

Maternal environmental effects on the phenotypic responses of the twining vine *Ipomoea purpurea* to support availability

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The presence of physical support elicits a number of morphological changes in the shoot of the common morning glory *Ipomoea purpurea*, including a shortening of internodes and petioles and a thickening of the main stem. Working with experimentally supported and non-supported plants of *I. purpurea*, I tested the existence of maternal environmental effects of physical support in this twining vine. I evaluated whether the offspring of supported plants differed from the offspring of non-supported plants in a number of morphological and reproductive characters. Stem diameter was the only shoot trait that showed a significant effect of the maternal environment (support). The stems of the progeny of supported mother plants were thicker than the stems of the progeny of non-supported mother plants. This was true for both supported and non-supported progeny. Stem diameter, however, was not significantly related to plant fitness (seed number) in supported or non-supported progeny plants. The maternal environment did not affect the magnitude of the phenotypic responses to support of shoot traits in the progeny plants. There were no maternal environmental effects of physical support on the proportion of flowering plants at week 10 in both non-supported and supported progeny. Likewise, the presence of physical support in the maternal environment did not affect reproductive traits (seed number, seed size, percentage of reproductive biomass) in supported and non-supported progeny plants. Finally, the relationship between seed size and seed number was affected by the maternal support environment. The progeny of supported mother plants showed a significantly negative association (trade-off) between seed size and number, whereas such a trade-off was not observed in the progeny of non-supported plants. This was true for both supported and non-supported progeny.

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The effects of maternal environment on plant phenotype have been amply demonstrated (Roach and Wulff 1987, Rossiter 1996, Donohue and Schmitt 1998) and can be of greater magnitude than those of maternal genotype (Stratton 1989, Schmitt et al. 1992, Sultan 1996). Most of the work on maternal environmental effects has dealt with nutritional or abiotic factors (Rossiter 1996) and has focused on their consequences on seed size (Roach and Wulff 1987, Donohue and Schmitt 1998). Furthermore, studies reporting maternal environmental effects on seedling or adult plant traits often explain these results as indirect maternal

effects via seed size (Stanton 1984, Wulff 1986, Stratton 1989, Schmid and Dolt 1994). Some studies, however, have found maternal environmental effects on later plant life stages that cannot be obviously related to differences in seed quantitative provisioning due to variation in parental resource availability/investment (Agrawal et al. 1999, Agrawal 2001). On the other hand, there is considerable evidence that the evolution of offspring provisioning may be constrained by a trade-off between seed size and number (Westoby et al. 1992, Mojonier 1998, Jakobsson and Eriksson 2000).

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The predictability of the offspring environment is a key issue for the adaptive value of maternal environmental effects. Thus, if the cue eliciting the maternal environmental effect also accurately predicts the environment of the progeny, then maternal effects on offspring traits positively related to fitness in that environment may be selectively advantageous (Donohue and Schmitt 1998). This requisite is more likely to be met in plants where fruits or seeds are not dispersed far from the mother plant. It is thereby assumed that the local environmental conditions are similar (or periodically variable) from one generation to the next. There is evidence that maternal environmental effects may take place even during seed formation, which may be interpreted as a “last minute” sensing and conveyance of the prevailing environmental conditions. (Roach and Wulff 1987). Thus, developing seeds exposed to light qualities characteristic of foliage shade may induce a phytochrome-mediated requirement of light for germination (Cresswell and Grime 1981).

Herbaceous vines depend on the availability of physical support to reach upper layers and thereby enhance the harvest of solar radiation and prevent shading by neighbouring plants. The consequences of finding support on the morphology, biomass allocation, and reproduction of vines have been described (Puntieri and Pyšek 1993, Klimeš and Klimešová 1994, Den Dubelden and Oosterbeek 1995, Schweitzer and Larson 1999, Gianoli 2001, 2002). Despite the central role of physical support in the fitness of vines, no study has yet addressed maternal environmental effects on the phenotypic responses of vines to support and their consequences on plant fitness. The availability of physical support for vines rarely varies from one generation to the next (e.g. crop plants, woody shrubs in ruderal habitats, forest trees, fences, etc.) and hence may be considered relatively predictable. Therefore, such maternal environmental effects should be expected to be verified. In this article, I used the common morning glory *Ipomoea purpurea* as a model vine species to test the hypothesis of the existence of maternal environmental effects of physical support. It has been recently shown that the availability of support elicits a number of morphological changes in the shoot of *I. purpurea* plants including a shortening of internodes and petioles and a thickening of the main stem (Gianoli 2002). Working with experimentally supported and non-supported plants of *I. purpurea*, I specifically addressed the following questions: i) what is the adaptive value of the morphological responses of *I. purpurea* to support availability, ii) does support availability in maternal plants affect shoot morphology, plant phenology, or reproductive traits of the offspring?, iii) once support is provided, does the offspring of supported mother plants show greater phenotypic responses to support than the offspring of non-supported mother plants?,

and iv) are maternal environmental effects mediated by seed size?

Materials and methods

Plant species and seed origin

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. Fruits contain typically 6 seeds (4 mm long, 2.5 mm wide). *I. purpurea* is distributed throughout the Americas (Austin and Huamán 1996) and occurs in cultivated fields, orchards, pastures, gardens and forest edges (Matthei 1995).

The maternal plants originated from seeds collected in several individuals (ca 20 plants) in the edge of orchards in Central Chile in April 1999 (autumn). These seeds were pooled before sorting them into experimental (maternal) treatments in order to minimise both genotypic and environmental maternal effects. Seeds were stored at room temperature.

Maternal plants

In October 1999 seeds of maternal plants were scarified and germinated. 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 $22 \pm 2^\circ\text{C}$ 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 × 8 m), and was previously weeded and covered with a layer of coarse sand. Experiments were performed during the austral summer (November 1999–February 2000), at a range of maximum and minimum temperatures of $29 \pm 3^\circ\text{C}$ and $12 \pm 3^\circ\text{C}$, respectively, and a day length of 15 h. Full daylight in clear days reached an average value of $1993 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD.

Plants were randomly assigned to two experimental treatments (N = 14 plants per treatment): with and without physical support. 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) were placed alternately within an area of 4 × 8 m. Inter-pot distances were sufficient to prevent mutual shading. Plants were watered with tap water to field capacity every second day.

Table 1. Coefficient of determination R^2 of the multiple regression model and partial regression coefficients \pm SE of *I. purpurea* shoot traits on seed number in supported (SUP) and non-supported (N-S) plants (n = 20 plants per treatment).

	SUP	N-S
R^2	0.58**	0.09
Internode length	$0.54 \pm 0.16^{**}$	-0.11 ± 0.25
Petiole length	$-0.55 \pm 0.16^{**}$	0.14 ± 0.24
Stem thickness	-0.01 ± 0.16	-0.25 ± 0.25

** P < 0.01.

These plants are a subset of the experimental plants utilised in Gianoli (2002). Fifteen weeks after plants were transferred to the plot, the shoot was harvested and the seeds collected. Seeds were stored at room temperature until the following experimental season.

Progeny plants

In November 2000, seeds obtained from supported and non-supported maternal plants were pooled within each maternal treatment before sorting them into progeny treatments in order to minimise maternal genotype effects. The initial mean seed mass in the two treatments (maternal-supported and maternal-nonsupported) was not significantly different ($P > 0.31$, t-test, sample of n = 30 seeds). Mean \pm SE (mg) were 26.88 ± 3.92 and 32.26 ± 4.59 for supported and non-supported plants, respectively. Seeds were scarified, germinated and grown to seedlings in the same way as was indicated above. Ten seedlings received experimental support (vertical stakes) and ten seedlings were left unsupported in each of the two maternal treatments. In this way, four experimental groups arose after a combination of generation (maternal and progeny) and support treatments (with and without physical support). Seven weeks after the plants were transferred to the experimental plot, stem diameter and the length of three consecutive internodes and petioles at mid shoot were measured in all the *I. purpurea* plants using a digital calliper (Mitutoyo Corporation; resolution 0.01 mm). Three weeks later, the number of flowering plants within each of the four experimental groups was recorded. Five weeks later, the shoot was harvested,

dried (48 h at 80°C) and weighed. Seeds were then collected, counted and weighed.

Statistical analysis

The relationship between plant fitness (seed number) and the shoot traits responsive to support in *I. purpurea* was evaluated by a multiple regression analysis, which was separately applied to supported and non-supported progeny plants. The effect of the maternal and progeny environment (physical support availability) on shoot morphology and reproductive traits (seed size, seed number, and % of reproductive biomass [$100 \times$ total seed mass/shoot mass]) of the progeny was tested by a two-way ANOVA. When there was a significant overall effect of the maternal environment, the significance of differences between means for the effect of maternal environment within the progeny environments was tested by a Tukey HSD test. Log- and arc sin-transformations were applied to values of seed number and % of reproductive biomass, respectively, in order to achieve data normality. The P-value of the interaction term of the two-way ANOVA (maternal environment \times progeny environment) is equivalent to the significance of a test of parallelism and hence was used to evaluate whether the plasticity (i.e. the slope of the reaction norms to support) of the progeny was affected by the maternal environment. The Bonferroni correction for multiple comparisons was applied to estimate significant P-values. To evaluate the effect of the maternal environment on plant phenology (number of plants attaining anthesis ten weeks after the onset of the experiment) a χ^2 test was applied to supported and non-supported progeny. The effect of the maternal environment on the relationship between seed size and seed number was evaluated comparing the outcome of linear regression analyses. This was done for supported and non-supported progeny.

Results

Stem diameter was not significantly related to plant fitness (seed number) in supported nor non-supported

Table 2. P-values corresponding to a two-way ANOVA of the effect of maternal (M) and progeny (P) environment (physical support) on morphological and reproductive traits of *I. purpurea* progeny plants. The significance of the interaction term is equivalent to the significance of a test of parallelism and hence it determines whether the plasticity (phenotypic response to support) of the progeny was affected by the maternal environment (Fig. 1). Significant P-values, after applying the Bonferroni correction for multiple comparisons, are shown in bold.

	Internode length	Petiole length	Stem thickness	Seed number ¹	Seed biomass	% reproduct ²
Maternal (M)	0.1511	0.2542	0.0001	0.1056	0.3769	0.0703
Progeny (P)	0.0001	0.0001	0.0001	0.0001	0.0149	0.0001
M \times P	0.8214	0.5950	0.6759	0.3796	0.0215	0.3744

¹ Shoot biomass was entered as a covariate.

² Percentage of reproductive biomass = 100 (total seed mass)/shoot biomass.

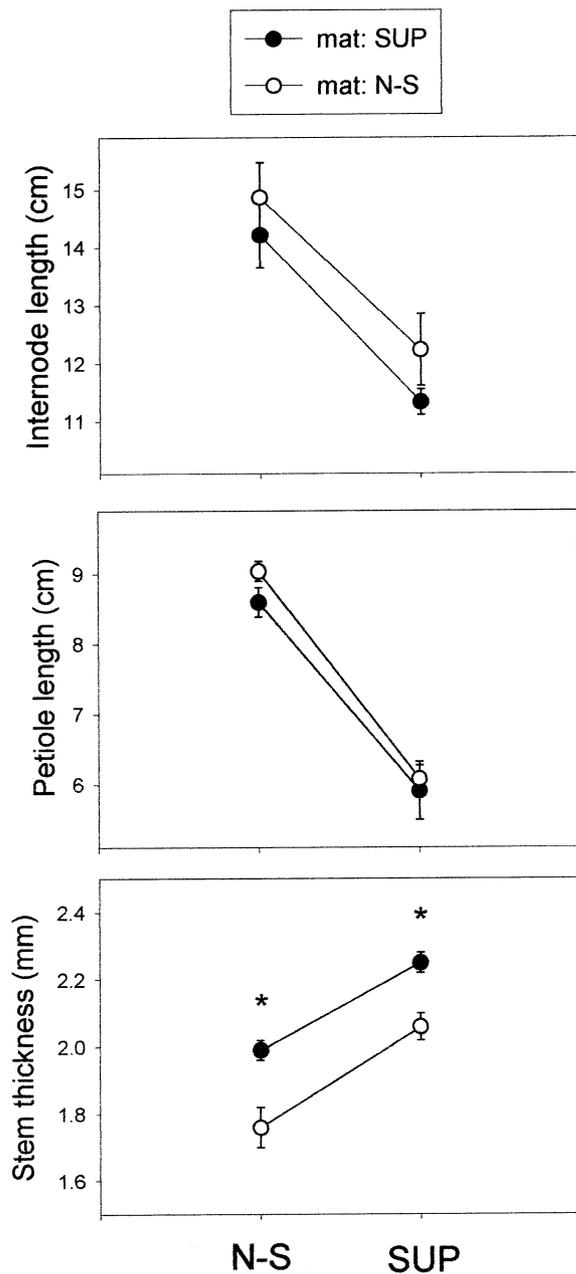


Fig. 1. Shoot traits of non-supported (N-S) and supported (SUP) *I. purpurea* plants. Black and white points correspond to the progeny of supported and non-supported mother plants, respectively. Each point is the mean (\pm SE) of 10 replicates. The asterisk indicates significant effects of the maternal environment within the progeny environment ($P < 0.05$, Tukey HSD test). See Table 2 for the whole statistical analysis.

progeny plants, as was the case for internode and petiole length (Table 1). However, stem diameter was the only shoot trait that showed a significant effect of the maternal environment (support) (Table 2). The stems of the progeny of supported mother plants were thicker than the stems of the progeny of non-supported mother plants. This was true for both supported and

non-supported progeny (Fig. 1). The maternal environment did not affect the plasticity (i.e. the phenotypic responses to physical support) of shoot traits in the progeny plants. Thus, the slopes of the reaction norms corresponding to the progeny of supported and non-supported mother plants (Fig. 1) were not significantly different (see P-values of the interaction of main effects in the two-way ANOVA, Table 2). There were no maternal environmental effects of physical support on the phenological trait of *I. purpurea* that was measured. Thus, the maternal environment did not affect the proportion of flowering plants at week 10 in non-supported ($\chi^2 = 2.73$, $P > 0.09$) and supported ($\chi^2 = 0.10$, $P > 0.74$) progeny. Likewise, the presence of physical support in the maternal environment did not affect reproductive traits (seed number, seed size, % of reproductive biomass) in supported and non-supported progeny plants (Table 3). The presence of support in the progeny environment produced a shortening of internodes and petioles, a thickening of the stem (Fig. 1, Table 2), an increase of seed number and an increase of the percentage of reproductive biomass (Table 2 and 3). Finally, the relationship between seed size and seed number was affected by the maternal support environment. The progeny of supported mother plants showed a significantly negative association (trade-off) between seed size and number, whereas such a trade-off was not observed in the progeny of non-supported plants (Fig. 2). This was true for both supported and non-supported progeny.

Discussion

The availability of physical support is essential for the fitness of vines. Data from earlier studies (Darwin 1875, Putz 1984, Puntieri and Pyšek 1993, Schweitzer and Larson 1999) and results of the present work make it evident. On the other hand, the effects of the maternal environment on the phenotype of progeny plants can be of fundamental importance (Stratton 1989, Schmitt et al. 1992, Sultan 1996, Weiner et al. 1997). Surprisingly, to my knowledge, this is the first report on maternal environmental effects of support on vines. Stem diameter was the only shoot trait that showed a significant effect of the maternal environment (support). Thus, the progeny of supported mother plants exhibited thicker stems than the progeny of non-supported mother plants. This is consistent with the phenotypic response of *I. purpurea* shoots to physical support, i.e. a thickening of the main stem (Gianoli 2002, Fig. 1 in the present article). Internode and petiole length showed non-significant tendencies for a maternal environmental effect similarly consistent with the phenotypic response to support of these traits, i.e. a shortening of the organ. Thus, the progeny of supported mother plants tended to produce shorter internodes and petioles.

In general, the maternal environment did not affect the plasticity (i.e. the phenotypic responses to physical support) of shoot traits in the progeny plants. It has been considered that the evolutionary response of plants to environmental heterogeneity may occur for traits and for trait plasticities (Galloway 1995). The latter would be a “cheaper” strategy because it involves the investment of plant resources into phenotypic changes only when they are suitable for the prevailing environment (Sultan 1987). In the present case, a greater response to physical support was expected for the progeny of supported mother plants, but it was not observed. In view of the results, it might be suggested that the process of twining, and hence the magnitude of its concomitant morphological changes in the shoot, is to some extent fixed in *I. purpurea*. However, a recent study shows that such phenotypic responses differ in magnitude in sun and shade conditions (Gianoli 2002).

The adaptive value of the phenotypic responses of the shoot to physical support (shortening of internodes

and petioles, thickening of the stem) is not clear. Thus, in supported progeny plants, while petiole length was significantly associated with plant fitness (seed number) in an inverse way, internode length showed a significant and positive association with plant fitness, which is somewhat contradictory to the direction of the morphological change (i.e. internode shortening). This apparent paradox may be solved if the two situations are analysed separately. Firstly, it might be considered that the process of twining on a physical support inevitably involves a significant reduction of internode length (ca 3 cm) as compared to prostrate plants (Den Dubbelden and Oosterbeek 1995, Schweitzer and Larson 1999, Gianoli 2001, 2002). Secondly, within the range of variation of internode length in supported plants (ca 5 cm) those plants with longer internodes exhibited a higher production of seeds. Interestingly, in non-supported progeny plants no significant associations of shoot traits with plant fitness were found. This corroborates earlier observations (Lechowicz and Blais 1988,

Table 3. Reproductive traits (mean \pm SE) of supported and non-supported progeny plants of *I. purpurea* originated from supported (SUP) and non-supported (N-S) mother plants. There were no significant effects of the maternal (Mat) environment within each progeny environment (see Table 2).

	Progeny:N-S		Progeny:SUP	
	Mat:N-S	Mat:SUP	Mat:N-S	Mat:SUP
Seed number (log)	1.83 \pm 0.16	1.54 \pm 0.16	2.42 \pm 0.07	2.32 \pm 0.08
Seed biomass (mg)	27.89 \pm 1.97	36.29 \pm 4.23	27.51 \pm 1.52	23.67 \pm 1.34
% reproductive biomass*	6.05 \pm 1.47	4.27 \pm 1.23	17.95 \pm 2.07	13.13 \pm 2.06

* 100 (total seed mass)/shoot biomass.

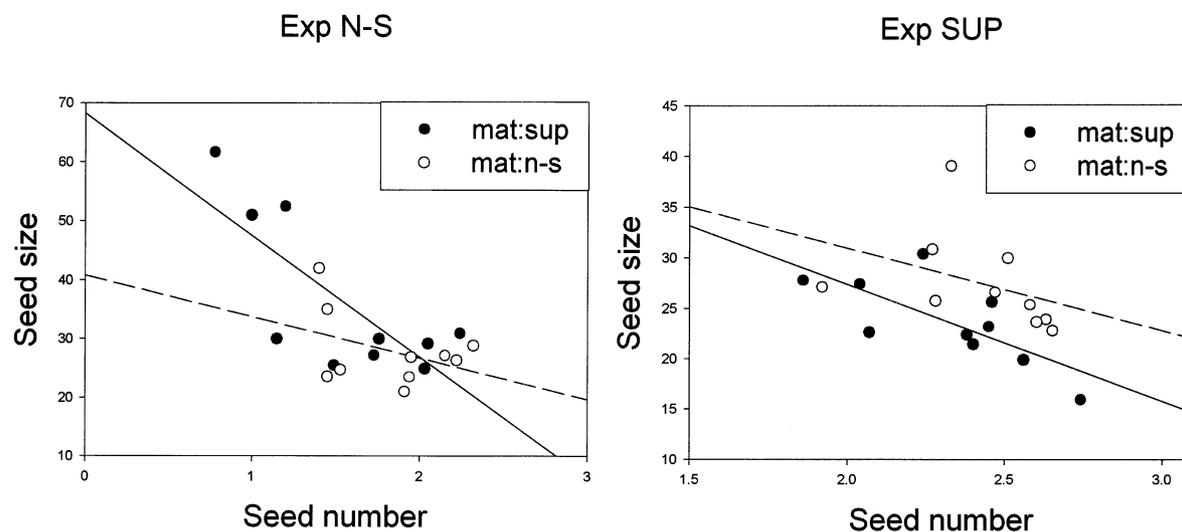


Fig. 2. The relationship between seed size (mg) and seed number (log) in experimentally non-supported (Exp N-S) and supported (Exp SUP) plants of *I. purpurea*. Black points and solid regression lines correspond to the progeny of supported (mat:sup) mother plants. White points and dashed regression lines correspond to the progeny of non-supported (mat:n-s) mother plants. The following are the results of the linear regression analysis. Exp N-S: solid line (mat:sup): $m = -20.7$, $R^2 = 0.59$, $P = 0.0096$; dashed line (mat:n-s): $m = -7.1$, $R^2 = 0.16$, $P = 0.2594$. Exp SUP: solid line (mat:sup): $m = -11.6$, $R^2 = 0.53$, $P = 0.0168$; dashed line (mat:n-s): $m = -8.2$, $R^2 = 0.15$, $P = 0.2723$.

Schlichting 1989) showing that the correlation of plant traits with fitness may vary with the environmental conditions (support availability, in this case).

Stem diameter, the only shoot trait exhibiting a significant effect of the maternal environment, was not significantly associated with seed number in either supported or non-supported progeny. The thickening of the stem of twining vines once they have met external support has been described in a number of species (Den Dobbelden and Oosterbeek 1995, Schweitzer and Larson 1999, Gianoli 2001, 2002). This putatively functional variation is probably a consequence of the biomechanics of the processes of twining and sustaining (Putz and Holbrook 1991). The twining stem puts itself into tension and uses a helical geometry to generate contact forces which are large relative to the stem weight (Silk and Hubbard 1991). In view of this, a significant association between stem diameter and plant fitness in supported plants could have been expected. A possible explanation for the lack of adaptive value of stem diameter in the present study is that the variation of both the trait value and the growth environment was too small for such an association to be detectable (Endler 1986, Chapter 4). Studies reporting the contribution to offspring fitness of maternal environmental effects have been usually conducted under a number of environments or in nature (Schmitt et al. 1992, Sultan 1996, Galloway 2001).

There were no significant maternal environmental effects on the phenology (flowering time) or reproductive traits (seed size, seed number, percentage of reproductive biomass) of *I. purpurea* plants. It is therefore concluded that, unlike the majority of the reported cases of maternal environmental effects (Roach and Wulff 1987, Rossiter 1996, Weiner et al. 1997, Agrawal 2001), the observed effect of the maternal support environment on stem diameter was not mediated by seed size. The mechanism underlying this pattern remains to be elucidated. It is likely that the stem thickening of the offspring of supported mother plants is a consequence of qualitative differences in seed composition (primary or secondary metabolites, hormones, etc.) that carry over to mature stages.

At first sight, the fact that the maternal environment affected the plants only during their vegetative growth could also appear as confirming a characteristic of environmental maternal effects: their transitory nature (Miao et al. 1991, Wulff and Bazzaz 1992). However, results showed that the maternal support environment affected the relationship between seed size (mass) and seed number. Interestingly, the progeny of supported mother plants exhibited a phenotypic trade-off between seed size and number, whereas such a trade-off was not observed in the progeny of non-supported plants. This was true for both supported and non-supported progeny. The bio-

logical interpretation of this pattern is not straightforward. Assuming that the trade-off between seed size and number is the rule (Harper et al. 1970, Venable 1992, Westoby et al. 1992, Jakobsson and Eriksson 2000, Leishman 2001), it might be speculated why the progeny of non-supported mother plants is released from the constraint that produces the trade-off. Prostate plants of vines possess a lower number of reproductive buds compared to supported plants because the foraging for support involves an extension of internodes (Peñalosa 1983, Ray 1992, Gianoli 2001, 2002) and hence a reduction of node number (main stem length is not different in supported and non-supported plants of *I. purpurea*, in sun conditions: Gianoli 2002). This not only translates into a greater quantity of seeds in supported plants, but also determines that, in non-supported plants, the seed number is limited and thereby the investment into seed provisioning (seed mass) is relatively unconstrained. In other words, the availability of relatively few reproductive buds allows the allocation of resources into seed size without paying with seed number. This explanation, however, contradicts the classical view that seed size is a plant trait of limited plasticity (Harper et al. 1970) and hence differences in reproductive output are thought to come mainly through variation in seed number (Weiner et al. 1997).

Maternal environmental effects in plants are expected to be found in systems where the environmental factor is relevant for plant fitness and the offspring environment is predictable from the maternal environment (Donohue and Schmitt 1998). Both conditions are met in the case of the twining vine *I. purpurea* because physical support has a great impact on plant fitness and seeds are not dispersed far from the mother plant, allowing the exploitation of the same support resource utilised by the mother plant. Consequently, I hypothesised that the existence of maternal environmental effects of physical support would be verified in *I. purpurea* plants. This was confirmed for stem diameter and the relationship between seed size and number, and was observed in both supported and non-supported progeny. Thus, unlike earlier reports (Schmitt et al. 1992, Wulff et al. 1994), the expression of maternal environmental effects did not depend upon the environment of the progeny. It is important to underline that the adaptive nature of such maternal effects of support in *I. purpurea* was not clear. Further research including a broader range of environmental conditions or field trials could shed light on the latter.

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