

Ecological implications of the determination of branch hierarchies

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Summary

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- The performance of the whole plant is largely dependent on its ability to allocate limited resources to branches that perform best throughout its life. Here, the hypothesis that the fate of young branches is determined by their growth rates and not merely by their relative physical sizes or net photosynthetic outputs was tested.
- The development of asymmetrical two-branch plants was followed after either one or both of the branches were restrained for short periods.
- The larger branch was invariably dominant in unrestrained or bilaterally restrained plants. However, when the larger branch was restrained while the smaller branch was not, the branch hierarchy inverted despite the pronounced photosynthetic advantage of the larger branch over its smaller counterpart.
- It is suggested that growth rates are more important than physical size or photosynthetic output in young plants, where they could serve as better predictors of the overall future performance of the branch. It is speculated that rate-sensitivity has been selected for when plastic responses cannot adequately track environmental changes in real time.

Key words: branch competition, branch hierarchy, branch vigour, developmental decisions, phenotypic plasticity, photosynthetic rates, rate-determined processes, redundant organs.

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Introduction

Plant branching and branching patterns have significant adaptive consequences. Branching intensity and positioning play a major role in the determination of the plant's canopy architecture (Hallé *et al.*, 1978; Prusinkiewicz *et al.*, 1996; Daviero *et al.*, 2000), photosynthetic rates (Reekie & Bazzaz, 1989; Kikuzawa, 1995; Perttunen *et al.*, 1998; Valladares & Percy, 1998; King & Maindonald, 1999), spatial spread (Hallé *et al.*, 1978; Oborny & Cain, 1997; Sinoquet & Rivet, 1997; Jensen & Bell, 2001), competitive ability (Callaghan *et al.*, 1990; Aarssen, 1995; Stoll & Schmid, 1998; Gautier *et al.*, 2000; Marcuvitz & Turkington, 2000) and fitness (van Kleunen & Fischer, 2001). Plastic branching intensity and positioning enable plants to forage effectively for favourable patches within their immediate environment and to avoid spreading into relatively poor or highly competitive patches (Cain *et al.*, 1996; Wijesinghe & Hutchings, 1996; McPhee *et al.*, 1997; Oborny & Cain, 1997; van Kleunen & Fischer,

2001; Wijesinghe & Whigham, 2001). Furthermore, plants are capable of allocating more limiting resources to branches that develop in more favourable conditions at the expense of other branches (Snow, 1931; Novoplansky *et al.*, 1989; Sachs *et al.*, 1993; Takenaka, 2000; Henriksson, 2001). For example, relatively small branches at the outer canopy of a tree develop in relatively advantageous conditions (Sachs & Novoplansky, 1995; Ackerly & Bazzaz, 1995; Valladares & Percy, 1998; Yamada *et al.*, 2000) and are expected to grow faster and produce more in the long run than larger branches that develop under inferior conditions within the canopy of the same tree. Hence, the size of a branch alone is not always the best predictor of its overall performance.

Most plants are capable of producing a great excess of similar functional organs from dormant buds (Harper, 1985; de Kroon *et al.*, 1991; Sachs, 1991; Matlack *et al.*, 1993, but see Watson *et al.*, 1997). However, under natural conditions, resource limitation dictates that the success of the whole plant depends on selection of, and allocation to, only a limited number

of organs (Sachs *et al.*, 1993; Aarssen, 1995; Novoplansky, 1996). This can be seen in the presence of many buds that do not grow and in the limited growth of most branches on any given plant. When the seminal branch of a plant is removed or physically prevented from growing (McCallum, 1905), it is usually replaced by one or more lateral branches that would not have grown otherwise. This expression of apical dominance (Rubinstein & Nagao, 1976; Cline, 1991) has potentially important ecological implications involving competition for light, pollination, seed dispersal, foraging for resources and avoidance of herbivory damage (Aarssen, 1995). The release of only a limited number of buds from dormancy following the removal of apical dominance raises a general question relevant to the way plants take advantage of variable and unpredictable environments: what gives some buds or branches precedence over others? In other words – what determines the hierarchy among ‘redundant organs’ (Sachs *et al.*, 1993) of the same plant?

The first factors that come to mind in the context of hierarchy determination of branches with equal age and position are their relative size and net photosynthetic rates. Certainly, larger branches are usually greater exporters of photosynthates and are supported by a greater proportion of vascular connections to the roots (Sachs, 1981; Sachs *et al.*, 1993). In the present study an additional possibility was tested: that competition between branches is not only dictated by their size or photosynthetic outputs but also by their ability to grow and by their growth rates (hereafter known as ‘branch vigour’). At least under some circumstances, more vigorous and fast-growing branches might be expected to possess an advantage over branches that are slower to grow, regardless of their photosynthetic ability. Such a possibility could have important ecological implications: while physical size is a relatively adequate correlate of the branch’s *past* performance and development, its vigour may serve as a predictor of its *future* size and long-term performance (Watson & Casper, 1984; Geber *et al.*, 1997). Branch size and vigour are often, but not invariably, positively correlated with each other. Young branches are usually small in size but may grow vigorously, while old branches are often large but slower to grow. Therefore, it is predicted that at least under some circumstances, vigour may play an important role in determining the hierarchy of relatively young branches, because it is in these branches that future performance is expected to be more meaningful than past development (Novoplansky *et al.*, 1990; Novoplansky, 1996).

Although the available evidence is not conclusive it suggests that this hypothesis is conceivable. Snow (1931) and Novoplansky *et al.* (1989), treated ‘two-branch plants’ in which cotyledonary buds had started growing. They showed that differential adverse growth conditions such as lack of light or physical damage made the affected branch inferior in size and caused it to wither and die if a competing branch was developing on the same plant. Furthermore, removing the

young expanding leaves (the main source of growth signals such as auxin) from one branch and the mature leaves (the main source of photosynthates) from the other branch gave the branch with the smaller but more vigorously expanding leaves a pronounced advantage (Snow, 1931; Sachs & Hassidim, 1996). Dostal (1967) and Desbiez *et al.* (1984) compared the growth of buds in the axils of opposite cotyledons that were released from dominance by the removal of the seminal branch. Damage to one cotyledon greatly increased the probability of growth of the bud in its axil. In an earlier study the determinants of bud fate were studied in two-branch plants (Novoplansky, 1996). It was found that the bud that became dominant was not necessarily the larger one, nor did it emerge from the axil of the larger branch. Instead, it was usually the bud that was inhibited for a shorter period by the branch next to it.

In order to study directly the relative importance of size, net photosynthetic rates and vigour for the hierarchy of redundant branches on the same plant, a system was sought in which the hierarchy between young branches could be manipulated. Such a system was found in a modification of two-branch plants (Snow, 1931). When the dominant seminal branch of a young *Pisum* plant is removed, its cotyledonary buds grow into branches. The resulting plant thus has two adjacent branches of variable symmetry (Novoplansky, 1996). The development of asymmetrical two-branch plants was followed after the growth of one or both of their branches was briefly inhibited by physical restraining (McCallum, 1905). This system allowed comparison of the growth of two branches developing on the same plant: one being smaller and vigorous while the other larger and slower to grow.

Methods

Pisum sativum var. *arvense* Poir. cv. Dunn plants were used throughout. Two-branch plants were prepared as described in Novoplansky (1996). When the seminal branch, the plumule, was removed, the seedlings naturally grew into plants with two branches with variable symmetry (Fig. 1). Two-branch plants were selected so that one of their branches had one leaf and was 26 ± 1.7 mm long and the other branch had two leaves and was 45 ± 2 mm long. Observations were made on the relative sizes and photosynthetic rates of the two branches developing on the same plant after one or both branches were either grown without interruption, or physically restrained, for 3 d (Fig. 1).

Growth conditions, restraining and plant measurements

The plants were grown at 25°C and under relatively low light levels ($110 \text{ mmol/m}^2 \text{ s}^{-1}$ photosynthetic photon fluence rate (PPFR) obtained from cool white fluorescent lamps) to increase the strength of correlative inhibition between their

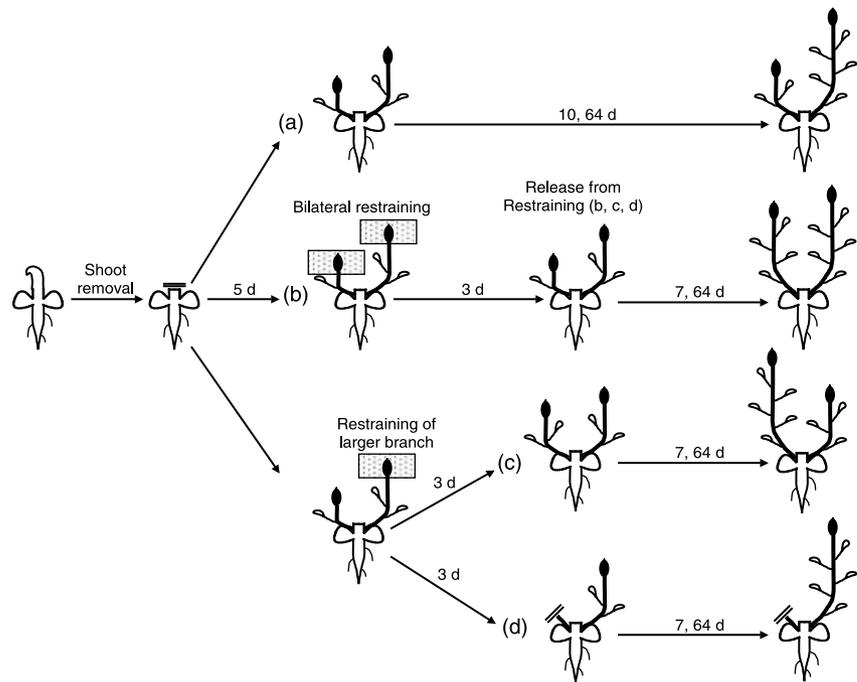


Fig. 1 Set-up of the experimental system. Asymmetrical two-branch *Pisum sativum* plants that developed following decapitation of young seedlings were used. The hierarchy of the branches was followed 7 and 64 d after the original two branches were simultaneously (a), left free restrained (b), or when only the larger branch was restrained for 3 d in the presence (c), or the absence (d) of the smaller branch on the same plant.

branches (Duffy *et al.*, 1999), and the probability of detecting differential branch development. The plants were individually planted in 10 cm diameter pots filled with extra-fine vermiculite. They were alternately irrigated with deionized water and 0.3 Hoagland solution (Hoagland & Arnon, 1950) at 3-d intervals.

The plants were grown so that their branches were aligned along a slightly slanted (20°) polycarbonate panel. Shoot restraining was carried out by fastening the uppermost part of the branch, including the apex and unfurled young leaves, to the polycarbonate panel with a piece of transparent adhesive tape (Scotch Magic Tape, 3M, Bracknell, UK). The plants were aligned so that the tape adhered to the outer (lower) surface of their youngest visible stipules, confining the young unfurled leaves to the tightly closed stipules. Preliminary observations confirmed that the restraining could efficiently prevent unfurling and expansion of new leaves and extension of the uppermost internodes of the restrained branches. Adhering the tape to the outer surface of the stipules ensured that no leaf surfaces were directly exposed to the adhesive tape. Release of restrained branches was done by carefully peeling off the adhesive tape. Microscopic observations verified that the peeling only scarified the uppermost layer of the stipule's cuticle, which is relatively thick in Dunn peas, leaving the epidermis unharmed.

The development of asymmetrical two-branch plants was observed after their branches were simultaneously restrained (RESTR-RESTR) or left free (FREE-FREE) for 3 d (Fig. 1a–b). Comparing RESTR-RESTR with FREE-FREE allowed assessment of the absolute effects of physical branch restraining on branch growth and net photosynthetic rates. In the

following treatment each plant had a relatively small but vigorous branch and a relatively large but slow to grow branch. The larger branch of each two-branch plant was restrained for 3 d, during which the smaller branch was left unrestrained. The larger branch was released from restraining when the smaller branch was 90% the length of the larger branch (RESTR-FREE, Fig. 1c). In an additional treatment the differential restraining was followed by the removal of the smaller branch immediately upon release of the larger branch from restraining (RESTR-X, Fig. 1d). Comparing RESTR-FREE and RESTR-X allowed assessment of the effect of correlative inhibition between the two branches.

Shoot size was determined 7 d after the release of the RESTR-RESTR branches from restraining and at harvest, 64 d after their release from restraining ($n = 29–31$ per treatment). Seven days after the release from restraining leaves were counted and the stem length and diameter of each branch measured. Leaves were large enough to be counted when their leaflets could be seen above the stipules. Shoot length was measured from the axil to the apex (± 2 mm). Stem diameter was measured 1 mm above the cotyledonary axils using a micrometer gauge (± 0.01 mm).

Sixty-four days after release from restraining the plants were harvested following the senescence of 20–25% of the leaves. The plants were dried for 3 d at 70°C in a ventilated oven and the dry masses of the vegetative (stem and leaves) and reproductive (pods and seeds) parts of each branch were measured.

Photosynthetic rates were measured on 14–15 FREE-FREE, RESTR-RESTR, and RESTR-FREE plants using a CIRAS-1 infra-red gas analyser and a Model-B probe (PP Systems,

Herts, UK). The photosynthetic measurements were carried out 6–7 h after releasing the larger branch of FREE-RESTR plants from restraining, and under the same light and humidity conditions experienced by the plants during the restraining period. Measurements were conducted on entire branches (all leaves and stem, except for the lowest 5 mm of the stem that was in the probe's peripheral insulation) whose upper leaf surfaces were perpendicular to the lights.

Statistical analyses were conducted using SYSTAT 10.0 (SPSS, 2000). All dependent variables met the assumptions of parametric statistics. One-way ANOVAs followed by Bonferroni-corrected comparisons were used to test differences among treatment averages. Differences between the sizes of the initially

larger and smaller branches of the same plants were analysed using paired *t*-tests.

Results

The effect of uniform branch restraining

Unrestrained two-branch plants (FREE-FREE) increased their asymmetry during the 64 d of the experiment (Fig. 2). At the beginning of the experiment the initially larger branch bore 67% of the plant's leaves and 74% of the total stem length, 10 d after the beginning of the experiment the initially larger branch bore 69% and 88% of the plant's leaves and

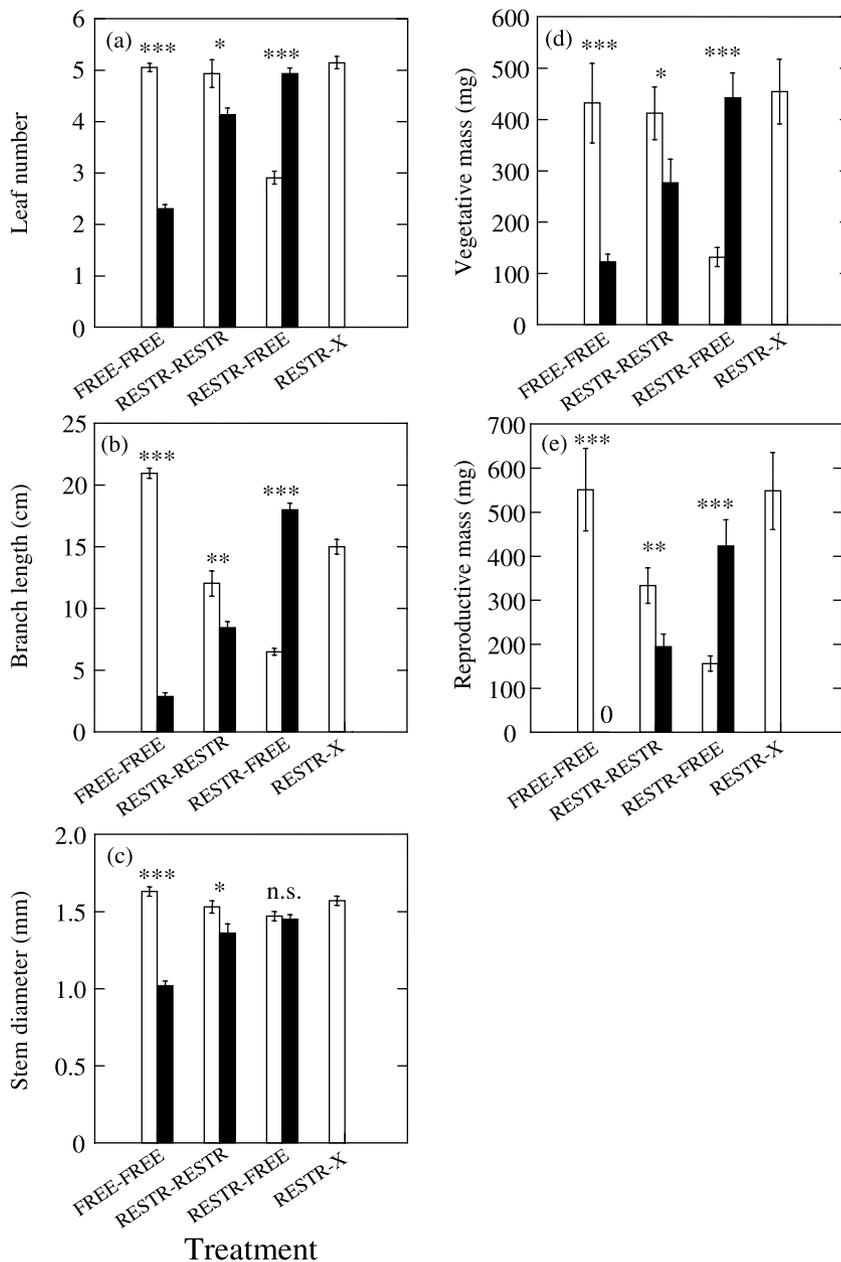


Fig. 2 Number of leaves (a), branch length (b), stem diameter (c) 7 d after the release from restraining, and dry mass of vegetative parts (stems and leaves) (d) and reproductive parts (e) of the initially larger (open bars) and smaller (closed bars) branches of the experimental *Pisum sativum* plants 64 d after the release from restraining. Values are means \pm SE. The significance values are for paired *t*-test comparisons between the larger and smaller branches of each plant at the time of the measurement. ***, $P < 0.001$, **, $P < 0.01$, *, $P < 0.05$, ns, $P > 0.1$.

total stem length, respectively, and by the end of the experiment the initially larger branch bore 78% of the vegetative mass and 100% of the reproductive mass on the plant. Bilateral restraining of two-branch plants (RESTR-RESTR) did not change the initial branch hierarchy, the number of leaves, or the stem diameter of the larger branch 7 d after release from restraining (Fig. 2a,c). However, bilateral restraining did benefit the initially smaller branch and 7 d after release from restraining it was significantly larger in RESTR-RESTR than in FREE-FREE ($P < 0.01$ in one-way ANOVAS for all growth variables, Fig. 2a–c). These differences were also evident at the end of the experiment in the branch's vegetative and reproductive masses (Fig. 2d–e). In branch length both an absolute decrease in the size of the initially larger branch and an increase in the size of the initially smaller branch were observed in RESTR-RESTR compared with FREE-FREE plants (Fig. 2b, $P < 0.01$ in one-way ANOVAS). This change in symmetry was not accompanied by any change in the combined total branch length of the plant ($P > 0.1$ in a one-way ANOVA, Fig. 2b). As expected, following release from restraining whole-branch net photosynthetic rates were significantly greater in the larger branches than in the smaller branches. Comparing FREE-FREE and RESTR-RESTR shows that plants in the 3-d long restraining treatment had slightly lower net whole-branch photosynthetic rates at the time of release from restraining.

Contrasting branch size and vigour

Differential restraining of the larger branch (RESTR-FREE) inverted the branch hierarchy and at the end of the experiment the initially larger branch was significantly smaller than its counterpart (Fig. 2). At the beginning of the experiment the initially smaller branch bore 33% of the leaves and 26% of the total branch length of the plant; 7 d after release from restraining it bore 63% and 73% of the leaves and the branch length of the entire plant, respectively (Fig. 2a–b), and by the end of the experiment it bore 77% of the vegetative mass and 64% of the reproductive mass of the entire plant. Furthermore, the initially larger branch was significantly smaller in RESTR-FREE than in both RESTR-RESTR and FREE-FREE plants 7 d after release from restraining ($P < 0.001$ in one-way ANOVAS for leaf number and branch length, Fig. 2a,b) and at the end of the experiment ($P < 0.001$ in one-way ANOVAS for vegetative and reproductive masses).

The hierarchy inversion was evident in RESTR-FREE plants despite the 3-fold photosynthetic advantage of the larger branch over its smaller counterpart upon its release from restraining (Fig. 3). Removing the smaller branch concurrently with the release of the larger branch from restraining (RESTR-X) resulted in normal development of the initially larger branch (Fig. 2a, c–e; nonsignificant differences in number of leaves and stem diameter of the initially larger

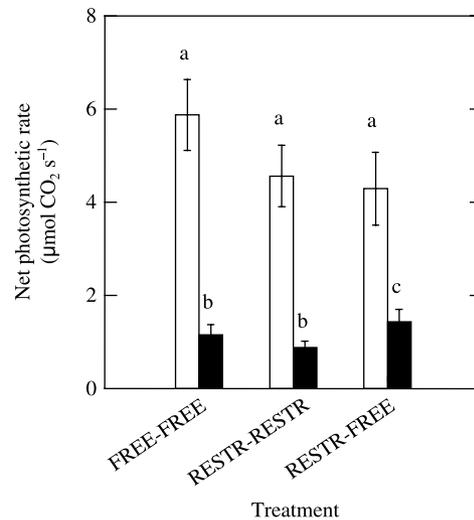


Fig. 3 Whole-branch net photosynthetic rates of the initially larger (open bars) and smaller branches (closed bars) of FREE-FREE, RESTR-RESTR, and RESTR-FREE *Pisum sativum* plants 7–9 h after their release from restraining and 7 d before the end of the experiment. Values are means \pm SE. Leaf area is missing from the units since they represent measurements of whole branches rather than of a fixed leaf area. Bars that share the same superscript are not significantly different ($P > 0.05$) in Bonferroni-corrected comparisons.

branch in RESTR-X and FREE-FREE 7 d after release from restraining, and in vegetative and reproductive masses at the end of the experiment, $P > 0.1$ in one-way ANOVAS), although it did not fully recover its length immediately following release from restraining (Fig. 2b).

Discussion

The results demonstrate that branch hierarchy is determined by both branch size and vigour. At least under some circumstances, branch hierarchy is more tightly correlated with its vigour than with its relative size or whole branch net photosynthetic rates. The short time that the initially smaller branch was free of the inhibitory effects of the larger branch gave it a significant developmental advantage that allowed it to overcome differences in both the relative sizes and the photosynthetic outputs of the branches.

In *Pisum*, branch hierarchy is normally correlated with the branches' relative sizes – the originally larger branch usually has a pronounced developmental advantage, leading to the inhibition or even death of its smaller counterpart (Fig. 2; Sachs, 1966). This expected result was only important as a reference for the other findings: bilateral restraining of a two-branch plant for 3 d reduced the ability of the larger branch to inhibit its smaller counterpart (Fig. 2). Furthermore, when the larger branch was restrained for 3 d while the smaller branch was left free, the smaller branch became dominant. Interestingly, this dominance inversion took place despite the 3-fold photosynthetic advantage of the initially larger branch

over its smaller counterpart at the time of its release from restraining (Fig. 3). Two different findings indicated that restraining alone did not change the branch hierarchy: (a) although the bilateral restraining reduced the inhibitory effects of the larger branch it did not change the original branch hierarchy (b) the inhibitory effects of the differential restraining occurred only in the presence of the smaller branch on the same plant.

The coexistence of branches in young two-branch *Pisum* plants is very unstable. The competitive interactions between the branches are severe and any minor interference is sufficient to instigate a pronounced developmental advantage of one branch over the other (Snow, 1931; Sachs, 1966; Desbiez *et al.*, 1984; Novoplansky, 1996; Sachs & Novoplansky, 1997). Once started, the developmental differences between the branches increase on a positive feedback course where developmental success leads to additional success and a relatively small disadvantage may result, under some circumstances, in total failure (Sachs, 1966; Novoplansky, 1996).

The results show that at least under some circumstances the prevailing branch was the more vigorous rather than the larger or the most photosynthetic. Therefore, interactions between branches, and probably other plant organs, are not exclusively mediated by sink-source relationships and the exchange of limiting resources (Sonnenwald *et al.*, 1994). Instead, interactions between branches may rely upon rapid nonresource signals such as auxin (Sachs, 1991), that carry information regarding the developmental vigour and morphogenetic status of the competing branches long before the products of their development are involved.

Ecological implications

The relationships between developing branches could be critical for the success of the entire plant. It is essential for a plant to allocate more resources to the branches with the greatest probability for high lifetime yield (Novoplansky, 1996; Sachs & Hassidim, 1996). However, at early stages the information regarding the future performance of any given branch is limited. The results demonstrate that young plants give the advantage to the branch with the greater probability to yield the most in the long run, rather than to the largest branch whose present performance is greater.

Allocation to larger but less vigorous branches at a young stage might translate into significant missed opportunities in the long run. It follows that somatic selection must take place even when all the competing organs are healthy and vigorous. In this context it is important to note that hierarchy determination among 'redundant organs' (Sachs *et al.*, 1993) is conceptually different from and complementary to the abortion of defective organs (Klekowski, 1988). It is suggested that vigour sensitivity is greater in relatively young plants where it can better serve to predict the future (thus overall) performance (Novoplansky, 1996). Theoretically, a large and highly

photosynthetic branch may become developmentally stagnant, for example due to mechanical damage or shading, and thus relatively inferior in terms of its overall future contribution to the plant, while a smaller but more vigorous branch might eventually become much larger and contribute significantly more in the long run. Accordingly, it is expected that vigour has only a relatively minor role in the determination of developmental processes in old (especially reproductive) annual plants. Such plants have relatively little 'future' (Novoplansky *et al.*, 1990) and are therefore expected to be more sensitive to the real-time performance of their branches.

It is suggested that similar vigour-sensitive selection mechanisms may play a role in other systems involving developmental hierarchies and where competition between surplus redundant organs such as flowers, fruits or ovaries is involved (Wiens *et al.*, 1987; Casper, 1988; Solomon, 1988; Garrish & Lee, 1989; De Lange *et al.*, 1993; Shaanker *et al.*, 1996; Huth & Pellmyr, 1997; Oliveira, 1997).

Since developmental processes take time, plastic responses often lag behind the ever-changing growth conditions (DeWitt *et al.*, 1998). Therefore, selection is expected to favour 'forecasting mechanisms' that enable plants to develop according to expected rather than prevailing growth conditions. The most studied forecasting system in plants is the red/far-red spectral sensitivity that enables the perception and avoidance of expected vegetative shade before actual competition for light materializes (Smith, 1982, 1994). It is suggested that vigour-sensitivity such as that demonstrated by the determination of branch hierarchy exemplifies yet another 'forecasting' mechanism. Hence, taking into account vigour allows the system to adapt with some limited accuracy to the expected rather than the prevailing conditions (Geber *et al.*, 1997).

The dependence of dynamic decisions on strength and directions of changes rather than absolute size parameters is well established in many disciplines. Canny stock trading is based on the allocation of capital to 'vigorous' shares and companies that are expected to grow more rapidly, certainly not the ones with the highest absolute values (Veale, 1991). Due to their great mass and inertia, the steering of heavy marine vessels necessitates the use of special 'rate-of-turn' indicators that help predict the future position of the vessel at any given moment following steering moves (Blanke *et al.*, 2000). The concept of rate perception is also well known in various biological systems. Skin thermoperception in humans is based on neurons whose firing rates are proportional to the rate of change rather than the absolute values of skin temperature (Livingston, 1990). Among the most studied examples of rate perception is chemotaxis in certain motile bacteria such as *Escherichia coli* or *Salmonella typhimurium*. Using their flagella these and other bacteria and algae are capable of swimming up nutrient gradients and navigating toward the richest patches in their immediate environment by responding to changes in the concentrations of these nutrients (Berg, 2000).

Although these systems are related to very different realms they share a common attribute: they are all adapted to perceive and react to some extrapolated future environment based on limited information. Furthermore, in most of these systems the need for vigour- or rate-sensitive controls is dictated by the system's limitation to follow environmental changes tightly in real time (DeWitt *et al.*, 1998; Givnish, 2002).

Finally, it is speculated that besides red/far-red sensitivity and vigour perception, plants might utilize other 'forecasting mechanisms' to pre-empt future resource availabilities and growth conditions in their environment. Other candidate mechanisms for which no evidence is currently available might involve the perception of resource gradients in space and time. As in the case of *E. coli* (Berg, 2000), such mechanisms might increase the foraging efficiency of plants by enabling them to allocate more resources to roots or branches that experience increasing (in contrast to decreasing or constant) resource gradients.

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