

# 藤本植物 *Potentilla reptans* 叶对风和遮阴的响应

刘 芸<sup>1 2</sup>

(1. 西南大学资环学院 ,三峡库区生态环境教育部重点实验室 ,重庆 400716 ;

2. 乌特勒支大学植物生态学系 ,荷兰乌特勒支 800.84 ,3508 TB )

**摘要** 生长在一个密集植物群中的植株由于相互遮蔽而不可能对风的影响做出反应 ,因为这样的环境条件 (有限的光资源 )对由风导致的矮小表型植株的生长是不利的。为弄清在密集植物群体中生长的植株对风的响应 ,利用藤本植物 *Potentilla reptans* 的 10 种基因型做实验材料 ,在温室条件下 (光照强度为日光照的 50% ,红光/远红光 = 1.2 )模拟冠层遮阴 (相当于 15% 的日光照 ,红光/远红光 = 0.3 ) ,研究了藤本植物叶对风的响应。结果表明 ,*Potentilla reptans* 的 10 种基因型植株在冠层遮阴下 (低的光红/远红光 )都表现出典型的避阴生长响应 :较少的叶 (叶生物量少 ) ,长而细但硬度系数高 (higher Young 's modulus )的叶柄 ;而受风影响的植株 ,无论遮阴或不遮阴 ,其植株的叶相对较多 ,叶柄短、粗且柔韧性强 (lower Young 's modulus ) ,说明 *Potentilla reptans* 叶对风的响应并未因遮阴而被压抑 ,其可塑性变化不过是对复杂生境做出的一种生长权衡 :尽可能增强抗风能力 (矮壮 )和获取最大光能 (足够高而避免被遮光 ) ,即保证在存活下去的前提下获取最大的生长效率。

**关键词** 生物力学 ;适合度 ;可塑性 ;形态趋同性 ;避阴 ;藤本植物

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## Differential response to wind and shade in mother leaf of *Potentilla reptans*

LIU Yun<sup>1 2</sup>

1 Key Laboratory of Eco-environments in Three Gorges Reservoir Region (Ministry of Education) , College of Resources and Environment , Southwest China University , Chongqing 400716 , China

2 Department of Plant Ecology , Utrecht University , P. O. Box 800.84 , 3508 TB , Utrecht , The Netherlands

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**Abstract** : Responses to mechanical stress (such as wind) should be suppressed in dense vegetation since the resultant shorter stature would lead to low fitness. However , this point has been debated , i. e. it has been argued that in dense vegetations a sensitivity to mechanical stress might provide an additional cue to shade avoidance. For 10 different genotypes of the clonal plant *Potentilla reptans* , the effects of shade (15% of daylight with a red :far red ratio , R/FR of 0.3 vs. 50% daylight and R/FR of 1.2 ) and wind (0 or 40 daily brushes with a duster) on the mother leaf properties were investigated. All genotypes exhibited typical "shade avoidance" responses under shade , such as the production of fewer leaves with longer petioles , reductions in petiole diameter , and the production of more rigid petiole tissue (petioles with a higher Young' modulus). Wind-treated plants produced more leaves with shorter and thicker petioles made of more flexible tissue (lower Young's modulus). All responses to wind are different from responses to shade. Interestingly the responses to wind

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作者简介 刘芸 (1966 ~ ) ,女 ,四川资中人 ,博士 ,主要从事植物生态学及区域生态学研究. E-mail liuyun19970205@163.com

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**Biography** LIU Yun ,Ph. D. ,mainly engaged in plant ecology. E-mail liuyun19970205@163.com

in leaf of *Potentilla reptans* were opposite in nature to the responses to light.

**Key Words :** biomechanics ; fitness ; plasticity ; thigmomorphogenesis ; shade avoidance ; stoloniferous plant

To acclimate to heterogeneous environments , plants display an important performance trait : phenotypic plasticity. For example , in crowded vegetations , many plants typically have “shade avoidance” responses , such as slender stems , strong apical dominance with low branching intensity , and high shoot :root ratios compared to plants growing in more open conditions [1–7]. However , when plants are exposed to above-ground mechanical stimuli , such as wind , touching , or rubbing , they typically have shorter and thicker stems [8–12] , lower shoot :root ratios [11 , 13–16] , and they have an increased stiffness and rigidity of stems [12 , 17]. These responses , termed thigmomorphogenesis by Jaffe [18] increase the resistance of plants to mechanical failure [16 , 19] and seem to be in the opposite direction to shade avoidance [12].

There is an interesting debate about interactive effects of shade and wind on plants. Some studies argue that in dense canopies , where plants compete for light , responses to wind (thigmomorphogenesis) should be suppressed [11 , 20] as the reduction in height growth would lead to reduced fitness ; however , other studies [1 , 21 , 22] have been arguing the opposite , that in dense vegetations plants are protected from wind and that sensitivity to this lower level of wind (hence enhanced height growth) leads to increased fitness ; i. e. also plants growing in dense stands should be sensitive to variation wind. According to the best of my knowledge , however , these studies just used erect plants and only at the individual level. No study has yet studied responses of stoloniferous plants to mechanical stress. Stoloniferous plants are more flexible in regulating the number and horizontal placement of leaves , leaf petioles serve as vertical support structures , and each leaf is separately supported [23–25] ①. These differences from erect plants in architecture probably have different response to mechanical stress. And , an analysis at the genotypic level [26–28] is even more valuable for experimental studies on plasticity , because in coarse-grained environments , reaction norms are properties of genotypes , not individuals , and effects on plasticity can only be measured at the genotype level [29]. The aim of the present study was to investigate , more precisely , the effects of shade (15% of daylight with a red :far red ratio , R/FR , of 0.3 vs. 50% daylight and R/FR of 1.2) and wind (0 or 40 daily brushes with a duster) on the leaf properties of 10 genotypes of the stoloniferous plant *Potentilla reptans*. The experiment was conducted in a greenhouse , i. e. a wind-protected environment , and the control plants can therefore be interpreted as wind-shielded plants [12]. The hypothesis was tested that thigmomorphogenesis was not suppressed under shade. If so , we expect that in dense stands , plants subjected to a wind-treatment , will produce shorter and thicker petioles , and more leaves relative to their counterparts. Quantifying these effects is a crucial step toward understanding the adaptive significance of thigmomorphogenesis and shade avoidance responses and their possible interaction [12].

1 Materials and methods

1.1 Plant material

During spring 1990 to 1997 , the stoloniferous , rosette-forming herb *Potentilla reptans* L. (Rosaceae) known 12 genetic identities were collected separately from a natural population in different habitats of the Netherlands and allowed to proliferate successively in the experimental garden of Utrecht University. Established rosettes produce horizontally growing stems (i. e. primary stolons) , which may root at their nodes and thereby give rise to potentially

① Dong M. Foraging through morphological plasticity clonal herbs. PhD thesis Utrecht University , 1994.

independent daughter rosettes<sup>[25, 30–32]</sup>. Unfortunately , genotype 6 and 11 were lost during cultured.

1.2 Experimental methods

Similar-sized rosettes of ten genotypes were taken from this garden population and used as experimental material. For clarity , the rosettes of *Potentilla reptans* plants were defined in such a way that the stolons were excluded , and the mother rosette is considered as the one that was initially planted. The leaves of a rosette are defined as the petiole and lamina together<sup>[30, 31]</sup>. The rosettes were transplanted into plastic trays (15 cm × 15 cm × 100 cm ) filled with river sand in the greenhouse of this garden , watered daily with tap water , and fertilized weekly with a nutrient solution which had previously been shown to provide non-limiting nutrition for *P. reptans*<sup>[32]</sup>. This watering and fertilization regime was continued until the end of the experiment. After 4 weeks , offspring ramets of ten genotypes were excavated and size-standardized by removing all but the youngest unfolded leaf from the rosettes , and by cutting roots to a length of 3 cm. Ramets were then planted into plastic pots (13 cm in depth and diameter ) filled with river sand supplied with water and nutrients as described above. After 2 weeks , 32 similar-sized plants of each genotype were randomly divided into four groups (8 replicate plants per group of each genotype ) and subjected to a combination of canopy shading (15% of daylight with a red far red ratio , R/FR , of 0.3 vs. 50% daylight and R/FR = 1.2 ) and a wind-treatment (0 or 40 daily brushes with a duster ) in a 2 × 2 factorial design. Control plants (HLc ) were exposed to 50% daylight and R/FR = 1.2 conditions shading by the greenhouse roof with no wind treatment. Wind-treated plants (HLm ) were exposed to the same as control light conditions with 40 daily brushes with a duster . In two shading treatments , whole plants were grown in cages covered by one layer of a plastic film (Lee Colortran International , Andover , UK ; no. 122 ) , which simulating canopy shading give 15% of daylight with R/FR of 0.3 (LLc ) , and one (LLm ) of the shading treatments additionally gave 40 daily brushes with a duster. Light was measured with a LI190 quantum sensor (LiCor , Lincoln , NE , USA ) connected to an LI1000 data logger. Red (655 — 665nm ) and far red (725 — 735nm ) light was measured with an LI1800 spectrometer. Wind-treatet plants were individually vibrated by applying 40 brushes for 40 s in the form of a mechanically operated duster (the tip of duster was covered with thick silks to prevent abrasion of epidermal cells ) with the same tense and speed (one brush s<sup>-1</sup> ) to simulate the effect of wind (the treatment was given once a day ).

Shade cages were constructed in a way , which allowed air circulation within cages and facilitated exchange of air with the surrounding environment in the greenhouse. Microclimatic measurements revealed no differences in temperature and air humidity between treatments. During the experiment , the position of treatments between control and wind , shadings were changed once a week to minimize the effects of sites.

The harvest was conducted 30 days after the start of the treatments. Plants were cut at ground level and divided into petioles , leaf lamine and stolons. The total mother leaf number was counted ; the length and basal diameter of the longest petiole of each plant were measured to the nearest 0.1 mm with a digital ruler and calliper ; mother leaf lamina area was measured with a leaf area meter (LI 3100 , LiCor , Lincoln , NE ). Dry masses of above petioles and lamine were determined after oven drying for at least 72 h at 70℃ . In addition , the Young ’s elastic modulus (*E* , MN m<sup>-2</sup> ) of the longest petiole of each plant was measured on the basal part of the petiole. The petioles were enclosed in plastic bags with moist filter paper and immediately put into a freezer at about 8℃ , brought to the laboratory within 30 min of collection (during the transport the temperature in the transport box was kept at the temperature at 8℃ , and all measurements were completed within 1h after cutting. In the actual measurement of Young ’s modulus , we used an Instron universal testing machine (5542 , Instron , Canton , MA , USA ). Sections of the basal part of the petiole were placed on two fixed pins , which were separated by a given distance *L* (in cm). The petiole sections were bended by a third pin , placed exactly between the two fixed pins. This third pin moved

with a controlled speed (given in  $\text{mm min}^{-1}$ .) Both the imposed force  $P$  (in Newtons) and the deflection  $\delta$  (in mm) were instantaneously measured by the equipment. The Young's modulus  $E$  (in MPascal) was automatically calculated from the linear part of the force-deflection curve. For a beam with free ends, the relation between deflection and force is given by<sup>[3]</sup>

$$\delta = (P L^3) / 48 E I$$

where  $E$  is the Young's modulus and with  $I$  the second moment of area

$$I = 16/175 a^3 b$$

That is, the cross section of the petiole was assumed to have a parabolic form, with 'long' axis  $a$  and width  $2b$  [delete  $x$ -symbol] (both  $a$  and  $b$  measured in mm)<sup>[9]</sup>.

1.3 Statistical Analysis

A three-way ANOVA was used to test for differences in response parameters, with shade ( $df = 1$ ), wind ( $df = 1$ ) and genotype ( $df = 9$ ) as fixed factors. Data transformation was based first on Levene's test for quality of variance second on the Shapiro-Wilk test of normality.

2 Results

2.1 The longest petiole length

The treatments had significant effects on petiole length (Fig. 1, Table 1). Shade increased length regardless of wind, while the wind-treatment decreased it regardless of shade. All genotypes displayed the same responses in petiole length to shade and wind. No significant interactive effects on petiole length were observed between low light and wind, and between low light and genotype. There was a significant interactive effect on petiole length between wind and genotype, suggesting differences in thigmomorphogenic responses between the 10 genotypes (Table 1).

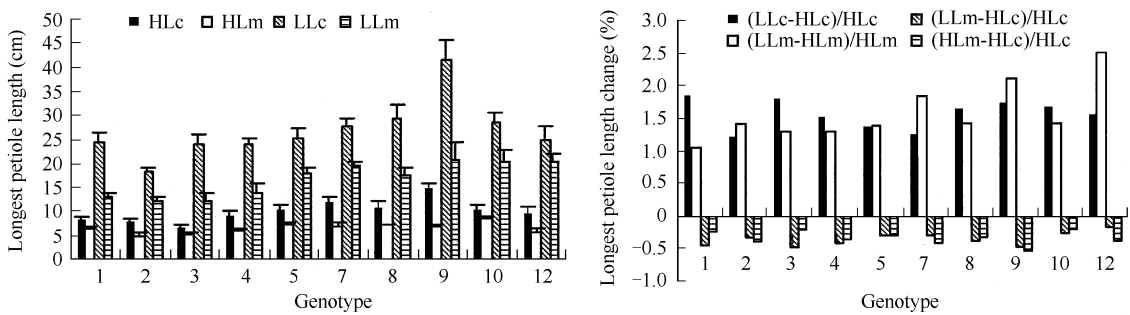


Fig. 1 Average longest petiole lengths and their changes in four treatments for ten genotypes. HLC = High light control; HLM = High light and wind; LLc = Low light control; LLm = Low light and wind. The change in length due to light effects is calculated by  $(LLc-HLC)/HLC$ ,  $(LLm-HLM)/HLM$  and for thigmomorphogenic effects the calculation is given by  $(LLm-LLc)/LLc$ ,  $(HLM-HLC)/HLC$ . Bars indicate standard errors ( $n = 8$ ); the same below

2.2 Petiole diameter

The shade and wind treatments had significant effects on petiole diameter (Fig. 2, Table 1). Low light decreased the petiole diameter in all genotypes, while wind increased it (except for genotype 2, 3 and 10 under the high light treatment). No significant interactions were observed between low light and wind, between low light and genotype, or between wind and genotype.

2.3 Petiole Young's modulus

Both treatments had a significant effect on petiole Young's modulus (Fig. 3, Table 1). Low light increase Young's modulus (except for genotype 4, 5 and 9), while wind decreases it (except for genotype 4, 5 and 12 under low light). No significant interactions were observed between low light and wind, between low light and

genotype , between wind and genotype.

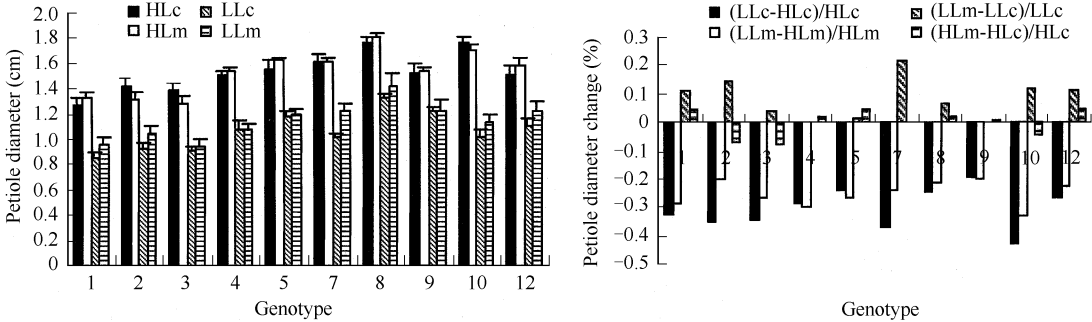


Fig. 2 Average longest petiole diameters and their changes in four treatments for ten genotypes

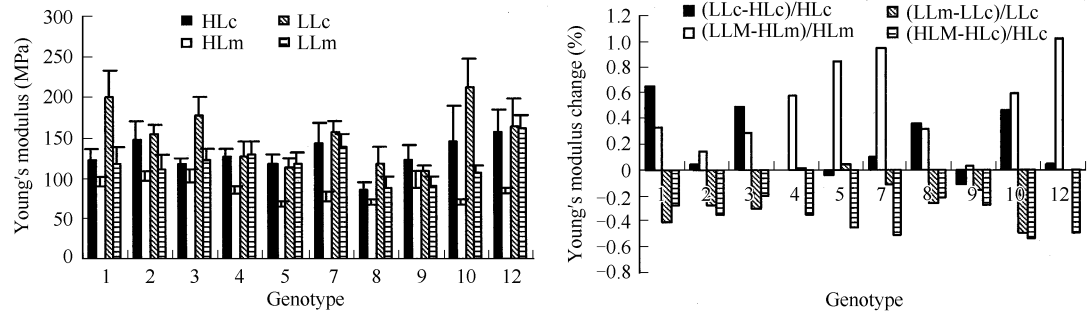


Fig. 3 Average petiole Young's modulus and their changes in four treatments for ten genotypes

2.4 Leaf number

The number of leaves in the mother rosette was reduced by shading. Wind on the other hand tended to increase the number of leaves in the mother rosette , and this effect was much stronger in the shading than in the non-shading treatment , as indicated by the significant wind and light interaction (Table 1 ).

Table 1 Results ( P values ) of analysis of variance with genotype (df=9 ) and wind ( df=1 ) and light ( df=1 ) as factors (for the genotype . wind interaction and genotype × light interaction df=9 ; for the wind × light interaction df=1 )

Item	Genotype	Wind	Light	Genotype × wind	Genotype × light	Wind × light
Total leaf number	0.000	0.000	0.000	0.541	0.291	0.001
Mother leaf area	0.000	0.034	0.000	0.953	0.074	0.009
Mother leaf dry mass	0.000	0.063	0.000	0.656	0.000	0.013
Specific leaf area (SLA )	0.000	0.007	0.000	0.000	0.000	0.040
The longest petiole length	0.000	0.000	0.000	0.042	0.624	0.424
The longest petiole diameter	0.000	0.049	0.000	0.961	0.083	0.091
The longest petiole mass	0.000	0.000	0.001	0.123	0.749	0.877
PetioleYoung's modulus	0.003	0.000	0.000	0.313	0.469	0.257

SLA = mother leaf area per unit mother leaf biomass

2.5 Leaf area and leaf mass in the mother rosette

Low light significantly decreased both the leaf area and leaf dry mass in the mother rosette , however , the degree of a reduction in leaf dry biomass was more than that in leaf area (Fig. 4 , Table 1 ) , thus plants had a higher SLA (leaf area per unit leaf mass ) under low light than under high light (Fig. 5 , Table 1 ). Under high light , the wind-treatment significantly decreased the leaf area of the mother rosette and marginally decreased the leaf dry mass ;but there was no consistent effect of the wind-treatment on the leaf area and leaf mass of the mother rosette under low

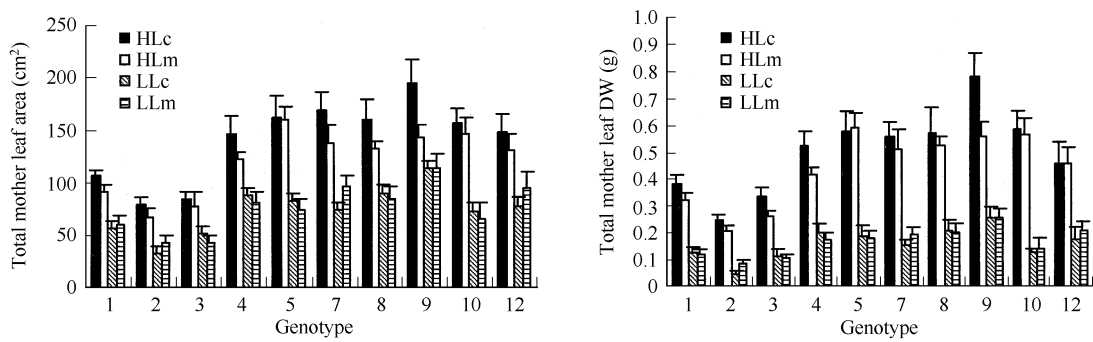


Fig. 4 Average total mother leaf area and total mother leaf DW in four treatments for ten genotypes

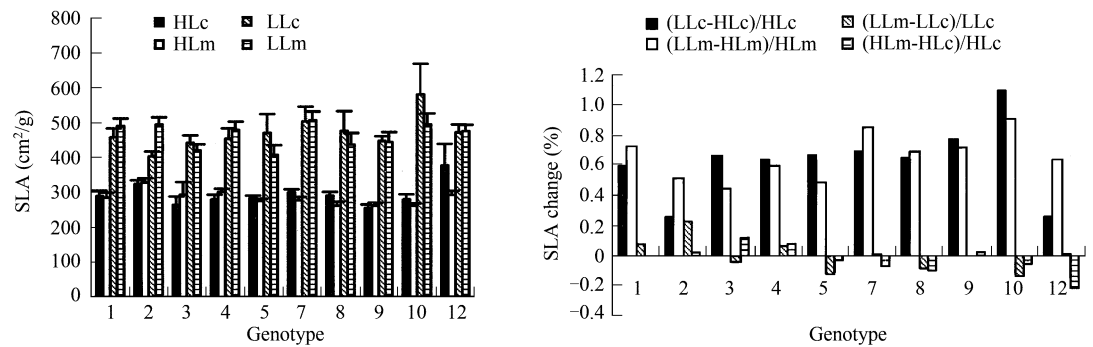


Fig. 5 Average SLA (Special Leaf Area) and their changes in four treatments for ten genotypes

light. There were significant interactions in SLA between wind and light ,between genotype and light ,and between wind and genotype ,suggesting that with respect to these traits the ten genotypes differed in their response to shade and wind.

3 Discussion

Our results demonstrate that the effects of shade and wind on morphology were independent and additive. For both the full light plants and the plants grown under shade , wind-treated plants had shorter , thicker petioles with lower Young’s modulus than untreated plants , which suggests that thigmomorphogenesis did not differ between high light and low light. These results are consistent with those of Mitchell [22] and Anten *et al.* [21] and contrary to those of Ashby *et al.* [20] and Henry and Thomas [11] ,who suggested that thigmomorphogenesis is suppressed when plants grow in dense stands (which they interpreted as an adaptive response because a shorter stature would confer a large disadvantage under those shade conditions ). It is well known ,however ,that wind exposure generally increases with plant height ;consequently ,also for plants grown in the shade an inappropriate stem elongation increases the risk of mechanical failure [52–55] . If maintaining the capacity for plasticity is costly , the optimal plastic response will be a compromise between the reaction norm expressing the optimal phenotype in each environment and the reaction norm with the lowest cost [56] . The adaptive value of plasticity to canopy shading may thus be diminished because of stem and/or petioles buckling or uprooting.

In our experiment , wind-treated plants had a lower Young’s modulus than the plants not subjected to such a treatment. This result is consistent with those of Goodman and Ennos [50] : more flexible stems (i. e. petioles with a lower Young’s modulus ) bend more easily in the wind and hence convey a smaller bending moment to their bases , which can increase the resistance to wind. On the contrary , plants grown under shade had a higher Young’s modulus compared to plants grown under high light (except for genotype 5 , 12 ). Furthermore , these shaded plants had quite

a longer petiole length and a smaller diameter. So ,we see that to maintain mechanical stability ,i. e. to prevent the petiole from falling over ,the plants increased their Young’s modulus. That is ,for example ,plants grown in canopy shading are longer and therefore might have more parenchyma cells (Puijalon , *et al* , 2006 , 14<sup>th</sup> New Phytologist Symposium<sup>①</sup> ). Because of the larger amount of parenchyma cells ,the mass density is lower. And ,because of this low mass density ,one would expect a lower Young’s modulus. However ,if the turgor pressure in this cells is increased ,relative to the petioles grown in light ,then this increase in pressure can lead to an increase in Young’s modulus ,and therefore maintains the mechanical stability. This could explain our above results ,in other words ,changes in petiole length are related with changes in the petiole anatomy but not necessarily to the expense of mechanical stability<sup>[11]</sup>.

Leaf architecture plays a major role in the light-harvesting efficiency of herb canopies ;petiole length even plays a dual role in leaf light harvesting<sup>[38 39]</sup> :For leaves organized in a rosette ,an increase in petiole length can decrease the clumping ,i. e. it can decrease the mutual overshadowing of the leaves. However ,an increase in petiole length may also lead to an increase in the lamina angle with respect to the horizontal ,and hence it can lead to a decrease in the average light intensity on the leaves. That is ,according to beam theory ,lamina deflection from the horizontal increases with the cube of petiole length<sup>[40 41]</sup> ,suggesting that modest changes in petiole length may have a large impact on light intensity. In herbaceous plants ,the petioles of stoloniferous plants and the internodes of erect plants can be regarded as analogous organs ,and then their strong increase in length due to shading can be viewed as a mechanism to try to enhance light harvesting<sup>[25]</sup>. Due to their low shade tolerance<sup>[1 34]</sup> ,rapid stem and/or petiole elongation may be especially pronounced in colonizing annual species like *Abutilon* and *P. reptans* ,growing under crowded conditions with strong vertical light gradients ,so that there is a low light availability at the bottom and increasingly higher light supply in the upper parts of canopy<sup>[35]</sup>. In this study ,canopy shading (low R/FR ) produced taller ,thinner petioles (table 1 ) ,indicating a trade-off between petiole height and diameter growth<sup>[1 42]</sup>. In this experiment ,wind-treatment had an effect on plants that was opposite in nature to that of canopy-shading ,producing shorter ,thicker petioles (Table 1 ). Plant responses to wind most likely increase the mechanical stability of plants<sup>[12 16 19]</sup>. That is ,petioles have to carry their own weight as well as the weight of leaves. So ,anyhow ,a minimum investment in carbohydrates is needed to guarantee a certain strength of the petiole to prevent buckling or breaking<sup>[45]</sup> ;Plants grown in crowded conditions experience a certain wind-shielding ,while plants grown under open field conditions are subjected to an extra loading in terms of wind and/or precipitation<sup>[46 47]</sup> requiring an extra investment in carbohydrates to resist mechanical failure. In open field situation there is a very strong increase in wind speed with height above the vegetation<sup>[12 48 49]</sup>. So ,plants with short stem and/or petiole therefore experienced less mechanical stress<sup>[12]</sup>. In the experiment ,it was found that the mean petiole diameter of winded plants was thicker than that of untreated plants (except for genotype 2 ,3 ,10 under high light ;Fig.2 ). This result is consistent with most literature on mechanical stress effects :mechanical stimuli tend to result in increased stem diameter growth relative to height growth<sup>[9 10 12]</sup> ,but the observed effects are contrary to those of Henry and Thomas<sup>[11]</sup>.

Shading reduced the number of leaves in the mother rosette. Mother SLA (leaf area per unit leaf biomass ) was higher in low light plants than in high light plants. The result is consistent with the low leaf thickness typically exhibited by shade leaves and is thought to minimize internal shading of chloroplasts<sup>[11 51]</sup>.

Overall ,changes in leaf properties hints at important trade-offs between light capture and stability ,this apparent

① Puijalon S ,Bornette G ,Sagnes P. Plastic responses to mechanical stress :adaptive significance of morphological and architectural adjustments (abstract ). 14th New Phytologist Symposium ,the Royal Society ,London ,UK. 2006 ,7

compromise possibly reflects conflicting requirements in terms of light capture and mechanical stability for biomass investments in petiole length and diameter , and in leaf thickness and leaf area. The morphological characteristics are generally employed in selection for genotypes of more adaptive variable environments ; such compromises may need further consideration at a genotype level <sup>[57]</sup> .

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