of two light treatments (100% and 5% of full daylight) and two support conditions (with and without physical support). A black shade cloth hung at 2 m over the ground in double layer provided the shade treatment. Full daylight in clear days reached an average value of $1993 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Plants under the shading treatment received on average a radiation of $88.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR (measured with a Li-250 light meter, LiCor Inc., at the ground level). Support consisted of a vertical plastic stake (0.8 cm diameter, 1.8 m long) placed just in contact with the stem. The 28 plants (14 supported, 14 non-supported) included in each of the two light treatments were placed alternately within an area of 4 m × 8 m. Inter-pot distances were sufficient to prevent mutual shading. Plants were watered with tap water to field capacity every second day.

Twelve weeks after plants were transferred to the plot, the shoot was harvested. Stem thickness, number of branches, length of the main branch, number of flowers (in the sun treatment only because there was no flower production in the shade), the length of three consecutive internodes and petioles at mid shoot, and the area and perimeter of three consecutive leaves were immediately measured in each plant. Leaves and the whole shoot were then oven-dried for 48 h at 80 °C and dry weight was determined. Thickness and length of organs was measured with a digital calliper (Mitutoyo Corporation; resolution 0.01 mm). Leaf area and shape (= $[4\pi \times \text{Area}]/[\text{Perime-}$

Table 1. Shoot and leaf traits (Mean \pm SE, N = 14) of plants of *I. purpurea* growing with (SUP) and without (NON) support availability in sun (100% full light) and shade (5% full light). Asterisks indicate significant differences ($P < 0.05$, LSD test) between means for the effect of support availability within light treatments.

	SUN		SHADE	
	SUP	NON	SUP	NON
Length of main stem (m)	1.01 \pm 0.07	0.86 \pm 0.06	*2.04 \pm 0.11	1.33 \pm 0.07
Number of branches	3.8 \pm 0.2	3.9 \pm 0.1	*1.3 \pm 0.1	2.5 \pm 0.1
Internode length (mm)	*64.2 \pm 3.3	91.1 \pm 6.2	*146.4 \pm 6.5	128.8 \pm 7.5
Petiole length (mm)	*35.5 \pm 2.5	59.9 \pm 3.6	48.2 \pm 2.9	50.2 \pm 2.1
Stem thickness (mm)	*2.08 \pm 0.05	1.67 \pm 0.03	*1.61 \pm 0.03	1.33 \pm 0.03
Leaf area (cm ²)	*19.80 \pm 0.90	24.48 \pm 0.99	*49.41 \pm 1.73	43.88 \pm 1.52
Leaf shape ¹	0.60 \pm 0.01	0.59 \pm 0.02	0.62 \pm 0.01	0.63 \pm 0.01
Leaf biomass (mg)	68.8 \pm 3.3	76.9 \pm 3.3	92.1 \pm 3.9	85.8 \pm 4.7
Specific leaf area (cm ² mg ⁻¹)	0.29 \pm 0.01	0.32 \pm 0.02	0.55 \pm 0.02	0.53 \pm 0.02
Shoot biomass (g)	13.00 \pm 0.78	11.80 \pm 0.71	6.65 \pm 0.52	5.12 \pm 0.32
Number of flowers ²	18.1 \pm 3.6	11.9 \pm 3.7	–	–

¹shape = $(4\pi \times \text{Area}) / (\text{Perimeter})^2$

²There was no flower production in the shade

ter]²) were estimated using the SigmaScan® software. The formula for leaf shape is a measure of how circular a two-dimensional object is; it generates values close to 0 for linear objects and close to 1 for circular objects.

Statistical analysis

The effect of treatments on shoot and leaf parameters was tested by a two-way ANOVA (main factors: light and support availability). The significance of differences between means for the effect of support availability within light treatments was tested by a post-hoc LSD test. The correlation among traits, both at the overall and at the within-treatment level, was evaluated by Pearson product-moment correlations. Finally, the plasticity of correlations among traits, i.e., the effect of environment on trait correlations, was estimated by a heterogeneity G-test (Sokal and Rohlf 1995) on z-transformed values, evaluating the goodness of fit of the within-treatment correlation coefficients to the overall correlation coefficient of each pair of traits. All the analyses were performed by the Statistica® program.

Results

In general, supported plants showed: i) a longer main stem, ii) reduced branching, iii) shorter petioles, iv) thicker stems, and v) greater shoot biomass compared to non-supported plants (Table 1). On the other hand, shading promoted: i) elongation of internodes and the main stem, ii) branching, iii) thinning of the stem, iv) increase of leaf area and specific leaf area, and v) a reduction in shoot biomass (Table 2). More related to the focus of the present work, the following traits exhibited a differential response to support availability in sun and shade as indicated by the significant interaction term in the two-way ANOVA (Table 2): length of main stem, branch number, internode and petiole length, and leaf area.

Several traits were significantly correlated when the analysis spanned all experimental plants (Table 3). At a finer scale of analysis, the number of significant trait correlations found in plants in the sun (5) and supported plants (6) was higher than those of shade (2) and nonsupported plants (1), respectively (data not shown to avoid extensive listing). On the other hand, the plasticity of trait correlations was verified. The heterogeneity G-test indicated that several of the correlations were sensitive to the environment (Table 3).

Flower number, a component of plant fitness, could only be determined in the sun treatment. Whereas no shoot or leaf trait was significantly cor-

Table 2. Two-way analysis of variance of *I. purpurea* traits listed in Table 1. Main factors: light and support availability. P-values are shown.

	Light (L)	Support (S)	L × S
Length of main stem	0.0000	0.0000	0.0016
Number of branches	0.0000	0.0001	0.0021
Internode length	0.0000	0.4698	0.0010
Petiole length ¹	0.7706	0.0001	0.0033
Stem thickness	0.0000	0.0000	0.1250
Leaf area	0.0000	0.7585	0.0005
Leaf shape	0.0547	0.9586	0.5002
Leaf biomass	0.0002	0.8227	0.07307
Specific leaf area	0.0000	0.7157	0.1855
Shoot biomass	0.0000	0.0370	0.7942
Number of flowers ²	–	0.2640	–

¹Leaf area was entered as a covariate

²A one-way ANOVA was applied because there was no flower production in the shade

related with flower number in supported plants, both petiole length and shoot biomass showed a significant correlation with such estimate of plant fitness in non-supported plants (Table 4).

Discussion

The non-significant tendencies of reduced branching and increased main stem length with support availability in the sun were highly significant in the shade. These findings are consistent with reported evidence that climbing plants are longer and/or have fewer branches when they are supported (Gartner 1991a; Den Dobbelden and Oosterbeek 1995). The results also agree with the “shade avoidance syndrome”, where the presence of neighbouring plants triggers changes in plant architecture that enhance light capture (Bazzaz and Harper 1977; Ellison and Niklas 1988; Schmitt and Wulff 1993; Dudley and Schmitt 1996). Both responses of *I. purpurea* plants are most probably independent phenomena and not a consequence of a positive correlated variation because the involved traits actually were, overall, negatively correlated. The pattern found for branching and main stem length is also consistent with the hypothesis I tested, i.e. greater phenotypic responses under shading conditions.

Internode length and leaf area decreased in the sun and increased in the shade with support availability. This result may be interpreted as a differential re-

sponse of plants to a non-stressful and a stressful environment. Under conditions of sufficient light, the investment in leaf production will repay in terms of productivity, while gradually climbing onto the available support. In contrast, an increased rate of vertical growth, which allows plants to attain better-lighted layers, would be more beneficial in the shade. Leaves produced in the shade, besides their low productivity, would divert resources from internode elongation. It has been shown before that the presence of support increases the relative growth rate of climbing plant species (Gartner 1991a, 1991b; Puntieri and Pyšek 1993). Likewise, the expansion of leaves in the shoots of twining vines is delayed behind the elongation of internodes (French 1977; Gartner 1991b).

Petiole length was responsive to support availability in the sun but not in the shade. This pattern is opposite to the hypothesis put forward in the Introduction. The relationship between petiole length and plant fitness (i.e., flower number) in the sun may contribute to the understanding of this pattern. It was observed that whereas petiole length was highly related to the number of flowers produced in non-supported plants, it had a null contribution to plant fitness in supported plants of *I. purpurea*. Similar environmental dependence of the contribution of individual traits to overall plant fitness has been reported before (Lechowicz and Blais 1988; Schlichting 1989). Consequently, the shortening of petioles observed in supported plants in the sun may be interpreted as petioles no longer playing an important role in the increase of the harvest of light, as was the case for non-supported plants. This has been suggested before in the context of the greater reliability of the vertical gradient of light compared to the horizontal one ((Ballaré 1994; Huber 1996; Huber et al. 1998); but see Gianoli (2001)). Unfortunately, there was no production of flowers in the shade treatment. Therefore, the involvement of the adaptive value of petioles on its phenotypic responsiveness could not be corroborated in conditions of shading. Likewise, the adaptive value of internode elongation, presumably more relevant in the shade (Dudley and Schmitt 1996; Cipollini and Schultz 1999), could not be assessed.

Results summarised in Table 3 indicate that phenotypic responses of *I. purpurea* are not independent phenomena. Several traits responsive to support availability were correlated, and the correlations between these traits changed with the environment. In addition, the direction of the effect of shading on the expression of some shoot traits of *I. purpurea* (namely,

Table 3. Correlation among traits (A) and plasticity of trait correlations (B) in *I. purpurea*. A) Values above the main diagonal are correlation coefficients r (Pearson product-moment correlations). B) Below the main diagonal: values of the G-statistic for heterogeneity (G-test for goodness of fit of the within-treatment correlation coefficients to the overall correlation coefficient of each pair of traits).

	SL	BN	ST	PL	IL	LA	LB	SB
Main stem length (SL)	1.00	-0.79***	-0.18ns	-0.11ns	0.72***	0.72***	0.46**	-0.47***
Number of branches (BN)	21.35**	1.00	0.36**	0.06ns	-0.71***	-0.77***	-0.42**	0.64***
Stem thickness (ST)	23.57**	93.02***	1.00	-0.38**	-0.55***	-0.57***	-0.31*	0.69***
Petiole length (PL)	11.25ns	14.8*	43.93***	1.00	0.18ns	0.13ns	0.19ns	-0.03ns
Internode length (IL)	66.59***	71.64***	64.08***	40.97***	1.00	0.81***	0.50***	-0.63***
Leaf area (LA)	50.67***	154.32***	105.11***	7.2ns	35.97***	1.00	0.60***	-0.74***
Leaf biomass (LB)	24.3**	58.94***	61.89***	4.22ns	64.86***	21.91**	1.00	-0.26ns
Shoot biomass (SB)	28.44***	103.15***	31.74***	6.52ns	131.8***	117.9***	3.84ns	1.00

ns non-significant, * $P \leq 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4. Correlation between the number of flowers and several shoot and leaf traits in *I. purpurea* plants growing in sun conditions with (SUP) and without (NON) physical support. Values shown are correlation coefficients r (Pearson product-moment correlation).

	Number of flowers	
	SUP	NON
Length of main stem	0.29	0.45
Number of branches	-0.20	0.40
Internode length	0.19	0.29
Petiole length	0.02	0.53*
Stem thickness	0.13	0.03
Leaf area	0.32	0.32
Leaf biomass	0.31	0.47
Shoot biomass	0.07	0.66**

* $P \leq 0.05$, ** $P \leq 0.01$

branching, stem thickness and shoot biomass) was opposite to that of support availability. These findings put together suggest that putatively adaptive phenotypic responses to shading related to the exploitation of support availability may be constrained by the internal structure of correlations as well as by their environmental sensitivity (Schlichting 1986, 1989; Schlichting and Pigliucci 1998). Furthermore, the relationship between a component of plant fitness and shoot and leaf traits may change dramatically with the inclusion of an environmental factor (physical support, in this case). Therefore, in a context of changing environments, the links within the phenotype and between the phenotype and the selective environment may be unstable.

I. purpurea plants showed increased phenotypic responses to support availability in shade conditions compared to sun conditions. This was true mainly for those morphological changes traditionally considered

functional to the enhancement of light capture by shaded plants (i.e., reduced branching, stem and internode elongation). This work contributes to the identification of potential sources of variation in the phenotypic patterns of response of vines to support availability. The fact that general phenotypic patterns remain detectable despite the seemingly daunting background complexity (see Pigliucci et al. (1995); Schlichting and Pigliucci (1995); Sultan et al. (1998); Stanton et al. (2000)) encourages continuing in the pursuit of general explanations.

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