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Height convergence in response to neighbour growth: genotypic differences in the stoloniferous plant *Potentilla reptans*

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Summary

- Using a new experimental set up, the way in which height growth of stoloniferous plants is adjusted to that of their neighbours, as well as differences between genotypes in their ability to keep up with neighbour height growth were tested.
- Five *Potentilla reptans* genotypes inherently differing in petiole length were subjected to three experimental light gradients, involving light intensity and red : far-red ratio. Each plant was placed in a vertically adjustable cylinder of green foil, and the treatments differed in the speed of cylinder height increase and final height.
- Total weight of plants decreased from the 'Slow' to the 'Fast' treatment, while petiole length increased. Leaves reaching the top of the cylinder stopped petiole elongation, resulting in similar final heights for all genotypes in the 'Slow' treatment. In the 'Fast' treatment only the fastest-growing genotype maintained its position in the top of the cylinder and genotypes differed strongly in final height within the cylinders.
- Plants adjust their height growth to that of the surrounding vegetation, leading to height convergence in short light gradients that slowly increase. These adjustments and genotypic differences in ability to keep up with fast-growing neighbours can influence the outcome of competition for light.

Key words: clonal plants, height convergence, height growth, light gradient, neighbours, petiole elongation, phenotypic plasticity, shade avoidance.

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Introduction

Game theoretical models predict that with increasing density plants should invest more mass in height in order to maintain their position in the canopy and prevent being shaded (Givnish, 1982, 1995; Iwasa *et al.*, 1985). The fitness benefits of this response have been experimentally demonstrated in various studies (Schmitt *et al.*, 1995; Dudley & Schmitt, 1996; Pierik *et al.*, 2003). These game theoretical models also predict that plants should not grow much taller than the surrounding vegetation as the minimal increase in light capture would not compensate the additional cost. This suggests that in dense stands a so-called height convergence will occur, where taller plants in the canopy have about the same height irrespective of other size measures and associated growth potential. Indeed, studies in dense stands of erect plants have documented such height convergence patterns (Weiner & Thomas, 1992; Nagashima & Terashima, 1995). This implies that plants should be able to adjust their rate of vertical spacer elongation to different rates of height increment of the surrounding vegetation.

Many studies have investigated the mechanisms through which plants respond to their neighbours. Generally, a reduced red : far red (R : Fr) ratio of light reflected by neighbours is believed to be a prominent cue (Ballaré *et al.*, 1997; Casal *et al.*, 2003), but other factors such as neighbour-produced

ethylene (Pierik *et al.*, 2006) and wind shielding (Telewski & Jaffe, 1986; Anten *et al.*, 2005) are also thought to play a role. Plants adjust their height growth using these cues, which can differ in strength and quality depending on the vertical position of the plant. Individuals that are positioned deeper in the canopy will experience strong photomorphogenetic signals that induce height growth (Weiner & Fishman, 1994; Yokozawa & Hara, 1995; Berntson & Wayne, 2000). At the top of the vegetation these signals are less strong, except for wind force, and further height growth is reduced (Vince-Prue *et al.*, 1976; Casal & Smith, 1988; Lötscher & Nösberger, 1997; Anten *et al.*, 2005). As a result plants that are initially shaded by taller plants may realize a stronger height growth than plants at the top, and these plastic responses work to mitigate the variation in height between individuals (Aphalo *et al.*, 1999; Ballaré, 1999). If the ability to respond plastically is reduced, for example through a mutation in the phytochrome, blue light photoreceptor or ethylene sensing, height inequality within the vegetation increases (Ballaré *et al.*, 1994; Ballaré & Scopel, 1997; Pierik *et al.*, 2004).

Many plant species show intraspecific differences in height growth and the plasticity therein, suggesting genotypic differences in height growth potential (Dudley & Schmitt, 1995; Turkington, 1996; van Kleunen & Fischer, 2001). If plants grow in vegetation that grows inherently slowly, genotypes with a low height growth potential or low height growth plasticity can probably still reach the top of the canopy, and height convergence may occur. However, plants of such genotypes will not be able to position their leaves in a high-light environment, in vegetation that grows rapidly. Since a small lag in height growth can result in low light availability when plants are growing in crowded vegetations (Ballaré *et al.*, 1988), genotypic differences in height growth plasticity and height growth of the surrounding plants can have large effects on plant performance.

Most studies that have experimentally investigated plasticity in height growth in response to shade have been carried out in a vertically homogeneous light environment using shade cages. Under such conditions height growth is probably maladaptive since it does not place the leaves in a better light climate (Schmitt, 1997; Leeflang *et al.*, 1998); thus, such studies do not properly evaluate the benefits of increased height. Others have used light gradients of fixed length (Huber & Wiggerman, 1997; Leeflang *et al.*, 1998; Weijschede *et al.*, 2006), mimicking the instantaneous light gradient that occurs in most dense herbaceous vegetation (Monsi & Saeki, 1953; Grime & Jeffrey, 1965). In these situations the performance of the plants depends only on the response of the plant itself and the experiment does not test the effects of a change in the light environment around the plant. The benefits of height growth are thus overestimated, as even a minimal height increment places the leaves in better light climate. In a dense vegetation of hemicryptophytes or annuals, all plants tend to increase in height together early in the season (Fliervoet, 1984), and the pay-off in terms of light capture to individuals increasing in height will depend on the general increase in height of the canopy as a whole. Therefore the experimental setting should mimic the surrounding vegetation's increase in height with time. Such a setup would also allow direct testing of the hypothesis that plants can adjust their rate of vertical spacer elongation to different rates of height increment of the surrounding vegetation by manipulation of the speed with which the light gradients increase in height.

Fine-tuning of the vertical positioning of leaves within upgrowing vegetation might be especially important for stoloniferous plants. Whereas in erect-growing plants increased investment in stem can be seen as an investment for future height of later-formed leaves, each new leaf of a stoloniferous plant has to start at the bottom of the light gradient. Height growth of such species might therefore be more costly than that of erect plants, because each leaf is supported separately from ground level upwards, which in terms of biomass use for vertical support is less efficient than the production of a single stem bearing several leaves (Liu *et al.*, 2007). Because the ability to elongate the petiole decreases with leaf age and does not come back once the lamina has reached high light conditions (Leeflang, 1999), the height of a lamina is more or less fixed once the petiole has stopped elongating. This means that when the vegetation around it is getting taller over time, existing leaves are shaded and new leaves will have to be formed which need to exhibit stronger elongation to reach the top of the canopy.

The stoloniferous plant *Potentilla reptans* was used in a new experimental setup in which surrounding vegetation with different speeds of height growth was mimicked through the use of vertically adjustable cylinders of light-filtering plastic sheet. The experimental period was equal for all treatments, so the treatments differed not only in the rate of height increase, but also in the final length of the cylinders. Genotypic differences in responses were studied by using five genotypes that were known to differ in the longest petiole in other shading experiments (Liu *et al.*, 2007; P. J. Vermeulen, unpublished).

Our goal was to investigate whether the plants adjusted their height growth to that of the surrounding light gradient. We expected that if the rate of cylinder height increase was relatively slow, and thus the resulting light gradient short, all genotypes would be able to put new leaves at the top of the gradient throughout the experiment but would not outgrow it (i.e. show height convergence despite differences in biomass and morphological traits such as the number of leaves, the root mass ratio, specific petiole length and specific lamina area). We also expected that when the shading gradient increased more rapidly in height, not all genotypes would succeed in reaching the top of the light gradient and that a height hierarchy would develop among them.

Materials and Methods

Plant material

Potentilla reptans L. is a stoloniferous herb found at moderately disturbed, productive pastures, mown grasslands, lake and river shores, road margins and several other man-made habitats (van der Meijden, 2005). The plant produces sympodially growing stolons with rooted rosette-forming ramets on its nodes. In the absence of physical disturbance the ramets remain interconnected throughout one growing season (Stuefer *et al.*, 2002). Each leaf consists of five to seven palmately arranged leaflets borne on a vertically orientated petiole attached to the ground rosette. The height of an individual leaf is thus the result of the length of its petiole (Huber, 1996; Stuefer & Huber, 1998).

A set of 10 genotypes was collected in 1997 from 10 different locations in the Netherlands and kept in the botanical gardens of Utrecht University (the Netherlands). From this set five genotypes were selected in 2006 on the basis of their potential petiole length: two genotypes with the shortest petioles (genotypes B and C), two genotypes with long petioles (genotypes F and I), and one genotype with an intermediate petiole length (genotype D). These characteristics had been determined in two previous experiments: an experiment with a light gradient of fixed length (P. J. Vermeulen, unpublished data) and an experiment with a vertically homogeneous light environment using shade cages (Liu *et al.*, 2007). Identification letters of the genotypes are the same as used in other experiments (J. F. Stuefer *et al.*, unpublished).

Experimental set up

On the 6 July 2006, 30 young ramets of similar size from each of these five genotypes were taken from the stock populations. All leaves except for the two youngest unfolded leaves were removed and the roots were cut to a length of 5 cm. The ramets were planted in pots with a diameter of 13 cm and height of 11 cm, filled with a 1 : 1 mixture of river sand and compost, with slow release fertilizer (Osmocote plus; Grace Sierra International, Heerlen, the Netherlands) to provide an added 13 mg nitrogen (N) wk^{-1} per pot. On the 10 July, 24 pots with ramets of similar size per genotype were selected. Six were used for the measurement of start biomass. The other 18 were randomly assigned to three treatments: light gradients that increase in height slowly (S), at medium speed (M) or fast (F).

The pots were placed on a water tray placed on 50-cm high columns, which were standing in three rows on a table in a plastic glasshouse (photosynthetic photon flux density (PPFD) 80% of outside PPFD, no change in R : Fr) in the botanical gardens. Around each column a 58.5 cm long, 14 cm diameter cylinder of green filter (Lee colortran international, Andover, UK; #139 HT primary green) was placed. Each cylinder was attached to a chain, which was hanging from a cable above the set up (Fig. 1). At the start of the experiment the top of the cylinder was 4.5 cm above the surface of the pots and the leaves reached to 1.5 cm beneath the top of the cylinder. All pots were randomly positioned in one of the rows on the table.

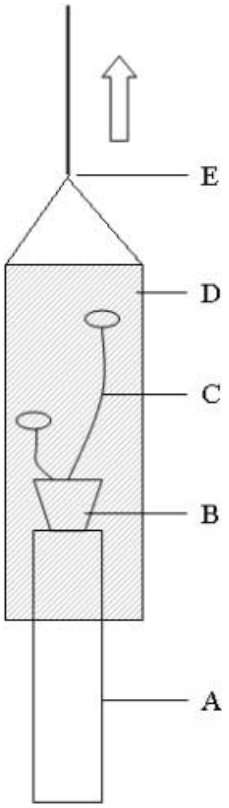

Fig. 1 Experimental setup. (A) Column, on which pot (B) is standing, (C) petiole of plant, (D) green filter cylinder around the plant, (E) chain, which is attached to the cable hanging above the table.

Starting on the 12 July, each cylinder was moved upwards three times a week, by moving the cylinder along the chain, placing the top 0.75 cm (Slow treatment), 1.5 cm (Medium treatment) or 2.25 cm (Fast treatment) higher above the soil surface. The light gradients thus increased in height at a speed of 2.25, 4.5 and 6.75 cm wk^{-1}. Measurements in a competition experiment with the full set of 10 genotypes had shown that height growth early in the season is ±4.5–6 cm wk^{-1}, with an average maximum height of 32 cm (P. J. Vermeulen, unpublished). As the experimental period was equal for the three treatments, this resulted in light gradients that differed in final length. Relative PPFD inside the cylinders was measured using a Li-185A photometer (Li-Cor, Lincoln, NE, USA), with a ceptometer (Delta-T Devices, Cambridge, UK) to simultaneously measure light at the top of the light gradient. The relative PPFD declined steeply to *c.* 22% over the first 10 cm from the top of the cylinders. Close to the bottom of the cylinders, at 50 cm depth, relative PPFD was on average 2.8% (Fig. 2a). The different speeds of the cylinders thus created three light gradients that differed in the rate at which

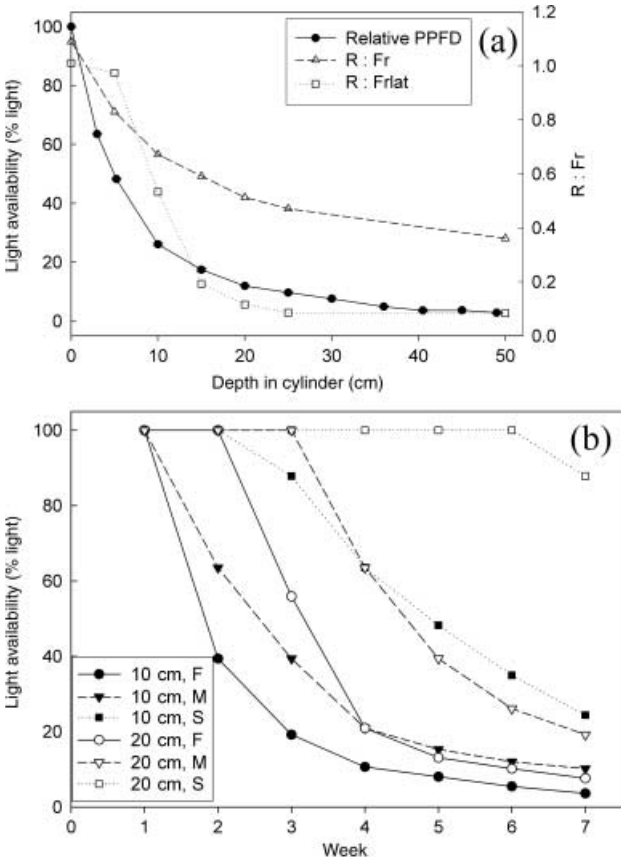

Fig. 2 Light characteristics of the light gradient with increasing depth in the shade cylinder. (a) Light availability (as % of light measured at the top of the light gradient), R : Fr ratio with sensor facing upwards and R : Fr ratio measured sideways (R : Fr_{lat}); PPFD, relative photosynthetic photon flux density. (b) Decrease of light availability over time of a hypothetical leaf placed at 10 cm height and 20 cm height for the three treatments Slow (S), Middle (M), and Fast (F). Note: (a) is based on depth, measured from the top of the cylinder downwards, (b) on height, measured from the soil surface.

the light availability at a certain height changed over time (Fig. 2b). The R : Fr ratio in the gradient was measured using a Li-Cor 1800 spectroradiometer connected to a remote cosine receptor. The R : Fr ratio was 1.09 at the top of the gradient, while it was 0.36 at the bottom (Fig. 2a). The R : Fr ratio of horizontally directed radiation inside the cylinders was also measured. This lateral R : Fr ratio (R : Fr_{lat}) decreased strongly below the top 5 cm to very low values lower down in the gradient (Fig. 2a). The R : Fr gradient showed similar differences over time between treatments as the relative PPFD did (data not shown).

The pots were watered daily. Each week the length of all petioles was measured (apart from week 6). Stolons produced by the rosettes were cut off to prevent crowding effects within the cylinder and dried. The experiment was harvested after 7 wk. Of each individual leaf we measured the petiole length, and the lamina area using a LI-3100 (Li-Cor) leaf area meter. We washed the roots free from soil particles. All parts were dried at 65°C for at least 3 d and then their mass was measured. From the individual leaf characteristics and the root biomass we calculated the total petiole mass ratio (PMR, total petiole mass : total plant mass), the lamina mass ratio (L_{am}MR, total lamina mass : total plant mass), the root mass ratio (root mass : total plant mass) and the stolon mass ratio (total stolon mass produced during the experiment : total plant mass). From the total lamina area and the total lamina mass we calculated the specific lamina area ($SL_{am}A$, m^2 lamina area g^{-1} lamina mass) and from the petiole characteristics the Specific Petiole Length (m petiole length g^{-1} petiole). All these characteristics are thus mean whole-plant trait values and will indicate how the treatments affected the allocation and morphology of the plants.

Statistics

Analysis of the start biomass, using a one-way ANOVA with genotype as fixed factor, showed no significant differences between the genotypes. Also, no difference between the genotypes in the height above the soil surface at the start of the experiment was found. Repeated measures ANOVAs were performed to test for differences in the length of the tallest petiole over time, one two-way repeated ANOVA with treatment and genotype as fixed factors (the genotypes were chosen on the basis of their height growth characteristics from a pool of 10 genotypes), and repeated ANOVAs for each separate treatment. The tallest petiole length is defined as the length of the tallest petiole at each census. The tallest petiole was a different, later-formed petiole every week.

To test for differences between treatments and genotypes and the genotype × treatment interaction a two-way ANOVA with both genotype and treatment as fixed factor was used for the five characteristics measured at the end of the experiment. Since the mass ratios are interdependent, the significance levels were adjusted in separate two-way ANOVAs with the four mass ratios as dependent variable, using a Bonferroni correction. To test if, within treatments, the genotypes differed in their tallest petiole length at final harvest, three separate one-way ANOVAs were performed with genotype as fixed factor. If necessary, data were transformed to meet the demands of normality and homoscedasticity (see Tables).

In our setup, differences between treatments may be caused by the confounding effect of the differences in both the rate of height increase and the absolute height. Therefore, in order to separate the effects of height growth rate of the cylinders from the absolute height, a two-way ANOVA was performed, with tallest petiole length at common cylinder height as dependent variable. This tested whether the genotypes responded differently to the rate of height increase alone. For the Medium treatment the tallest petiole length at week 7 was used for this analysis, while for the Fast treatment the length at week 4 was used. A one-way ANOVA showed that at these two different points in time the height of the cylinder was not

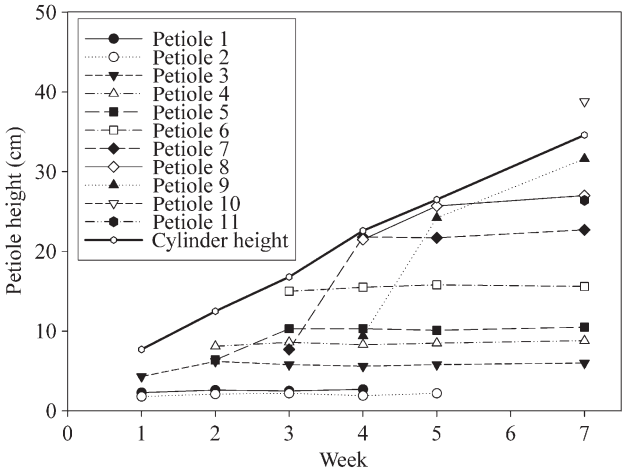

Fig. 3 Petiole height development through time of a *Potentilla reptans* genotype 6 plant in the Medium treatment. Order of petioles is the order in which they were formed. The tallest petioles at each census of this plant are 3, 4, 6, 7, 8, and 10, respectively.

significantly different between the two treatments ($F = 2.61$, $P = 0.101$). It was not possible to include the Slow treatment in such a comparison, because there were no time-points at which the cylinder height in all three treatments was not significantly different.

Results

All genotypes followed the same general pattern of leaf placement in response to the three treatments (see Fig. 3 for an example). Petiole elongation of a single leaf lasted between 1 wk to a little over 2 wk. With time, newly formed leaves were placed above the older leaves. As a result, the tallest petiole was a different petiole at every census. The tallest petiole of the previous week had more or less stopped elongating by the time the next census took place and did not restart elongation when the shading cylinder was moved up.

In general, at final harvest of the plants petioles were tallest in the Fast treatment, and petioles were taller in the Medium treatment than in the Slow treatment (Fig. 4, Table 1). The tallest petiole at harvest of genotype F, however, did not differ in length between the Fast and Medium treatment. Total plant weight decreased from the Slow to the Fast treatment (Fig. 5a), as did the number of leaves that were produced during the experiment (Fig. 5b). Plants invested relatively more biomass in petioles and laminas, and less in roots and stolons from the Slow to the Fast treatment (Fig. 5, Table 1). specific petiole length (SPL, Fig. 5 g) and specific lamina area ($SL_{am}A$, Fig. 5 h) were also greater in the Fast treatment.

The repeated measures ANOVA on the tallest petiole lengths showed a significant time × treatment × genotype interaction (Table 2), showing that treatment had an effect on the difference between genotypes in the height at which they placed their leaves with time. Analysis of the tallest petiole length

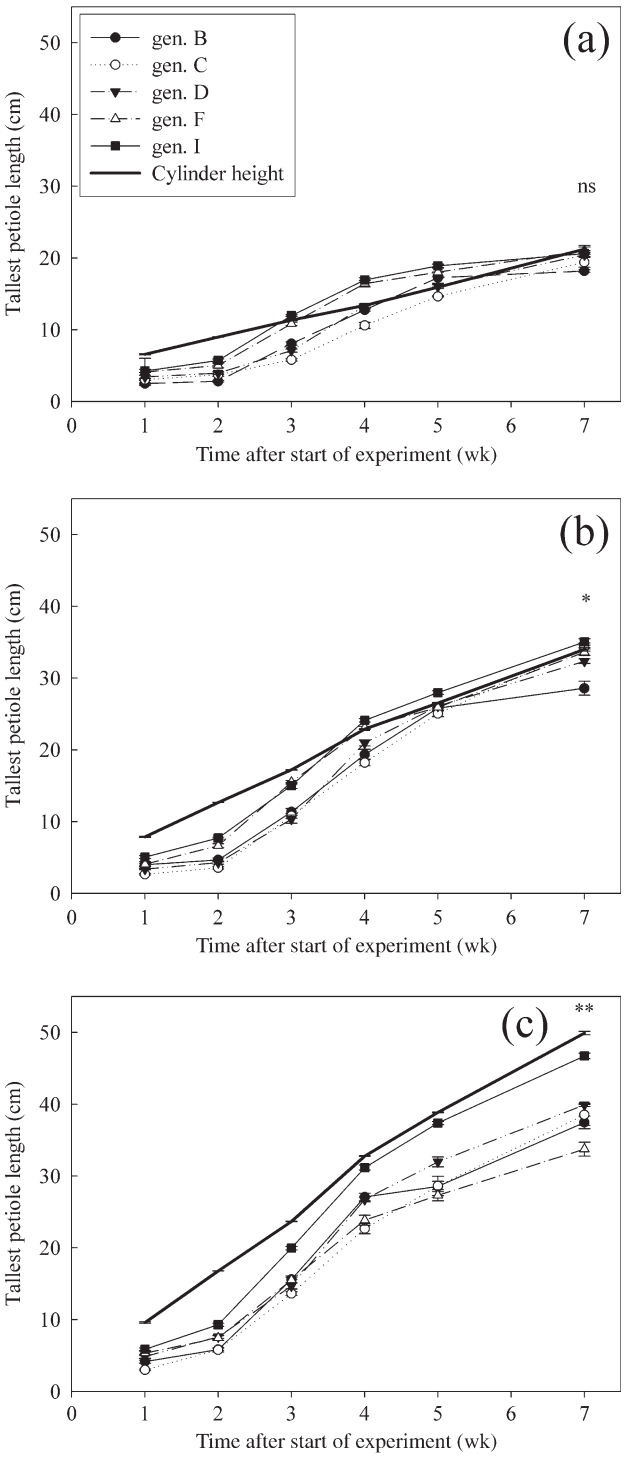

Fig. 4 Height (± 1 SE) of tallest petiole of *Potentilla reptans* genotypes (gen.) in time for (a) Slow treatment, (b) Medium treatment and (c) Fast treatment. Symbols above petiole height in week 7 indicate significance of the one-way ANOVA tests: ns, $F = 1.088$, $P > 0.05$; *$F = 3.059$, $0.01 < P \leq 0.05$; **$F = 5.385$, $P < 0.01$.

Table 1 Results of the two-way ANOVAs examining the effects of treatment and genotype and their interaction

Analysis	Trait	Treatment	Genotype	Treatment × genotype	Error
Two-way ANOVA	df	2	4	8	75
	Total plant mass^{log}	40.22***	20.68***	2.37*	
	Number of leaves	25.18***	5.58**	2.35*	
	Specific petiole length	19.87***	20.84***	2.17*	
	Specific lamina area	35.93***	4.88**	1.96^{ns}	
	Tallest petiole at harvest	184.77***	6.43***	2.94**	
Two-way Bonferroni	Petiole mass ratio	49.18***	4.61**	2.04^{bns}	
	Lamina mass ratio	18.04***	3.93**	2.32^{bns}	
	Root mass ratio	58.24***	2.97^{bns}	2.20^{bns}	
	Stolon mass ratio	25.36***	8.74***	0.57^{bns}	
Two-way at similar cylinder height	Tallest petiole length	53.41***	4.43**	4.45**	

Table shows three separate analyses: two-way ANOVA, the two-way ANOVA with Bonferroni correction, and two-way ANOVA at similar cylinder height.
F-values and their significance: ns, $P > 0.05$; *$0.05 \geq P > 0.01$; **$0.01 \geq P > 0.001$; ***$P < 0.001$; bns (Bonferroni corrected significant level), $P > 0.0125$.
^{log}, log-transformed data.

Table 2 Results of the repeated measurement ANOVAs examining the effects of treatment, genotype and time and their interactions on the tallest petioles

Analysis		Treatment	Genotype	Treatment × genotype	Time	Time × treatment	Time × genotype	Time × treatment × genotype	Error
Two-way repeated	df	2	4	8	5	10	20	40	75
	F	225.43***	17.16***	2.76*	2056***	75.99***	4.14***	1.85**	
One way	df		4		5		20		25
Slow	*F*		8.21***		508.5***		2.53**		
Medium	*F*		7.62***		996.4***		2.56**		
Fast	*F*		7.59***		682.7***		2.67**		

In the two-way analysis, time was the within subject factor, while treatment and genotype were treated as fixed between factors. In the one-way repeated analysis done separately per treatment, time was the within-subject factor with genotype a fixed factor.
F-values and their significance: ns, $P > 0.05$; *$0.05 \geq P > 0.01$; **$0.01 \geq P > 0.001$; ***$P < 0.001$.

at final harvest showed that the genotypes differed in response to the different treatments (significant treatment × genotype interaction, Table 1). Further analysis in separate one-way ANOVAs showed no significant difference between the genotypes for the tallest petiole length at final harvest in the Slow treatment (Fig. 4). In the Medium and Fast treatment, however, there was a significant difference between genotypes. The separate repeated ANOVAs showed that in all three treatments there was a significant time × genotype interaction for tallest petiole length (Table 2), indicating that in all treatments genotypes differed in their ability to place their leaves higher up in the light gradient with time.

The analysis of tallest petiole length at similar cylinder height showed that genotypes responded differently to a higher rate of cylinder increase (Table 1). More variation seemed to occur between the genotypes in the Fast treatment at week 4 than in the Medium treatment at week 7 (Fig. 4). Overall, tallest petiole length was higher in the Medium treatment at week 7 than in the Fast treatment at week 4.

The genotypes also differed in all other measured parameters (Fig. 5, Table 1). A significant treatment × genotype interaction was found for most plant characteristics, except for $SL_{am}A$, where the interaction was only marginally significant (Table 1). The ratios also did not show significant treatment × genotype interactions. The total mass of the plants did show a treatment × genotype interaction, with the rank order of the genotypes changing with treatments (Table 1, Fig. 5a).

Discussion

Our setup is a valuable tool for studying plastic responses in a light environment that changes while plants are developing. The benefit of this setup is that growth differences between genotypes at final harvest resulted both from the ability of the

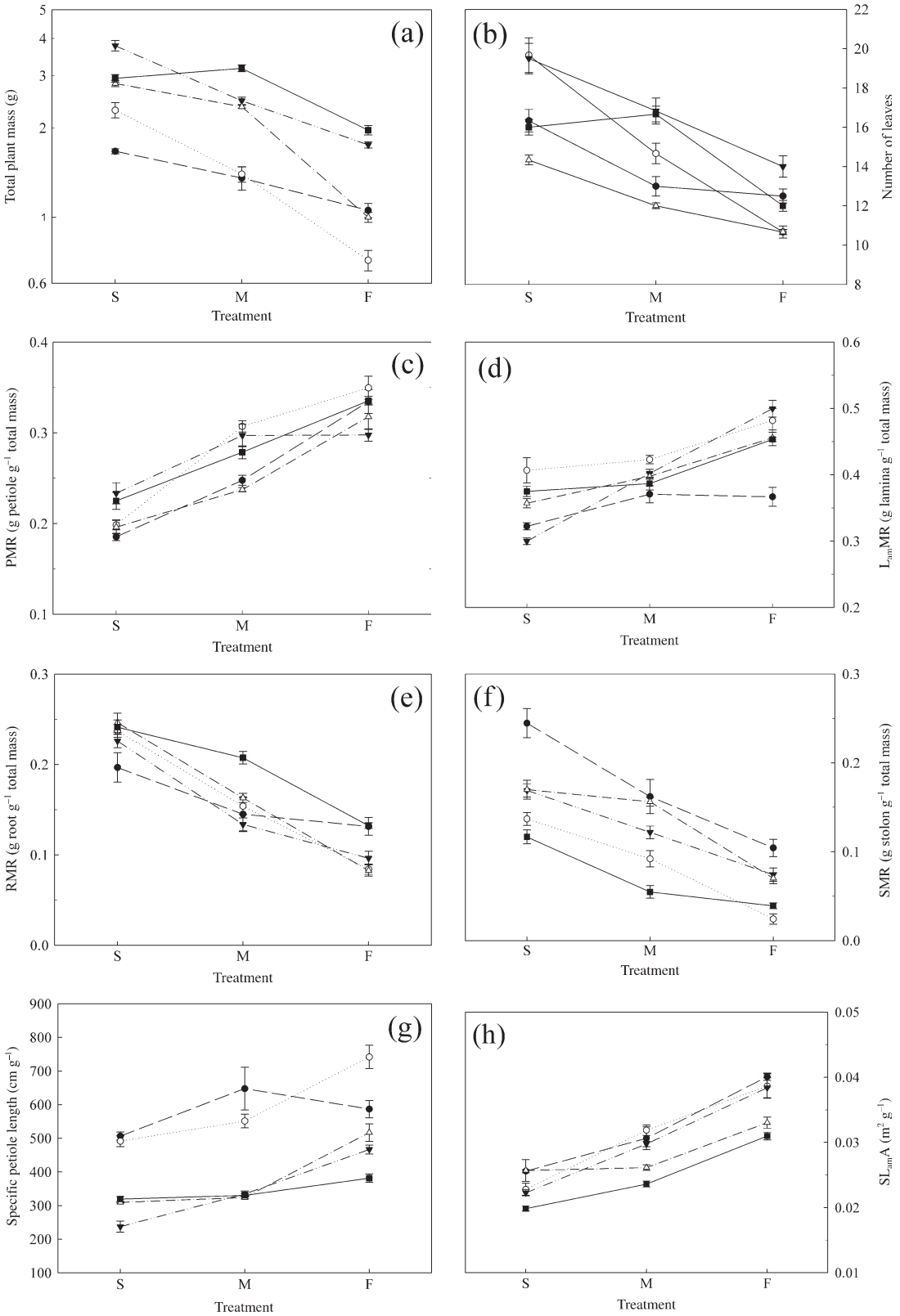

Fig. 5 Morphological characteristics of the five *Potentilla reptans* genotypes in response to the treatments (S, Slow; M, Medium; F, Fast). (a) Total plant mass, (b) total number of leaves produced at week 7, (c) petiole mass ratio (PMR), (d) lamina mass ratio (L_{am}MR), (e) root mass ratio (RMR), (f) stolon mass ratio (SMR), (g) specific petiole length, (h) specific lamina area ($SL_{am}A$). Note the differences in scales, with (a) log-transformed. Symbols of genotypes can be found in the key of Fig. 4a.

genotype to place newly formed leaves at high light levels, and the ability of these leaves to perform at lower light levels once they were shaded later in time. Also, in our experiment, the plants started at high-light levels. This means that light conditions did not strongly change when the plants were moved from precultivation to the experimental conditions. It is important to note that the differences between treatments reflect both the rate of cylinder height increase and the cylinder's absolute final height, since our setup confounds these two aspects of neighbour canopy height. This resembles height growth in natural stands, where an increase in height growth rate will lead to taller vegetation, and to a faster decrease of light availability of lower placed leaves.

From the Slow to the Fast treatment plants showed responses that are also found as crowding gets more intense (Geber, 1989; Ballare *et al.*, 1991; Schmitt & Wulff, 1993): an increased allocation to height growth (i.e. to the petioles), a decreased allocation to the roots and higher values of the SLA.

Plants increased the length of their petioles from the Slow to the Fast treatment. Total mass of the plants, however, decreased, while the number of leaves produced and the amount of stolon mass that was cut off during the experiment was lower. This shows that an increase in speed of elevating the vertical shade gradient and the resulting increase in absolute height reduced the production of biomass, delayed the formation of new leaves, and increased the allocation to the petioles at the expense of allocation to the roots and stolons.

From the Slow to the Fast treatment, the petiole length per unit mass, the SPL, increased. This contrasts with the findings of Huber & Wiggerman (1997) and Leeflang *et al.* (1998) in light gradients of fixed length. They argued that in order to place a lamina higher up in the canopy an increase in mass per unit petiole length (i.e. a decrease in the length per unit mass) is necessary to support the weight of the lamina. Liu *et al.* (2007) showed that *P. reptans* produces shorter, more flexible petioles in response to mechanical stress, a response that is likely to decrease the chance of buckling. The higher SPL that found in our study indicates that the increased elongation in response to the increased height of the cylinders may have reduced the mechanical stability of the petioles.

In all our treatments, the significant genotype × time interaction for tallest petiole indicates that genotypes differ in their ability to quickly place their new leaves at the top of the light gradient. The differences between genotypes in tallest petiole length at harvest in the medium and fast treatment also show that they differ in height growth potential. In the Slow treatment, however, the length of the tallest petiole at harvest was similar for all genotypes, while they did differ in biomass, allocation patterns, specific lamina area and other morphological characteristics. This indicates that when height growth of surrounding vegetation is slow and the resulting light gradient relatively short, height convergence of clonal plants can occur, despite differences between genotypes in height growth potential.

Ballaré (1999) and Aphalo *et al.* (1999) argued that photomorphogenic signalling among neighbours can buffer the development of differences in height between plants because shorter plants experience a stronger signal and thus have a stronger height growth. The responses of the genotypes in our Slow treatment support this view. After an initial period in which leaves were located in shade below the top of the cylinder, some genotypes had grown new, elongated petioles, which placed their laminas at the top of the light gradient at the third census. The other, initially shorter genotypes had their laminas at lower light levels, experienced stronger signals and thus had a stronger height growth later in time. As a result, all genotypes had placed leaves at similar height at final harvest in the Slow treatment, and thus at similar light levels.

Elongation stopped once the laminas were in high-light conditions, while petioles of the same age became taller in the Fast treatment compared with the Medium and Slow treatment. Several studies working with stoloniferous species have shown that petiole elongation slowed down or even stopped once the plants reached the top of a light gradient (Price & Hutchings, 1996; Lötscher & Nösberger, 1997; Leeflang *et al.*, 1998). This indicates that the detection mechanism for these stoloniferous plants is located near the lamina, as was found by Thompson (1995) for *Trifolium repens*, and that the sensing of radiation reflected by neighbours works in a similar way to that found in erect species (Ballaré, 1999). To date, however, no study has investigated the effect of cues such as ethylene and blue light on stoloniferous plants. Also, the fact that elongation of the petioles starts at the bottom of the light gradient, and that elongation, and thus meristem activity, stops, suggests that the regulation of height growth in stoloniferous plants could be different from that of the stems of erect plants.

Whether a genotype can place its laminas at the top of the vegetation can be influenced by both the absolute length of the light gradient and its rate of increase. Leaves that start at ground level need to elongate the length of the initial light gradient, plus the elongation rate of the vegetation during leaf development in order to place their laminas at the top. Genotypic differences in leaf positioning can therefore result from differences in elongation rate, the time-period a petiole elongates and a possible maximum petiole length a genotype can reach. In the Medium and Fast treatment there was a clear differentiation between genotypes with regard to the height they reached and the time that they needed to reach that height. Despite the stronger photomorphogenic signals that the shorter genotypes experienced, they could not place their leaves at similar height as taller genotypes did. Our results therefore suggest that if height growth of surrounding vegetation is fast and results in tall vegetation, differences between genotypes in height growth potential will result in leaves of different genotypes occupying different positions in the vertical light gradient of the stand. Moreover, our analysis of the longest petiole, at similar cylinder height in the Medium and Fast treatments,

indicates that the rate of height change of the light gradient alone can induce these genotypic differences.

The fact that petioles were longer in the Medium treatment at week 7 than in the Fast treatment at week 4 suggests that petiole length is limited by the production capacity of the plants, as plants in the Fast treatment were smaller. This could in part explain why genotype F, which was chosen because of its long petioles in other experiments, had the lowest values for tallest petiole length in the Fast treatment. Analyses of leaves in the stock populations revealed that it had higher dark respiration than the other genotypes (unpublished data), indicating a lower carbon gain at low light levels. The rapid decrease in light availability of lower placed leaves may have resulted in low carbon gain, which in turn may have limited its ability to place leaves at the top of the cylinder.

Differences between individuals in leaf positioning at the beginning of the season may affect the positioning later on. In even-aged stands of herbaceous plants rank correlation in height of plants is fixed shortly after canopy closure, as differences in final height between plants are determined at an early stage of canopy development and plants that fall behind will not be able to catch up (Ford, 1975; Anten & Werger, 1996; Nagashima, 1999; Xiao *et al.*, 2006). Our results indicate that the same applies for competition between genotypes of a stoloniferous plant in a fast-growing canopy. This can strongly affect the outcome of competition between these genotypes.

In dense stands, either monospecific or multispecific, smaller plants can be excluded from the vegetation as they are shaded by neighbours and as a result develop a lower biomass use efficiency for light harvesting than their taller neighbours (Anten & Hirose, 1998; Werger *et al.*, 2002; Hikosaka *et al.*, 2003). Similarly, since the differences in length of the tallest petioles between genotypes in our study increased from the Slow to the Fast treatment, rapid height growth of the surrounding neighbours, leading to taller vegetation, may lead to competitive exclusion of the shortest or least plastic genotypes. Our results also show that more genotypes are able to place their leaves at the top of the light gradient when height growth of the vegetation is low. This would suggest that in such vegetations more genotypes can coexist for longer periods in the top of the canopy than in faster-growing, taller vegetation.

In conclusion, our results show that although stoloniferous plants have the disadvantage of starting new leaves from ground level, they can adjust their height growth well to that of the surrounding vegetation. Our findings confirm that height convergence can occur between different genotypes of stoloniferous plants. Our results also indicate that, depending on the height growth of the canopy, genotypes may differ in their abilities to keep up with neighbouring plants. Genotypes that are limited in height growth potential can only link up with potentially higher-growing genotypes in a light gradient with a restricted height increase. Since leaf positioning affects the light harvesting efficiency of a plant, height growth and plasticity therein can be an important factor explaining the outcome of competition between different genotypes.

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