

# Self/non-self discrimination in roots

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## Summary

**1** Competition usually involves the allocation of limiting resources to non-reproductive functions. Natural selection is expected to favour mechanisms that increase competition with non-self neighbours and limit wasteful competition with self.

**2** We used *Pisum sativum* plants that had two roots and ‘double plants’ with two shoots and two roots that could be either longitudinally separated into two genetically identical but physiologically distinct individuals or left intact.

**3** Root development was significantly greater in split-root plants whose neighbours belonged to different plants. Furthermore, root development was relatively greater in the presence of roots of a different plant, regardless of its identity. This discrimination had a vectorial component whereby plants developed more and longer lateral roots towards neighbouring roots of different plants than towards other roots of the same plant.

**4** The results thus demonstrate a mechanism of avoiding self-competition that is based on physiological co-ordination among different organs of the same plant rather than on allochemical recognition that depends on genetic differences.

**5** The ability to discriminate between self and non-self could be expected to increase resource use efficiency and ecological performance in plants. It could also be expected that tight physiological co-ordination will be selected for between organs of the same plant that have greater probability of being engaged in direct competitive interactions with each other.

*Key-words:* allorecognition, clonality, competition, double plants, physiological co-ordination, physiological integration, phenotypic plasticity, roots, split roots, two-shoot plants

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## Introduction

In both plants and animals, competition has led to two main types of evolutionary responses, those that increase competitive ability and those that minimize competitive interactions (e.g. for plants, Schmitt *et al.* 1995; Smith 1995; Nardini *et al.* 1999; Schmitt *et al.* 1999; Grime 2001). In animals, niche specialization is widely thought to be a common adaptation to minimize interspecific competition (Tokeshi 1999). In contrast, the potential to minimize interspecific competition has been thought to be relatively limited in plants, because they depend on the very same resources and niche specialization is less likely (e.g. Goldberg & Barton 1992).

Competition usually entails allocation of limiting resources to non-reproductive functions (Novoplansky

*et al.* 1990; Dudley & Schmitt 1996; Weinig 2000). Consequently, natural selection should favour mechanisms that minimize competition among parts of the same individual (e.g. Kimura & Simbolon 2002), clones and kin (e.g. Grosberg & Hart 2000). Both plants and animals use internal chemical signals to coordinate the form and function of different parts of the same individual (e.g. for humans, Dubey *et al.* 2002; for plants, Snow 1931; Honkanen & Haukioja 1994; Whitehead *et al.* 1996; Sachs & Novoplansky 1997; Henriksson 2001). In the absence of movement plants also use genetically deterministic architectural rules to decrease self-interference among photosynthetic organs (e.g. Honda & Fisher 1978; Hallé *et al.* 1978; Bell & Tomlinson 1980), and roots (Fitter *et al.* 1991). However, the potential to minimize self-competition has been thought to be relatively limited in plants, because only animals were known to possess self/non-self discrimination capabilities (Grosberg 1988; Frank *et al.*

1996; Grosberg *et al.* 1996; Hart & Grosberg 1999; Penn & Potts 1999; Richman 2000). Clonal animals, such as sea anemones, can attack individuals belonging to different genetic clones while avoiding attacking individuals of the same clone (Sebens 1986; Ayre & Grosberg 1995; Ishii & Saito 1995). Furthermore, many social animals are able to discriminate behaviourally between individuals with different degrees of genetic relatedness (e.g. Krebs & Davies 1997).

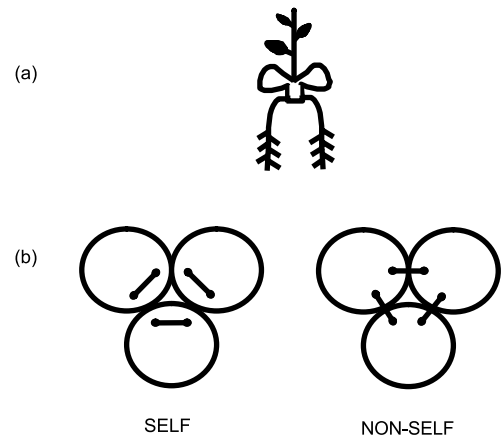
However, recent evidence suggests that roots are able to detect and avoid the presence of neighbouring roots (Krannitz & Caldwell 1995), and to segregate spatially in 'territories' (Schenk *et al.* 1999). The evidence suggests that there appear to be at least two different types of self/non-self discrimination. Mahall & Callaway (1991, 1996) found that roots of *Ambrosia* are capable of reducing root elongation following interplant but not intraplant root contacts, and Gersani *et al.* (2001) demonstrated that *Glycine max* plants increase root development in the presence of neighbouring conspecifics but not in the presence of other roots on the same plant. Avoidance of root competition among clone members was also observed in *Fragaria chiloensis*, where clonal integration allowed higher clonal performance (Holzapfel & Alpert 2003). These findings raise questions regarding self/non-self discrimination in roots: (a) How common is the ability of plants to discriminate between self and non-self neighbours? (b) What mechanisms are used in root self/non-self discrimination? Is it based on allogenic recognition such as in other self/non-self systems (e.g. Penn & Potts 1999; Grosberg & Hart 2000; Dixit & Nasrallah 2001) or on physiological coordination among roots that are part of the same plant (Snow 1931)?

Using *Pisum sativum* plants we were able to create plants that had two equal roots ('split roots') and 'double plants' that had two equal shoots and two equal roots (Sachs & Novoplansky 1997). We used split-root plants to compare roots that developed in the presence of another root of the same plant vs. the root of another plant. We then compared the development of intact and severed double plants, in order to define the role of physiological coordination. The severed plants were arranged so that both of their halves either originated from the same mother plant (i.e. they were genetically identical but physiologically separated) or from two different mother plants (genetically and physiologically alien to each other). In a third experiment we studied the possibility that roots develop differentially towards self and non-self neighbours.

## Materials and methods

### SELF/NON-SELF DISCRIMINATION: THE SPLIT-ROOT EXPERIMENT

*Pisum sativum* var. arvense Poir. cultivar Dunn plants were grown so that they developed two equal roots following removal of the seminal root ('split-root plants';



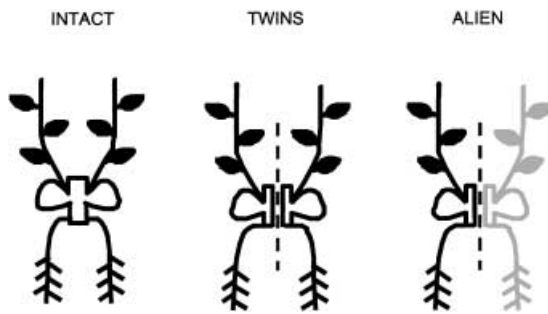
**Fig. 1** Split-root plants generated two equal roots (a) following the removal of their seminal roots. Triplets were grown so that the roots in each pot were separated by the same distance in both treatments (b).

Fig. 1a, e.g. Jeschke & Wolf 1988). Two days from germination, the seminal root was severed 5 mm below the hypocotyl and the plants were replanted in damp vermiculite. By 7 days from germination the stump of the seminal root had developed two to five lateral roots. All but two of these roots were removed. Seedlings with two 25–30 mm long roots were planted in triplets so each pot contained either two roots of the same plant (SELF) or of two different plants (NON-SELF) (Fig. 1).

This design allowed identical positioning of shoots and roots of neighbouring plants in the two treatments. Special attention was paid to ensuring that roots were vertical and that there was identical spacing between the roots and between the roots and the pot wall in all cases. The plants were grown in standard 60-mm diameter 0.085 L polyethylene pots filled with extra-fine vermiculite, which were glued together in triplets to fix their relative positions. Plants belonging to the same triplet had the same initial root and shoot sizes ( $\pm 1$  mm). As the development of different plants sharing the same non-self triplet was interdependent, the scores in both treatments were based on triplet averages (i.e. number of replications equals the number of triplets, each triplet represented by the average score of three root pairs). Measurements were made 18 days after the experiment started, 25 days after germination.

### MECHANISMS OF SELF/NON-SELF DISCRIMINATION

*Pisum sativum* arvense Poir. cultivar Dunn plants were grown so that they had two shoots and two roots ('double plants'; Sachs & Novoplansky 1997). Seeds were soaked for 24 h in aerated water. They were germinated in damp vermiculite with their radicle pointing downwards. Three days later the plumule was removed and two shoots then developed from the cotyledonary buds (Snow 1931). Eight days from germination, the seminal root was severed and regenerated as described for the



**Fig. 2** 'Double-plants', with two identical halves regenerated following the removal of their seminal shoots and roots (Sachs & Novoplansky 1997), were planted INTACT, or as TWINS, or ALIEN. Interactions could be compared between neighbouring roots that belonged to the same or different physiological individuals and between those with potentially the same or different genetic identities.

split-root experiment above. The regenerative 'double plants' were selected so that they had two equal, 47–59 mm long shoots and two equal, 25–36 mm long roots. The length variation allowed between the two shoots or the two roots of the same plant was less than 3 mm. Plants fulfilling these criteria constituted approximately 5% of the seedling batch.

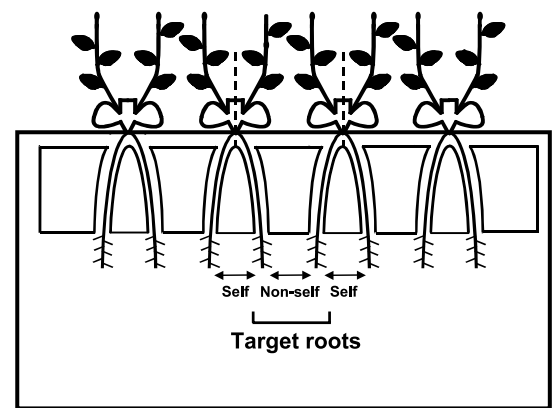
'Double plants' were either longitudinally severed into two genetically identical but physiologically separate individuals or left intact. Each plant (or set of two plant halves) was planted in the middle of a 0.085-L well-drained pot filled with extra-fine vermiculite. They were assigned to one of three treatments (Fig. 2): INTACT, in which the two plant halves remained physiologically integrated; TWINS, in which the two plant halves originated from the same individual plant but were physiologically separate; and ALIEN plants, in which the two plant halves originated from two different individual plants and were physiologically separate.

A strip of Parafilm (Brand, Germany) was placed between the severed halves of the shoot and the hypocotyl of TWINS and ALIEN plants to prevent direct contact while allowing the same physical alignment of the plant halves as in INTACT plants. Measurements were made 18 days after the experiment started, 31 days after germination.

#### VECTORIAL SELF/NON-SELF DISCRIMINATION

An experimental system was developed so that the directional growth of *Pisum sativum* roots could be directly observed and measured without perturbation. Double plants were grown and treated as described above, but plants were arranged to allow free development of roots that were equidistant from neighbouring roots of either the same or other plants (Fig. 3).

In order to avoid edge effects additional plants were planted at equal distances on each side of the target plants (Fig. 3). Each experimental pot therefore included four plants but only the inner 'target roots'



**Fig. 3** Vectorial root responses in INTACT and TWINS treatments (vertical broken line indicates severing in latter). Each target root faced a self root on one side and a non-self root on its other side. ALIEN plants were similarly arranged but both neighbouring roots belonged to non-self plants. Plants were added on both sides of the target plants to avoid edge effects. Roots were directed by 4-mm thick Plexiglas spacers along the initial 50 mm of their length and could develop freely thereafter. When emerging from the spacers the roots were 25 mm away from their neighbouring roots.

(the right root of the left target plant and the left root of the right target plant) were scored (Fig. 3). At the beginning of the experiment the plants were 9 days old and each plant had two  $25 \pm 3$  mm long roots and shoots. The growth chambers were 50 cm deep, 40 cm wide and 4 cm broad, and were slanted at  $30^\circ$  to promote growth of roots along the lower transparent wall of the chamber (e.g. Kuchenbuch & Ingram 2002). Pots were randomly assigned to INTACT, TWINS or ALIEN treatments and their position on the bench was altered every 3–4 days. The transparent walls were covered by opaque plastic sheets and were exposed only for the purpose of root tracing. At the end of the experiment 74–87% of the total root length of the plants could be observed along the transparent wall of the growth chamber and traced on celluloid transparencies. Root systems could be clearly distinguished from one another.

#### GROWTH CONDITIONS, MEASUREMENTS AND STATISTICAL ANALYSES

The plants were grown at  $25^\circ\text{C}$  under continuous  $170 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD of cool-white fluorescent light. The plants were alternately watered with deionized water and 0.1 Hoagland solution (Hoagland & Arnon 1950) at 3-day intervals. Lateral roots were counted if they were longer than 0.5 mm. Root lengths and average diameters that also served to calculate root surface areas were recorded by scanning the freshly harvested roots using DT-Scan software (Delta-T, Cambridge, UK). Dry biomass was estimated after drying the plants at  $70^\circ\text{C}$  in a ventilated oven for 3 days.

Statistical analyses were conducted using SYSTAT 10.0 (SPSS 2000). All dependent variables met the assumptions of parametric statistics. We used one-way

**Table 1** Self/non-self discrimination in *Pisum sativum* seedlings as expressed by various root growth variables. Scores represent triplet means ( $\pm$  SE),  $n = 20$  per treatment. Analyses are for one-way ANOVAs between SELF and NON-SELF treatments

Variable	SELF	NON-SELF	d.f., <i>F</i>	<i>P</i>
Number of lateral roots	21.44 (0.85)	26.63 (0.80)	1, 19.9	< 0.001
Total root length (mm)	418.78 (17.87)	490.90 (21.90)	1, 6.5	0.015
Average root diameter (mm)	0.588 (0.026)	0.689 (0.032)	1, 5.2	0.023
Total root mass (g)	0.0072 (0.0004)	0.0126 (0.0013)	1, 26.9	< 0.001
Proportion of root (root mass/total mass)	0.25 (0.035)	0.37 (0.038)	1, 6.1	0.019

ANOVAs to test differences among treatment averages (randomly assigned pots). Differences between individual treatment averages were further estimated using Fisher's LSD comparisons. Paired *t*-tests were used to analyse differences in root development towards self and non-self neighbours.

## Results

### SELF/NON-SELF DISCRIMINATION

The results indicate that the identity of neighbouring roots could be important for the determination of root development. By the end of the experiment, root development was significantly greater in NON-SELF than SELF treatments (Table 1). NON-SELF roots had, on average, 24% more lateral roots, 17% greater root length, 17% greater root diameter, and 71% greater biomass (Table 1).

### MECHANISM OF SELF/NON-SELF DISCRIMINATION

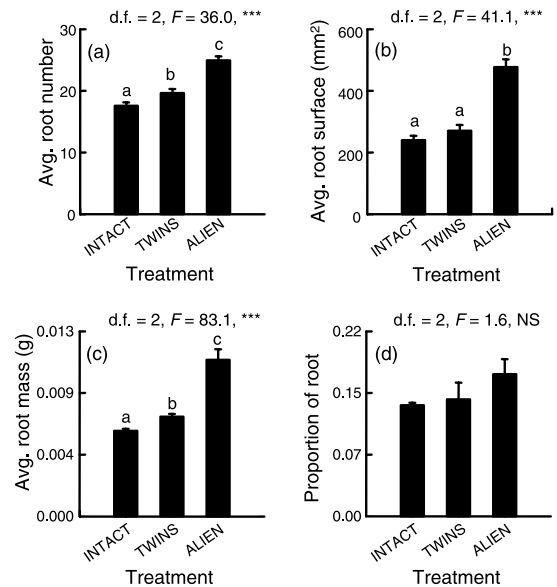
Although a significant difference between INTACT double plants and TWINS (severed, but from same plant) could be found only in number of lateral roots and root mass, all root growth variables were greater in TWINS than in INTACT plants (Fig. 4).

The greatest root development was, however, observed in the ALIEN treatment (27% more roots, 76% greater total root surface, and 57% greater biomass than INTACT plants, Fig. 4), pointing at a general possibility of the involvement of allogenic recognition.

Nevertheless, as both plant halves in INTACT and TWINS originated from the same individual, the increased root development in TWINS (Fig. 4) indicated self/non-self discrimination that was at least partly based on physiological coordination among roots that developed on the same plant, rather than allogenic recognition.

### VECTORIAL SELF/NON-SELF DISCRIMINATION

No dead roots, overlapping roots or direct root contacts among separate root systems were observed throughout the 18 days of the experiment. Such con-



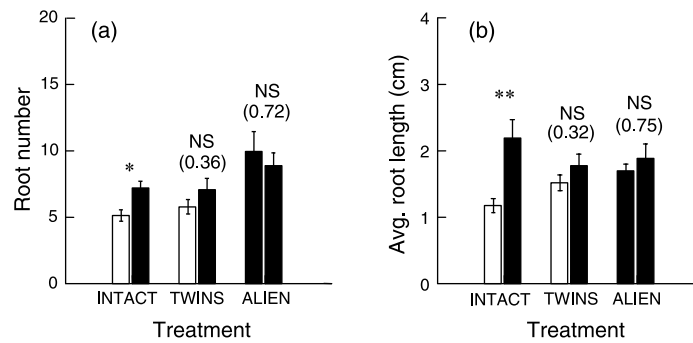
**Fig. 4** Self/non-self discrimination in *Pisum sativum* seedlings as expressed by means ( $n = 46-48$  per treatment)  $\pm$  SE of number of lateral roots (a), root surface (b), root biomass (c), and proportion of total plant biomass allocated to roots (d). Roots developed in the presence of another root on the same plant (INTACT), another detached root that originated from the same individual (TWINS), or a root of a different plant (ALIEN). Results of one-way ANOVAs appear above each figure. Bars that share the same superscript were not significantly different ( $P > 0.05$ ) in LSD comparisons. \*\*\*  $P \leq 0.001$

tacts would have been expected had the roots been insensitive to their neighbours.

Discriminatory root development depended on whether the plants were intact or severed. INTACT plants developed 22% more and 86% longer lateral roots towards non-self than towards self neighbouring roots (Fig. 5). In contrast, pairs of severed plants developed similarly towards their neighbours, regardless of whether these neighbours originated from the same plant (TWINS) or different plants (ALIEN) (Fig. 5).

## Discussion

Our results show that *Pisum sativum* plants appear to be able to differentiate between self and non-self neighbours and develop fewer and shorter roots in the presence of other roots of the same plant. This self/non-self discrimination has a vectorial component whereby plants develop more and longer roots towards roots of



**Fig. 5** Vectorial self/non-self discrimination in root development of *Pisum sativum* seedlings, represented by (a) numbers and (b) lengths of lateral roots that developed towards roots that were part of the same plant (open bars) and roots that originated from different plants (solid bars). The results represent the average scores of the two target roots in each pot,  $n = 8-9 \pm \text{SE}$  per treatment. Significance values (\* $P < 0.05$ , \*\* $P < 0.01$ , NS =  $P > 0.05$ ; numbers in parentheses represent the statistical power of non-significant comparisons) represent the results of paired  $t$ -tests. Neighbouring roots belonged to either the same (INTACT) or different (TWINS) physiological individuals or to different plants (ALIEN).

other plants, regardless of their genetic identity. The increased root development in TWINS compared with INTACT (Fig. 4) and the dependence of the discrimination on the physiological integrity of the plants (Fig. 5) suggest that at least some of the observed self/non-self discrimination was mediated by *physiological coordination* among roots that developed on the same plant rather than *allogenic recognition*. However, the greater root development in ALIEN compared with TWINS implies that the theoretical existence of an additional, *allogenic recognition* mechanism in *Pisum* roots cannot be ruled out. Nevertheless, the following evidence suggests that the probability of the existence of such *allogenic mechanisms* is low.

- There is good evidence that *Pisum sativum* cultivars are genetically uniform (e.g. Mendel 1866; Rathore *et al.* 1993). Genetic uniformity of the experimental plants would mean that the observed self/non-self discrimination could not be due to *allogenic recognition*.
- Vectorial root discrimination was observed in spite of the fact that none of the neighbouring roots ever contacted each other. Known *allogenic recognition* mechanisms are based on direct contacts and involve highly specific cell-surface determinants (e.g. Grosberg & Quinn 1989; Dixit & Nasrallah 2001).
- Complex organic ‘identifying molecules’, such as glycoproteins that are known from self-incompatibility systems (Dixit & Nasrallah 2001), can be expected to be susceptible to rapid decomposition by soil bacteria and fungi (Kjoller & Struwe 1989). This makes chemically based *allogenic recognition* of roots highly unlikely.
- Plants of totally different genotypes (even across plant families) can generally be grafted to each other (e.g. Sinnott 1960; Jones 1969) and roots of some plants are known to cross-graft spontaneously in the wild (e.g. Basnet *et al.* 1993). It can be expected that the existence of chemical *allogenic recognition* systems would prevent such grafts.

Although additional work is needed to ascertain the precise mechanism by which roots of the same physiological individual avoid self-competition (or in-

crease allocation to non-self competition), coordination among organs belonging to the same physiological individual is well documented for the development of shoots and roots (e.g. Sachs 1991), different shoots (Snow 1931; Novoplansky *et al.* 1989; Novoplansky 1996), and roots (e.g. Snow 1938; Gersani & Sachs 1992). Physiological mechanisms have also been mentioned in relation to the avoidance of self-inhibition (rather than the opposite effects seen here) between roots of the same plant in *Ambrosia dumosa* (Mahall & Callaway 1996). Physiological coordination among organs that develop on the same plant is known to be controlled by hormones such as auxin and cytokinins that can be readily transported within intact plants (Sachs 1991). We can offer the speculation that the individual specificity of roots depends on individual hormone(s) and/or electrical oscillations (Goodwin & Cohen 1969) that might be perceived by neighbouring roots without direct contact. The perception of ‘self’ signals might be based on resonant amplification of oscillatory signals in the vicinity of other roots of the same individual plant. Such resonant amplification could not occur in roots that are not oscillating at the same rhythm. The morphogenetic role of hormone and electric oscillations was indicated in internal processes such as xylogenesis in the cambial region of pine trunks (Kurek 1992) and root development (Souda *et al.* 1990). Interestingly, endogenous electric currents can be perceived and monitored outside roots (Weisenseel *et al.* 1992). Regardless of the precise nature of the coordination mechanism among roots that develop on the same plant, it is reasonable to assume that the same internal signals (e.g. hormone oscillations) are retained in the roots for some time after they are no longer physiologically integrated. This might explain why TWINS plants that were separated just before the onset of the experiment demonstrated relatively weaker self/non-self discrimination than ALIEN plants that originated from different individuals (Figs 4, 5).

It is suggested that the demonstrated self/non-self abilities are ecologically advantageous because they

help plants avoid wasteful allocation of resources to competition with self. The ability to discriminate between roots of the same plant and roots of other plants could reduce allocation to competition with self and allow greater resource availability for other functions, including greater reproductive outputs (Gersani *et al.* 2001). Our results are consistent with the findings of Gersani *et al.* (2001) and Holzapfel & Alpert (2003), representing a new 'root communication' phenomenon whose implications complicate existing allocation models. Accordingly, root development is expected not only to increase under limitation of root resources (Bloom *et al.* 1985; McConnaughay & Coleman 1999), but also when non-self competition is perceived.

We suggest that the advantages of self/non-self root discrimination might be especially high in clonal plants that form physiologically integrated groups of closely spaced ramets (e.g. Herben & Hara 1997; Holzapfel & Alpert 2003). Although the ecological rationale of plant clonality is often attributed to the ability of integrated clones to cope with, and take advantage of, environmental heterogeneity (Jackson *et al.* 1985; van Groenendael & de Kroon 1990; de Kroon & van Groenendael 1997; Alpert *et al.* 2003), our findings imply an additional role of clonal integration: avoiding competition among members of the same clone. Accordingly, it could be predicted that physiological coordination and avoidance of competitive interactions with self would be the greatest among closely spaced members of the same clone that are potentially in direct competitive interaction with each other.

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### References

- Alpert, P., Holzapfel, C. & Slominski, C. (2003) Differences in performance between genotypes of *Fragaria chiloensis* with different degrees of resource sharing. *Journal of Ecology*, **91**, 27–35.
- Ayre, D.J. & Grosberg, R.K. (1995) Aggression, habituation, and clonal coexistence in the sea-anemone *Anthopleura elegantissima*. *American Naturalist*, **146**, 427–453.
- Basnet, K., Scatena, F.N., Likens, G.E. & Lugo, A.E. (1993) Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **25**, 28–35.
- Bell, A.D. & Tomlinson, P.B. (1980) Adaptive architecture in rhizomatous plants. *Botanical Journal of the Linnean Society*, **80**, 125–160.

- Bloom, A.J., Chapin, F.S. III & Mooney, H.A. (1985) Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics*, **16**, 363–392.
- Dixit, R. & Nasrallah, J.B. (2001) Recognizing self in the self-incompatibility response. *Plant Physiology*, **125**, 105–108.
- Dubey, R.K., Oparil, S., Imthurn, B. & Jackson, E.K. (2002) Sex hormones and hypertension. *Cardiovascular Research*, **53**, 688–708.
- Dudley, S.A. & Schmitt, J. (1996) Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *American Naturalist*, **147**, 445–465.
- Fitter, A.H., Stickland, T.R., Harvery, M.L. & Wilson, G. (1991) Architectural analysis of plant root systems. I. Architectural correlations of exploitation efficiency. *New Phytologist*, **118**, 375–382.
- Frank, U., Bak, R.P.M. & Rinkevich, B. (1996) Allorecognition responses in the soft coral *Parerythropodium fulvum* from the Red Sea. *Journal of Experimental Marine Biology and Ecology*, **197**, 191–201.
- Gersani, M., Brown, J.S., O'Brien, E.E., Maina, G.M. & Abramsky, Z. (2001) Tragedy of the commons as a result of root competition. *Journal of Ecology*, **89**, 660–669.
- Gersani, M. & Sachs, T. (1992) Developmental correlations between roots in heterogeneous environments. *Plant Cell and Environment*, **15**, 463–469.
- Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities: field experiments with plants. *American Naturalist*, **139**, 771–801.
- Goodwin, B.C. & Cohen, M.H. (1969) A phase shift model for the spatial and temporal organization of developing systems. *Journal of Theoretical Biology*, **25**, 49–107.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. John Wiley, Chichester.
- van Groenendael, J. & de Kroon, H. (1990) *Clonal Growth in Plants: Regulation and Function*. SPB Academic, The Hague.
- Grosberg, R.K. (1988) The evolution of allorecognition specificity in clonal invertebrates. *Quarterly Review of Biology*, **63**, 377–412.
- Grosberg, R.K. & Hart, M.W. (2000) Mate selection and the evolution of highly polymorphic self/nonself recognition genes. *Science*, **289**, 2111–2114.
- Grosberg, R.K., Levitan, D.R. & Cameron, B.B. (1996) Evolutionary genetics of allorecognition in the colonial hydroid *Hydractinia symbiolongicarpus*. *Evolution*, **50**, 2221–2240.
- Grosberg, R.K. & Quinn, J.F. (1989) The evolution of selective aggression conditioned on allorecognition specificity. *Evolution*, **43**, 504–515.
- Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978) *Tropical Trees and Forests: an Architectural Analysis*. Springer, Berlin.
- Hart, M.W. & Grosberg, R.K. (1999) Kin interactions in a colonial hydrozoan (*Hydractinia symbiolongicarpus*): population structure on a mobile landscape. *Evolution*, **53**, 793–805.
- Henriksson, J. (2001) Differential shading of branches or whole trees: survival, growth, and reproduction. *Oecologia*, **126**, 482–486.
- Herben, T. & Hara, T. (1997) Competition and spatial dynamics of clonal plants. *The Ecology and Evolution of Clonal Plants* (eds H. de Kroon & J.M. van Groenendael), pp. 331–357. Backhuys, Leiden.
- Hoagland, D.R. & Arnon, I. (1950) The water culture method for growing plants without soil. *California Agriculture Experiment Station Circular*, **347**.
- Holzapfel, C. & Alpert, P. (2003) Root cooperation in a clonal plant: connected strawberries segregate roots. *Oecologia*, **134**, 72–77.

- Honda, H. & Fisher, J.B. (1978) Tree branch angle: maximizing effective leaf area. *Science*, **199**, 888–890.
- Honkanen, T. & Haukioja, E. (1994) Why does a branch suffer more after branch-wide than after tree-wide defoliation? *Oikos*, **71**, 441–450.
- Ishii, T. & Saito, Y. (1995) Colony specificity in the marine Bryozoan *Dakaria subovoidea*. *Zoological Science*, **12**, 435–441.
- Jackson, R.B.C., Buss, L.W. & Cook, R.E. (1985) *Population Biology and Evolution of Clonal Organisms*. Yale University Press, London.
- Jeschke, W.D. & Wolf, O. (1988) External potassium supply is not required for root growth in saline conditions experiments with *Ricinus communis* L. Growth in reciprocal split-root system. *Journal of Experimental Botany*, **39**, 1149–1168.
- Jones, W.J. (1969) *Plant Chimeras*, 2nd edn. Methuen, London.
- Kimura, M. & Simbolon, H. (2002) Allometry and life history of a forest understorey palm *Pinanga coronata* (Arecaceae) on Mount Halimun, West Java. *Ecological Research*, **17**, 323–338.
- Kjoller, A. & Struwe, S. (1989) Fungi and bacteria as decomposers of organic matter in soil. *Opera-Botanica*, **100**, 147–152.
- Krannitz, P.G. & Caldwell, M.M. (1995) Root-growth responses of 3 Great-Basin perennials to intraspecific and interspecific contact with other roots. *Flora*, **190**, 161–167.
- Krebs, J.R. & Davies, N.B. (1997) *Behavioural Ecology: an Evolutionary Approach*, 4th edn. Blackwell Science, Oxford.
- de Kroon, H. & van Groenendael, J. (1997) *The Ecology and Evolution of Clonal Plants*. Backhuys, Leiden.
- Kuchenbuch, R.O. & Ingram, K. (2002) Image analysis for non-destructive and non-invasive quantification of root growth and soil water content in rhizotrons. *Journal of Plant Nutrition and Soil Science*, **165**, 573–581.
- Kurek, W. (1992) Endogenous oscillations of electric potential difference in the cambial region of the pine stem. II. Possible involvement of the oscillations in xylogenesis. *Acta Societatis Botanicorum Poloniae*, **61**, 221–230.
- Mahall, B.E. & Callaway, R.M. (1991) Root communication among desert shrubs. *Proceedings of the National Academy of Sciences of the USA*, **88**, 874–876.
- Mahall, B.E. & Callaway, R.M. (1996) Effects of regional origin and genotype on intraspecific root communication in the desert shrub *Ambrosia dumosa* (Asteraceae). *American Journal of Botany*, **83**, 93–98.
- McConnaughay, K.D.M. & Coleman, J.S. (1999) Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology*, **80**, 2581–2593.
- Mendel, G. (1866) Versuche über Pflanzen-Hybriden. *Verhandlungen Des Naturforschenden Vereines in Brünn*, **4**, 1–47.
- Nardini, A., Lo, G.M.A. & Salleo, S. (1999) Competitive strategies for water availability in two Mediterranean *Quercus* species. *Plant, Cell and Environment*, **22**, 109–116.
- Novoplansky, A. (1996) Hierarchy among potentially similar buds in two-shoot plants. *Plant, Cell and Environment*, **19**, 781–786.
- Novoplansky, A., Cohen, D. & Sachs, T. (1989) Ecological implications of correlative inhibition between plant shoots. *Physiological Plantarum*, **77**, 136–140.
- Novoplansky, A., Sachs, T., Cohen, D., Bar, R., Budenheimer, J. & Reisfeld, R. (1990) Increasing plant productivity by changing the solar spectrum. *Solar Energy Materials*, **21**, 17–23.
- Penn, D.J. & Potts, W.K. (1999) Evolution of mating preferences and major histocompatibility complex genes. *American Naturalist*, **153**, 145–164.
- Rathore, P.K., Gupta, V.P. & Plaha, P. (1993) Nature of variation and interrelationships among seed yield and some physiological traits in pea. *Crop Improvement*, **20**, 51–54.
- Richman, A. (2000) Evolution of balanced genetic polymorphism. *Molecular Ecology*, **9**, 1953–1963.
- Sachs, T. (1991) *Pattern Formation in Plant Tissues*. Cambridge University Press, Cambridge.
- Sachs, T. & Novoplansky, A. (1997) What does a clonal organization suggest concerning clonal plants? *The Ecology and Evolution of Clonal Growth in Plants* (eds H. de Kroon & J.M. van Groenendael), pp. 55–78. Backhuys, Leiden.
- Schenk, H.J., Callaway, R.M. & Mahall, B.E. (1999) Spatial root segregation: are plants territorial? *Advances in Ecological Research*, **28**, 145–180.
- Schmitt, J., Dudley, S.A. & Pigliucci, M. (1999) Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants. *American Naturalist*, **154** (Suppl.), S43–S54.
- Schmitt, J., McCormac, A.C. & Smith, H. (1995) A test of the adaptive plasticity hypothesis using transgenic and mutant plants disabled in phytochrome-mediated elongation responses to neighbours. *American Naturalist*, **146**, 937–953.
- Sebens, K.P. (1986) Agnostic behavior in the intertidal sea anemone *Anthopleura xanthogrammica*. *Biological Bulletin*, **166**, 457–472.
- Sinnott, E.W. (1960) *Plant Morphogenesis*. McGraw-Hill, New York.
- Smith, H. (1995) Physiological and ecological function within the phytochrome family. *Annual Review of Plant Physiology and Plant Molecular Biology*, **46**, 289–315.
- Snow, R. (1931) Experiments on growth and inhibition. II. New phenomena of inhibition. *Proceedings of the Royal Society of London, Series B*, **108**, 305–316.
- Snow, R. (1938) On the upwards inhibiting effect of auxin in shoots. *New Phytologist*, **37**, 173–185.
- Souda, A.M., Toko, K., Hayashi, K., Fujiyoshi, T., Ezaki, S. & Yamafuji, K. (1990) Relationship between growth and electric oscillations in bean roots. *Plant Physiology*, **93**, 532–536.
- SPSS Inc. (2000) *Systat for Windows*, Version 10.0. SPSS Inc., Chicago, Illinois.
- Tokeshi, M. (1999) *Species Coexistence: Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford.
- Weinig, C. (2000) Plasticity versus canalization: population differences in the timing of shade-avoidance responses. *Evolution*, **54**, 441–451.
- Weisenseel, M.H., Becker, H.F. & Ehlgötz, J.G. (1992) Measurements using a novel three-dimensional recording probe. *Plant Physiology*, **100**, 16–25.
- Whitehead, D., Livingston, N.J., Kelliher, F.M., Hogan, K.P., Pepin, S., McSeverny, T.M. *et al.* (1996) Response of transpiration and photosynthesis to a transient change in illuminated foliage area for a *Pinus radiata* D. Don tree. *Plant, Cell and Environment*, **19**, 949–957.

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