Root navigation by self inhibition

OMER FALIK[1,*], PERLA REIDES[1], MORDECHAI GERSANI[1] & ARIEL NOVOPLANSKY[2]

[1]*Department of Life Sciences, Ben-Gurion University of the Negev, Beer-Sheva, Israel and* [2]*Mitrani Department of Desert Ecology, Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion 84990, Israel*

ABSTRACT

Circumventing physical obstacles is critical for a plant's survival and performance. Although the ability of roots to circumvent obstacles has been known for over 100 years, the phenomena and its mechanisms have received relatively little attention. In this study it is demonstrated that roots of *Pisum sativum* are able to detect and avoid growth towards inanimate obstacles and the hypothesis that this behaviour is based on the sensitivity of roots to their own allelopathic exudates that accumulate in the vicinity of physical obstacles is tested. The development of lateral roots of *Pisum sativum* towards an obstacle (a piece of nylon string, similar in dimensions to a plant root) was followed. Lateral roots were similar in number, but significantly shorter in the direction of the nylon string. In addition, up to half of the lateral roots that developed towards the nylon string withered, whereas no withering was observed in the absence of the nylon string. These avoidance growth patterns were suppressed in the presence of potassium permanganate or activated carbon, indicating a role of allelopathic exudates in promoting obstacle avoidance. The demonstrated obstacle avoidance by self inhibition could increase plant performance by limiting resource allocation to less promising parts of the root system.

Key-words: *Pisum sativum*; activated carbon; lateral roots; obstacle avoidance; phenotypic plasticity; potassium permanganate.

INTRODUCTION

The fundamental architecture of plant roots is dictated by genetically determined architectural plans that are related to the expected availability and distribution of limiting soil resources (e.g. Fitter *et al*. 1991, 2002; Doussan, Pages & Pierret 2003). Nevertheless, the fate and morphology of individual roots are often determined by complex interactions with various environmental factors. The range of adaptations of roots to spatial and temporal heterogeneity of resource availability, stresses, and interactions with other

Correspondence: Ariel Novoplansky. Fax:+ 972 8 6596821; e-mail: anovopla@bgumail.bgu.ac.il

*Present address: Pennsylvania State University, Department of Horticulture, 103 Tyson Building. University Park, PA, 18602–4200, USA.

organisms is enormous (Gregory, Lake & Rose 1987; Caldwell & Pearcy 1994; Altman & Waisel 1997). Various mechanisms allow plants to take advantage of the most favourable soil patches in their immediate environment (Crick & Grime 1987; Caldwell & Pearcy 1994; Hutchings & de Kroon 1994; de Kroon & Hutchings 1995; Alpert & Stuefer 1997). For example, plants are capable of growing along positive gradients of water and minerals (Audus 1975; Jackson & Barlow 1981) and preferentially proliferate in patches relatively rich in resources, such as water (Takahashi 1994), nutrients (Drew & Saker 1975; Jackson & Caldwell 1989; Fitter 1994; Grime *et al*. 1997), and oxygen (Porterfield & Musgrave 1998). Roots are able to avoid various toxins (Miyasaka & Hawes 2001), competition with root of other plants (Mahall & Callaway 1991; Schenk, Callaway & Mahall 1999) and other roots of the same plant (Gersani *et al*. 2001; Holzapfel & Alpert 2003; Falik *et al*. 2003; Gruntman & Novoplansky 2004).

When confronted by physical obstacles, roots grow toward areas of least resistance (Kozlowski 1999; Clark, Whalley & Barraclough 2003). Circumventing physical obstacles could be critical for the plant's survival and performance, especially in rocky environments or when the soil is compacted. Early studies by Charles and Francis Darwin showed that roots tend to avoid inanimate obstacles and that this behaviour is more dominant than the root's tendency to develop geotropically (Darwin & Darwin 1896). They noted that when the tip of *Vicia* roots came in contact with a thin glass plate at a steep angle it changed its morphology and growth direction. These responses were based on the sensitivity of the root apex to tactile stimuli (negative thigmotropism) and the transmission of these stimuli to more remote parts of the root, resulting in curvature and redirection of the root away from the obstacle (Darwin & Darwin 1896). Similarly, when moss protonemata grow towards neighbouring protonemata or a physical obstacle, such as a thin glass plate, they usually stop growing or veer off even before coming into contact with the obstacle (Bopp 1952; Sachs 1997). It was suggested that this behaviour is related to inhibitory effects of substances that are exuded by the protonemata and accumulate in the vicinity of physical obstacles (Bopp & Klein 1963; Klein 1967; Sachs 1997).

In preliminary experiments we found that the seminal roots of *Pisum sativum* developed relatively shorter lateral roots towards nearby vertical obstacles, such as thin bamboo sticks or nylon strings (Novoplansky, unpublished results). In this study we characterize some obstacle-

avoidance responses in roots of *Pisum sativum* and test the hypothesis that this behaviour is based on the sensitivity of roots to their own allelopathic exudates that accumulate in the vicinity of physical obstacles. For that purpose we developed experimental systems in which the directional responses of roots to inanimate obstacles could be observed and quantified non-destructively.

MATERIALS AND METHODS

Characterizing root–obstacle interactions

Growth chambers were designed so the directional growth of *Pisum sativum* roots in the vicinity of physical obstacles could be quantitatively observed without perturbation. Plants were grown in half cylinders of opaque PVC and flat transparent Perspex walls through which the roots could be observed. The flat transparent walls of the chambers were 15 cm wide and 50 cm deep. The chambers were slanted at 30° to promote root growth along the lower flat transparent wall (Gross, Maruca & Pregitzer 1992; Falik *et al.* 2003). The transparent walls were covered by opaque plastic sheets and were exposed only for the purpose of root tracing. Plants with 50 mm long roots were planted in red Rhodoxeralf soil (Dan, Koyumdjisky & Yaalon 1962) or fine vermiculite and the development of lateral roots was observed through the transparent wall. A piece of monofilament nylon string, 0.8 mm in diameter, similar in shape and size to a neighbouring root (Bordallo *et al.* 2002), was secured along the vertical axis of the transparent wall, 1.5, 2.5 or 4.0 cm from the plant (see Fig. 1a). The nylon string was tightly stretched along the wall of the chamber so roots could not penetrate the gap between the nylon string and the wall of the chamber. Root responses to physical obstacles were similar in plants that developed in soil and vermiculite. For simplicity, results are presented only for plants grown in vermiculite, which allowed greater accuracy in root characterization and measurements.

The mechanism of root obstacle avoidance

We tested the tendency of roots to develop toward patches in which root exudates had been inactivated. We observed lateral root development in *Pisum sativum* plants whose lateral roots were confronted by physical obstacles with and without the presence of potassium permanganate, which is a strong oxidizer of organic compounds (Gates-Anderson, Siegrist & Cline 2001; Shaabani, Teimouri & Lee 2003). Plants with 50 mm long roots were planted in the middle of transparent growth chambers as described above, but equidistantly away from two vertical nylon strings that were stretched along the flat transparent wall of the growth chamber 100 mm apart (see Fig. 3a). Sleeves made of fine nylon mesh (3600 holes inch^{-2}), 20 mm in diameter and 150 mm long, were positioned along the nylon strings away from the roots (see Fig. 3a). One of the mesh sleeves in each chamber was filled with 15 g of damp fine vermiculite (control sleeve) while the other sleeve was filled with 15 g of damp fine vermiculite mixed with 5 mg of potassium permanganate (KMnO$_4$, > 99% purity; Sigma-Aldrich, St Louis, MO, USA). The fate, number, and length of lateral roots that developed towards the potassium permanganate and the control mesh sleeves were recorded 18 d after the beginning of the experiment, 21 d after germination. We predicted that if root development was inhibited by their own root exudates, the growth of lateral roots near obstacles would be greater in the direction of the potassium permanganate sleeves.

We assessed the possible role of root exudates near inanimate obstacles in determining the spatial distribution of entire root systems. The directional growth of *Pisum sativum* roots was observed when roots were confronted by physical obstacles with and without the presence of activated carbon, which is a strong absorber of organic compounds (e.g. Mahall & Callaway 1992). Plants with 50 mm long roots were planted in the middle of 20 mm diameter 150 mm long cylindrical sleeves made of fine nylon mesh (3600 holes inch^{-2}) filled with damp fine vermiculite. Preliminary experiments demonstrated that the mesh prevented penetration of roots while allowing free transfer of liquids. The mesh sleeves were surrounded by 150 mm long cellulose dialysis sleeves (Serva, Heidelberg, Germany) evenly filled with 5 g of fine powder of either activated carbon (Innerspace, Two Little Fishies, Coconut Grove, FL, USA) or non-activated carbon (> 99% pure, Fluka) (see Fig. 4). In order to prevent confounding growth responses of the roots we used powder carbon grades that had negligible concentrations (< 0.03 p.p.m) of phosphate. The carbon powder was confined to the dialysis sleeves (hole size 25 Å) so it could absorb organic compounds without contacting the roots. In different treatments the mesh sleeves were aligned with dialysis sleeves so (a) the entire perimeter of the mesh sleeve was surrounded by non-activated carbon; (b) the entire perimeter of the mesh sleeve was surrounded by activated carbon; (c) half of the sleeve's perimeter was surrounded by non-activated carbon while its other half was surrounded by activated carbon; or (d) it was not aligned by dialysis sleeves (see Fig. 4).

Each sleeve with its surrounding dialysis sleeves was positioned vertically in the middle of a 80-mm diameter, 240-mm-deep plastic pot filled with damp fine vermiculite. The plants were harvested 18 d after planting and 21 d after germination. The roots were carefully separated from the vermiculite and the number, length and biomass of lateral roots that developed towards each half sleeve were recorded. Root biomass was measured after drying the roots in a ventilated oven at 70 °C for at least 3 d. We predicted that if root development is inhibited by root exudates, the growth of lateral roots would be greater in the presence and the direction of activated carbon.

Growth conditions and statistical analyses

The plants (*Pisum sativum* var *arvense* Poir. cv. Dunn) were grown at 25 °C under continuous 170 μmol m^{-2} s^{-1} photosynthetic photon flux density of cool-white fluorescent

light. In order to avoid accumulation of minerals in the growth medium the plants were irrigated with deionized water every 3 d with no added minerals. Seeds were soaked for 24 h in aerated water and were germinated in damp vermiculite with radicles pointing downwards. Lateral roots were counted if they were longer than 0.5 mm. Root length was measured from root tracings using a map measure (± 1 mm).

Statistical analyses were conducted using SYSTAT 10.0 (SPSS 2000). Dependent variables were tested for normality and were log-transformed when they did not meet the assumptions of parametric statistics. We used one-way analyses of variance to test differences among treatment averages. Differences between individual treatment averages were estimated using Tukey's HSD comparisons. Paired *t*-tests were used to analyse differences in root development towards different directions.

RESULTS

The fate of roots encountering obstacles

The development of lateral roots was negatively affected by the presence of inanimate obstacles. Seedlings that were planted 1.5 to 4.0 cm away from a vertical nylon string developed a similar number (11 ± 0.42), but 32–36% shorter lateral roots towards the string compared to the opposite direction (Fig.1b & c). The greater the distance of the seminal root from the nylon string the longer the lateral roots (Fig. 1b & d). In no case did any of the lateral roots pass the nylon string, but 36–67% of the roots passed the equally distant reference line on the opposite side of the

seminal root. Although a similar proportion of roots stopped elongating before reaching the nylon string and the reference line, 18–49% of the lateral roots that developed toward the nylon string withered when in close proximity (<5 mm) to the nylon string (Fig. 2). Between 6 and 11% of the lateral roots that developed towards the nylon string changed their original azimuth and grew downwards ('continue') when reaching the nylon string (Fig. 2). Neither withering nor changes in azimuth were observed in lateral roots that developed towards the opposite unobstructed side of the seminal root. The proportion of withered lateral roots was highest (49%) when the plants were planted 1.5 cm away from the nylon string and it decreased to 31 and 18% when the roots were planted 2.5 and 4.0 cm away from the nylon string, respectively.

The mechanism of root obstacle avoidance

The development of lateral roots was affected by the suppression of organic compounds in the growth medium. Plants grown equidistantly from mesh sleeves filled with $KMnO_4$-soaked vermiculite and plain vermiculite developed a similar number, but 50% longer, lateral roots towards $KMnO_4$ sleeves compared with control sleeves (Fig. 3b & c). The greater root development towards $KMnO_4$ sleeves was also apparent after normalizing for the distance between the seminal root and the nylon string. The average ratio of the length of the lateral roots and the distance to their emergent point on the seminal root from the nylon string was 53% greater in the roots that developed towards $KMnO_4$ sleeves compared with the roots that
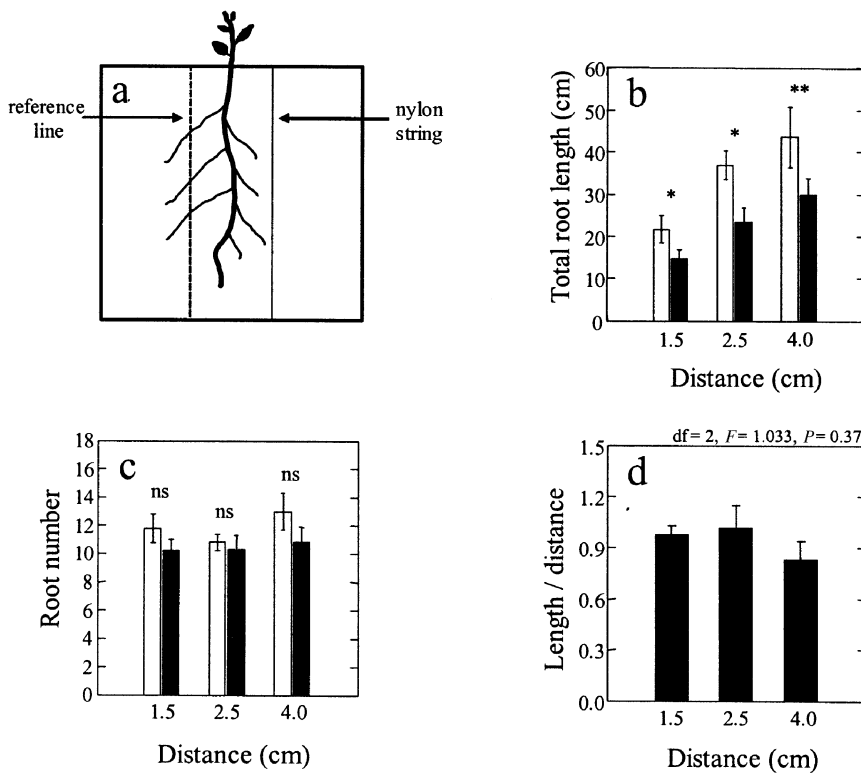

Figure 1. The response of *Pisum sativum* roots to inanimate obstacles. Plants were grown in slanted pots so most roots developed along the pot's transparent wall 1.5, 2.5 or 4.0 cm away from a 0.8-mm monofilament nylon string (a). The average total length (b) and number (c) of lateral roots that developed towards (black) and away (white) from the nylon string, and the average ratio between the length of each lateral root that developed towards the nylon string and the distance of its point of origin from the nylon string (d) recorded from root tracings 18 d after planting. Each bar represents the average ±SE of 7–10 replicates. The significance values above the bars in (b) and (c) are for paired *t*-tests (*$P < 0.05$; ns, $P > 0.05$).
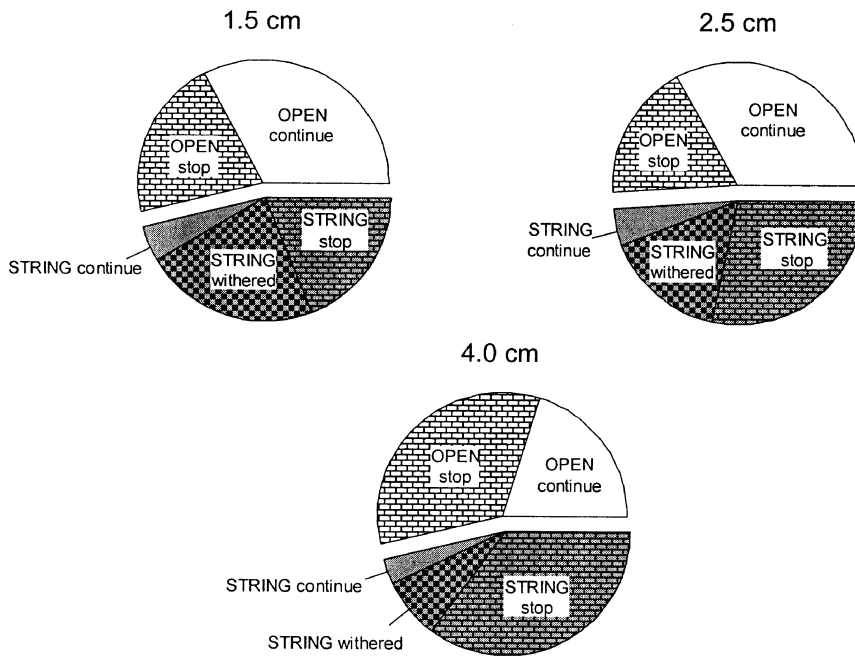
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2.5 cm

4.0 cm

Figure 2. The fate of lateral roots that developed towards and away from an inanimate obstacle (Fig. 1a). Proportions of lateral roots that stopped developing, withered or continued to grow (i.e. changed direction and continued growing downwards) before reaching the nylon string (STRING) or a reference line at the same distance on the opposite side of the plant (OPEN), after roots were grown for 18 d 1.5, 2.5 and 4.0 cm away from a vertical nylon string (Fig. 1).

developed towards control sleeves (Fig. 3d). The proportion of lateral roots that continued to elongate downwards after reaching the nylon string ('continue') was 36 times greater on the potassium permanganate side than on the opposite side (Fig. 3e). A total of 3.9% of the roots that developed towards the potassium permanganate sleeve crossed the nylon string whereas none of the roots that developed towards the opposite side crossed (unpublished
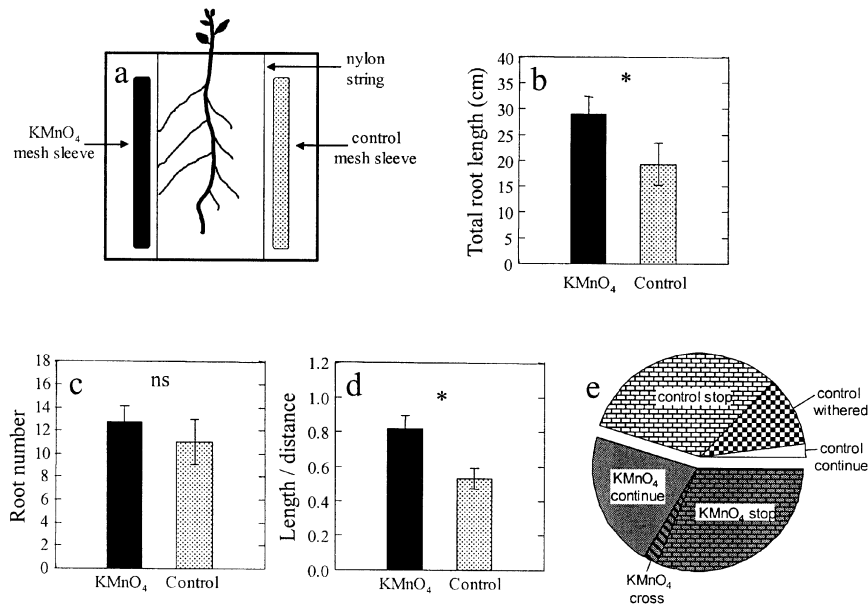

Figure 3. The response of lateral roots of *Pisum sativum* to reduction of root exudates near obstacles. Plants were grown equidistantly away from two vertical nylon strings that were stretched along the flat transparent wall of the growth chamber 5 cm away from the seminal root (a). Sleeves made of a fine nylon mesh were positioned along the nylon strings. One of the mesh sleeves in each chamber was filled with fine vermiculite soaked in potassium permanganate ($KMnO_4$) while the other sleeve (CONTROL) was filled with damp fine vermiculite. Average length (b) and number (c) of the roots that developed towards the potassium permanganate and the control sleeves was determined and the average ratio between the length of each lateral root and the distance of its point of origin from the nylon string was calculated (d) from root tracings that were made 18 d after the experiment started. Each bar represents the average ±SE of eight replicates. The significance values above the bars are for paired *t*-tests, *$P < 0.05$, ns, $P > 0.05$. Proportions of lateral roots that stopped developing, withered, continued to grow before reaching or crossing the nylon string were estimated at the end of the experiment for both control and potassium permanganate sleeves (e).
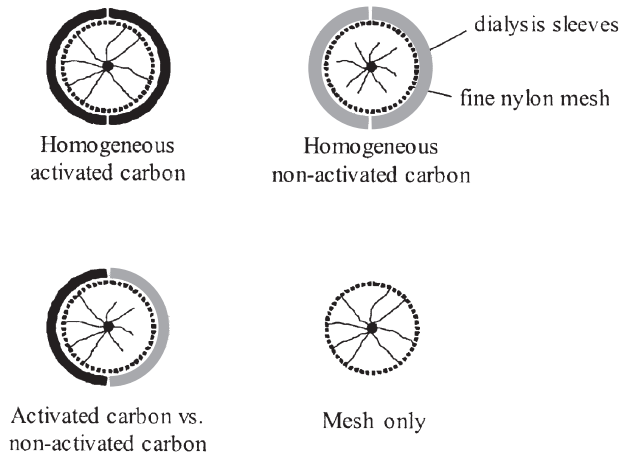
Figure 4. The design of the three-dimensional experiment. Individual *Pisum sativum* seedlings were planted in the middle of a nylon mesh sleeves filled with damp vermiculite. The perimeter of each sleeve was aligned by dialysis sleeves filled with activated carbon (a), non-activated carbon (b), half activated carbon and half non-activated carbon (c), or left free (d).

data). Withering was observed in 24.7% of the roots that developed towards the control sleeves but in none of the roots that developed towards the potassium permanganate (Fig. 3e).

Roots that were surrounded by nylon mesh developed differentially towards cellulose dialysis sleeves that were filled with activated and non-activated carbon (Figs. 4 & 5). Lateral roots developing in the direction of activated carbon were longer and heavier than those growing toward non-activated carbon (Fig. 5a & c). When surrounded by homogeneous activated carbon or mesh only, plants developed 20% longer and 34% heavier lateral roots than when surrounded by homogeneous non-activated carbon (Fig. 5a & c). Differences were more extreme in the heterogeneous treatment where plants developed 51% longer and 57% heavier lateral roots towards the activated carbon than towards the non-activated carbon portion (Fig. 5a & c). Throughout, the number of lateral roots was the least responsive to the treatments and demonstrated a slight dif-

ferential response only to the heterogeneous treatment (Fig. 5b).

DISCUSSION

Root development is prone to interference by obstacles such as rock surfaces, stones, gravel, lumps of compacted or cemented soil and neighbouring roots (Laboski *et al.* 1992; Tsegaye & Mullins 1994; Montagu, Conroy & Francis 1998; Croser, Bengough & Pritchard 2000; Chassot, Stamp & Richner 2001). Although the ability of roots to circumvent obstacles has been known for many years (Darwin & Darwin 1896; Montagu *et al.* 1998; Simojoki 2001), the topic has received relatively little attention in the ecological and physiological literature. Our results suggest that the development of lateral roots of *Pisum sativum* is strongly affected by inanimate obstacles. When developing next to a physical object as small as a monofilament nylon string that resembled in size and shape a neighbouring root, lateral roots stopped elongating or even withered before getting in contact with the string (Figs 1 & 2). Our results also suggest that the extreme sensitivity of roots to inanimate obstacles is mediated by the roots' own allelopathic influences (Figs 3–5). Accordingly, the effect of inanimate obstacles on lateral roots is mediated by reduced diffusion and accumulation of inhibitory root exudates in the vicinity of obstacles. This interpretation is supported by the following findings: (a) lateral root length (including those that developed away from the nylon string) was always inversely correlated to the distance of the main root from the string (Fig. 1b); (b) while a substantial proportion of the lateral roots that developed towards the nylon string withered, no withering was observed in lateral roots that developed away from the nylon string (Fig. 2); (c) the greater the distance of the roots from the nylon string the lower was the proportion of withering roots (Fig. 2); (d) the inhibitory effect of the inanimate obstacles could be reduced by eliminating the root exudates from the growth medium using potassium permanganate or activated carbon (Figs 3–5). Thus, this rather simple mechanism means that roots are not only able to grow away from inanimate obstacles (Dar-
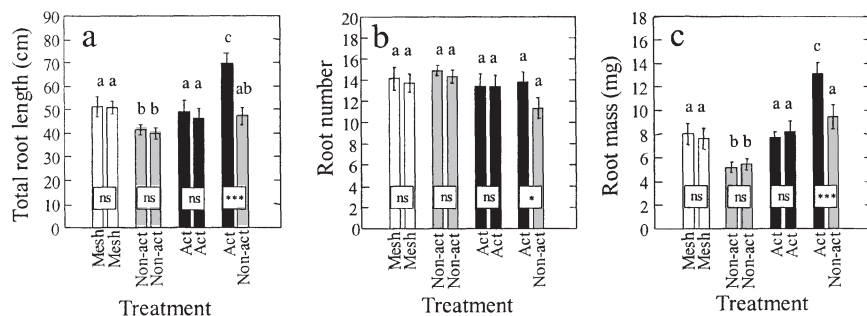

Figure 5. Average length (a), number (b) and biomass (c) of lateral roots that developed in nylon mesh sleeves in the direction of dialysis sleeves filled with activated carbon (Act), non-activated carbon (Non-act) or control sleeves (Mesh) (Fig. 4). Each bar represents the average ±SE of 14–18 replicates. Bars that share the same lettering were not significantly different from each other at a 0.05 probability level in Tukey HSD comparisons. The significance value inserts are for paired *t*-test comparisons between the two sleeve halves, $*P < 0.05$; $***P < 0.001$; ns, $P > 0.05$.

win & Darwin 1896; Leyser & Day 2003) but also roots that develop towards such obstacles are more likely to wither and die (Fig. 2), avoiding further resource allocation to less promising parts of the root system. Interestingly, the observed obstacle-avoidance responses were not accompanied by a greater number of lateral roots toward the preferred direction (Figs 1, 2, 3 & 5). It is hypothesized that the distance of the seminal root from the obstacle (1.5–5.0 cm) was large enough to significantly attenuate the effects of the allelopathic substances on the initiation of lateral roots. Support for this hypothesis comes from experiments in which plants developed no lateral roots towards vertical nylon strings or bamboo sticks that were less than 3 mm away from the seminal root (Novoplansky, unpublished results). Nevertheless, diffusion properties, accumulation and effectiveness of allelopathic substances are expected to be highly dependent on the physical properties of the growth medium and its micro-organismic flora. The importance of these factors as well as the availability of nutrients will have to be studied in a more natural setting in order to understand the relevance of our findings in an ecological context.

The responses of *Pisum* roots to inanimate obstacles are comparable with those of moss protonemata (Bopp & Klein 1963; Sachs 1997). Despite the differences in ontogenetic origin between roots and protonemata, this similarity is not surprising as the underlying mechanism of both of these responses is chemical allelopathy. For plants to utilize such a mechanism they need only be sensitive to their own allelopathic root exudates, and for the diffusion coefficients of the allelopathic substances to generate meaningful gradients that are detectable by the roots. Therefore, it is expected that obstacle avoidance by self inhibition is common among plants with root allelopathy (Hierro & Callaway 2003; Bertin, Yang & Weston 2003). Although obstacle avoidance is probably not the primary evolutionary driving force of allelopathy, it could certainly be a secondary adaptation that is 'hitchhiking' on the more apparent competitive role of allelopathy.

The determination of root development by self inhibition exemplifies an important principle in the mode of operation of phenotypic plasticity. Plastic development necessitates that a plant co-ordinates its responses according to the detected conditions in the immediate environment (Pigliucci 2001; Schlichting & Smith 2002). Recent evidence suggests that in many cases the very same mechanisms are responsible for mediating both the internal interactions between different tissues and organs of the same plant and the interactions of the plant with its external environment (Novoplansky, in preparation). The sensitivity of roots to their own allelopathic exudates means that in addition to root competition (*external function*), allelopathy might be also involved in spacing of roots belonging to the same plant (*internal function*) and avoidance of neighbouring roots and physical obstacles (*external function*). An additional example for such versatility of morphogenetic controls in plants is the multifaceted role of red/far-red spectral signals in the organization of shoot organs; Red/far-red signals are used by plants to perceive and avoid shade by both competitive neighbours (*external*) (Smith 1982; Novoplansky, Cohen & Sachs 1990; Aphalo & Ballarè 1995; Schlichting & Smith 2002) and other organs of the same plant (*internal*) (e.g. Gautier *et al.* 2000).

Pisum sativum is known to possess allelopathic capabilities (Hisashi 2003) and field experiments have shown that residues and extracts of *Pisum sativum* suppressed the growth of several plant species (Schenk & Werner 1991; Akemo, Regnier & Bennett 2000; Hisashi 2003). At least some of the allelopathic compounds in *Pisum* such as pisatin, are exuded by roots (Bagga & Straney 2000; Morandi, Gollotte & Camporota 2002). In this study we did not attempt to identify the substances that are responsible for its ability to avoid obstacles. Some studies have suggested that ethylene might be involved in the inhibitory effects of compacted soil on root development (e.g. Simojoki 2001). However, the efficient elimination of the relevant allelopathic compound by activated carbon (Fig. 5), which is known to be a poor scrubber of ethylene (S.A.S. 2004), implies ethylene may not play a major role. The precise identity of the involved allelopathic compounds might not be of great importance, for the described mechanism can operate using almost any combination of allelopathic compound(s) to which roots are sensitive. The mode of action and adaptive implications of navigation by self inhibition highly resemble those of other, well-documented, plant signalling systems such as the sensitivity to red/far-red signals (Schlichting & Smith 2002) or the dependence of the initiation of new vascular strands on fluxes of auxin (Sachs 1991).

Avoiding growth toward positive gradients of inhibitory substances might improve the efficiency of resource allocation. Instead of merely giving precedence to roots that develop in richer soil patches (Drew & Saker 1975; Crick & Grime 1987; Jackson & Caldwell 1989; Gersani & Sachs 1992; Fitter 1994; Grime & Mackey 2002), this mechanism could cater to improved root spacing as well as the avoidance of inanimate obstacles, well before root resources are limited by these factors.

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