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Root cooperation in a clonal plant: connected strawberries segregate roots

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Abstract The ability to selectively avoid competition with members of the same clone should be highly advantageous but has not been demonstrated in plants. We found that physical connection between plants in a clone of the wild strawberry *Fragaria chiloensis* induced them to segregate their roots, significantly increasing clonal performance. Such increase in performance was not found when plants were grown in containers that artificially divided their rooting zones. There was no effect of connection in a different clone of *F. chiloensis* with a lower degree of carbon transport between connected plants, suggesting that the mechanism for root segregation depended upon transport of a signal through the strawberry runners. We suggest that clonal integration allows some clones to coordinate below-ground resource foraging with other clone members, thus exhibiting a type of root cooperation.

Keywords Clonal plant · Self-competition · *Fragaria chiloensis* · Physiological integration

Introduction

Many animals cooperate with their kin by selectively avoiding competition within families or clones. These animals include clonal invertebrates that are relatively sessile and lack central nervous systems (Sebens 1986; Ayre and Grosberg 1995; Ishii and Saito 1995). Since these animals are relatively "plant-like", it seems plausible that plants might also possess the ability to avoid competition within clones. Roots of the desert shrub *Ambrosia dumosa* decrease their rates of elongation in response to contact with roots of conspecific plants from the same population but not when they contact roots of conspecific plants from a different region (Mahall and Callaway 1996), suggesting that plants can respond differently to other members of the same species depending upon genetic relatedness. Studies in which neighboring plants tended to place their roots away from each other (Brisson and Reynolds 1994; Schenk et al. 1999) or close to each other (Gersani et al. 2001) further indicate that plants can adjust root placement in response to the presence of neighbors. However, no previous study has shown that plants can selectively avoid interference within clones via root segregation.

The potential for cooperation between plants within clones seems especially high in species that bear asexual offspring along creeping stems or roots, i.e., "clonal plants" (de Kroon and van Groenendael 1997). In many of these species, asexual offspring are morphologically and functionally equivalent to whole plants but possess the ability to exchange substances via vascular transport as long as they remain connected by the parental stem or root (Pitelka and Ashmun 1985; Hutchings and Mogie 1990; Jónsdóttir and Watson 1997; Hutchings et al. 2000). This type of physiological integration between connected offspring in clonal plants provides the mechanism for several types of coordinated growth. Such coordination includes specialization to acquire resources that are abundant for one plant but scarce for connected plants ("division of labor"; Alpert and Stuefer 1997; Hutchings and Wijesinghe 1997), and elongation of internodes in response to differences in light availability to different, connected plants (Méthy et al. 1990; Evans and Cain 1995).

We therefore tested the hypothesis that physiological integration in clonal plants can enable them to selectively minimize interference between connected plants of the same clone via root segregation. We used the stoloniferous herb *Fragaria chiloensis* (L.) Duchesne (beach strawberry), in which connected plants along the same stolon exchange carbon compounds and nitrogen (Alpert and Mooney 1986; Alpert 1996). We predicted that, if the hypothesis were true, then: (1) connected plants would

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segregate their roots; (2) disconnecting plants would eliminate root segregation, showing that physiological integration was the mechanism for segregation; (3) connected plants would accumulate more biomass than disconnected ones, under conditions of nutrient limitation, showing that root segregation increased resource capture; (4) clones with a lower degree of physiological integration would show less effect of connection on biomass than clones with a higher degree of integration when nutrients are limited, further linking integration and root segregation.

Materials and methods

Collection and propagation

Plants were collected from a natural population on coastal sand dunes at Año Nuevo State Reserve (37° 3' N, 122° 13' W), about 100 km south of San Francisco, California (see Alpert and Mooney 1996 for a description of the site), and propagated through at least ten vegetative generations in a greenhouse at the University of Massachusetts in Amherst before use. Plants of *Fragaria chiloensis* consist of a short, usually unbranched, partially buried stem with a rosette of leaves and fibrous roots. The axillary bud of a leaf can produce a stolon or an inflorescence. Stolons rarely branch and typically produce a new plant at every other node, generally 20–40 cm apart.

Experimental designs

For the first experiment (Fig. 1a), newly produced plants, still connected to their parent plants and several sibling plants by a stolon, were rooted in pots (12 cm diameter × 12 cm depth) filled with fine, acid-washed sand. After 2 weeks of establishment, plants were separated into pairs of adjacent offspring by severing the stolon between every other plant along a stolon. Severing stolons between plants has no direct effect on plant growth in *F. chiloensis* (Alpert 1991). Four weeks later, 25 pairs were selected for the experiment on the basis of similarity in plant size. Twenty pairs, selected at random, were each transplanted into a single pot (12 cm × 12 cm) to initiate potential root competition, and the connection between plants was severed midway between them in half of the pairs, also selected at random. The other pairs were each transplanted into two pots, so that plants could not experience competition, and disconnected. All three treatments (connected, two plants per pot; disconnected, two plants per pot; and disconnected, one plant per pot) were randomly arranged on the same greenhouse bench. Plants were watered with a 1/4 strength Hoagland's solution (Alpert and Mooney 1986) containing 10 mg $N\text{-}NO_3\ l^{-1}$ (0.71 mM). This nitrogen concentration was selected on the basis of previous work (Alpert 1991) to be limiting to growth but sufficient to support growth. All pots were watered whenever the surface of the sand in any pot became dry. Enough solution was added at each watering to flush the sand and help prevent any buildup of nutrients. Plants were placed on a single bench in the greenhouse and grown from November to April under fluorescent light at approximately 500 $\mu M\ m^{-2}\ s^{-1}$ for 12 h per day. After 22–24 weeks, cores (1.5 cm diameter × 8 cm depth) were collected with a metal cylinder and plants were harvested. Roots were separated from the sand by hand, and roots from cores and plants were dried at 60°C and weighed. To eliminate variation due to genetic differences between plants, all plants were from the same clone.

The second experiment was intended to test whether effects of connection and plant density on distribution of root mass and accumulation of total dry biomass by plants could be repeated using plants of a different age and whether root segregation could be further documented using a second technique. For this experiment, we rooted newly produced plants directly in the experimental pots, so that plants were 2 weeks old (i.e., "juveniles") rather than 6 weeks old (i.e., "adults") at the start of treatments. We used 45 pairs of plants, 25 distributed among treatments as in the first experiment and 10 additional pairs in each of the two treatments with two plants per pot. Other features of the experimental design were the same as in the first experiment. After 7 weeks of treatment, each of the plants in the additional pairs was fed dye through plastic tubing attached to two cut leaf petioles. One plant in each pair received a green dye (1% acid fast green in water) and the other a red dye (0.5% acid fuchsin in water). Previous trials showed that dye could be traced in the root systems when plants were sufficiently droughted and all leaves were cut prior to dye application. Such treatment ensured a sufficient downward movement of the dye solution into the roots. A core was then taken halfway between the two rosettes, and the dyed root fragments of each color in a sample of the core were counted. These plants were not included in the measurements of root mass distribution or final plant mass.

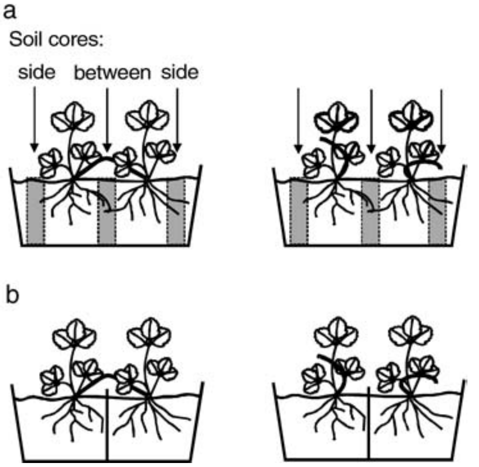

Fig. 1. Plant connection and pot partitioning treatments: connected and unconnected pairs of plants of *Fragaria chiloensis* in **a** unpartitioned and **b** partitioned pots, showing location of cores used to measure root mass distribution

For the third experiment (Fig. 1a, b), we crossed connection treatments (connected, two plants per pot; or disconnected, two plants per pot) with two rooting volume partitioning treatments (pots not partitioned as in the first two experiments or pots partitioned) and applied the treatments to two clones, the one used in the first two treatments and a clone known to have a lower degree of physiological integration (Alpert 1999). In the partitioned treatment, pots (again 12 cm × 12 cm) were divided into two equal volumes with a tightly fitted, vertical plastic divider, and one plant was rooted on either side of the partition. The unpartitioned treatment permitted roots to overlap; the partitioned treatment prevented that without changing total resource availability per plant.

Data analysis

We analyzed the first and second experiments together, using ANOVAs run with SYSTAT 9.0. Effects of connection (connected, two plants per pot; or disconnected, two plants per pot), position (between plants, or on the side of each plant away from the other plant), and experiment/developmental stage (first experiment, adults; or second experiment, juveniles) on root mass density were tested in a three-way ANOVA. Orthogonal comparisons were used to test for selected differences between individual means. Effects of

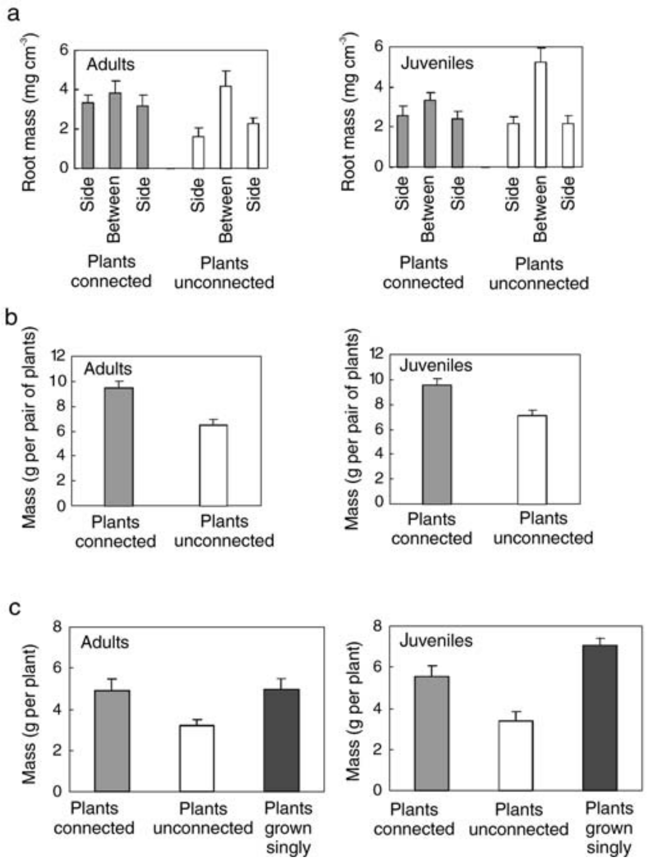

Fig. 2 Effect of connection between plants on **a** distribution of root mass between and on the sides of plants, **b** total dry biomass of pairs of plants, and **c** total dry biomass of single plants within pairs. Values are means + SE, *n*=10

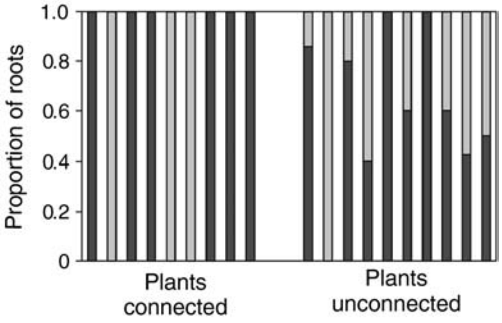

Fig. 3 Proportion of root fragments in cores placed halfway between plants by each plant in a pair. Each *bar* represents results for one pair, with a *shaded* portion for one plant and an *unshaded* portion for the other. Data are shown for nine connected and ten unconnected pairs

Table 1 Analysis of variance in root mass due to position (core taken between plants or to the side), connection (plants connected or unconnected), and experiment (first experiment, starting with adult plants or second experiment, starting with juvenal plants). See Fig. 2a for data

Source of variation	SS	*df*	*F*	*P*
Position	0.034	1	19.99	<0.001
Connection	0.001	1	0.191	0.664
Experiment	0.001	1	0.003	0.957
Pos. x Conn.	0.011	1	6.601	0.012
Pos. x Exp.	0.001	1	0.595	0.443
Conn. x Exp.	0.005	1	3.190	0.078
Pos. x Conn. x Exp.	0.001	1	0.184	0.669
Error	0.121	73		

connection and experiment/developmental stage on total final dry mass per pair of plants were tested in a two-way ANOVA. Effect of connection and density (connected, two plants per pot; disconnected, two plants per pot; or disconnected, one plant per pot) on total final dry mass per plant was tested in a one-way ANOVA; in the first two treatments, mass of one plant in each pair was chosen at random to use in this analysis.

Effect of connection on the proportion of dyed roots belonging to each plant in the dye-labeled pairs in the second experiment was tested with Fisher's exact test (Siegel and Castellan 1988). In the third experiment, effects of connection and partition (pot partitioned or pot not partitioned) on mass per pair of plants were tested in two separate two-way ANOVAs, one for the clone with high degree of integration between connected plants and one for the clone with lower degree of integration.

Results

Root segregation

Plants placed less root mass between them and more on the side away from the other plant when they were connected than when they were not (Fig. 2a, Table 1). This effect of connection on distribution of root mass did not differ between experiments (no significant interaction effect between root position, connection and experiment effects, Table 1), although the underlying components of the effect may have differed. Adult pairs responded to connection mainly by increasing rooting on the sides, whereas juveniles responded mainly by limiting rooting between plants (Fig. 2a). Overall, data on distribution of root mass thus showed that connection between plants resulted in root segregation. Connected and unconnected plants did not differ significantly in their root/shoot ratios (data not shown).

In the dye-labeled plants (Fig. 3), each core taken halfway between the plants in a pair contained roots from just one plant if the plants were connected, whereas most cores contained roots from both plants if the plants were unconnected (Fisher's exact test: 9.98, *df*=1, *P*=0.003). This suggested that one plant in each connected pair might have dominated the rooting volume between them; if so, that did not cause inequality in their performance, since variability in the total biomass of plants within pairs was not consistently greater in connected than in unconnected or singly grown plants (see SEs in Fig. 2c). Results from dye-labeling thus also suggested that connection induced root segregation.

Table 2 Analysis of variance in combined final dry mass of plants within pairs due to connection (plants connected or unconnected) and experiment (first experiment, starting with adult plants or second experiment, starting with juvenal plants). See Fig. 2b for data

Source of variation	SS	*df*	*F*	*P*
Connection	62.61	1	41.21	<0.001
Experiment	3.92	1	2.58	0.117
Conn. x Exp.	2.68	1	1.77	0.192
Error	56.21	37		

Table 3 Analysis of variance in combined final dry mass of plants within pairs due to connection (plants connected or unconnected), and partition of pot (entire or divided). See Fig. 4 for data

Source of variation	SS	*df*	*F*	*P*
(a) Clone used in all experiments				
Connection	50.53	1	4.99	0.032
Partition	31.68	1	3.13	0.086
Conn. x Part.	61.05	1	6.03	0.019
Error	354.20	36		
(b) Clone with a lower level of transport through stolons				
Connection	0.08	1	0.004	0.952
Partition	143.16	1	6.03	0.019
Conn. x Part.	0.02	1	0.0004	0.976
Error	853.59	36		

Accumulation of biomass

In the first two experiments, connected plants accumulated more combined biomass than disconnected plants did (Fig. 2b, Table 2). The effect of connection did not differ significantly between experiments or developmental stage. Disconnected plants that were grown one to a pot accumulated more biomass than the disconnected plants that were grown two to a pot (Fig. 2c; *P* [orthogonal comparisons]: adult, first experiment 0.001; juveniles, second experiment <0.001). Connected adults accumulated about as much mass as singly grown adults (*P* [orthogonal comparison] = 0.9). Connected juveniles grew more than unconnected juveniles (*P*<0.001) but less than singly grown juveniles (*P*<0.001).

In the third experiment, pairs of plants of the same clone as in the first two experiments again accumulated more mass if connected than if unconnected and grown in unpartitioned pots (Fig. 4a, Table 3; *P* [orthogonal comparison] = 0.001). In contrast, mass of pairs grown in pots with a partition (i.e., without the potential for root overlap) was not affected by connection (*P*=0.7).

This corroborated the results from the first two experiments and further indicated that the effect of connection on the mass of plant pairs in this clone was specifically due to avoidance of root overlap. Connection had no effect on the mass of plant pairs from a different clone previously shown (Alpert 1999) to have a lower degree of physiological integration between connected plants (Fig. 4b). This was true both in partitioned (*P* [orthogonal comparison] = 0.7) and unpartitioned pots (*P*=0.9). This suggested that not all clones of *Fragaria chiloensis* are capable of avoiding root overlap between connected plants. Ramet pairs of the highly integrated clone unexpectedly produced less mass in partitioned pots than pairs of the clone with lower level of transport (Fig. 4a, b, (*P* [orthogonal comparison between clones] = 0.03)).

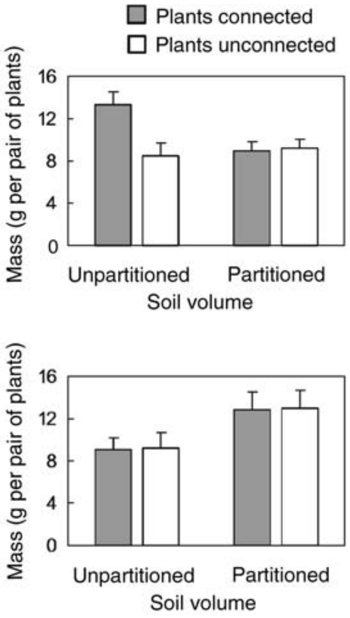

Fig. 4 Effects of connection and pot partitioning on the total dry biomass of pairs of plants (mean + SE, *n*=10), in **a** the clone used in all experiments and **b** a clone with a lower level of transport through stolons

Discussion

We conclude that physical connection between plants in at least some clones of *Fragaria chiloensis* can induce root segregation and that root segregation can increase plant performance; this most likely due to increased resource capture. Such root segregation clearly will have important implications for the avoidance of root self-competition between members of a plant clone. The fact that plants within connected pairs were able to accumulate as much (adults) or nearly as much (juveniles) biomass as plants grown singly suggests that connection enabled them to avoid self-competition at least to some degree. We suggest the term "root cooperation" for this phenomenon, because it shows both of the essential elements of cooperation, coordinated behavior and mutual benefit (e.g., Alpert and Stuefer 1997). Root cooperation could be of considerable benefit to *F. chiloensis* in natural populations because there is strong potential for self-competition between roots of plants of the same clone in natural populations. Plants along a stolon are typically close enough that their roots can intermingle, and soil resources such as nitrogen strongly limit the growth of *F.*

chiloensis in natural habitats on sand dunes along the west coast of North America (Alpert 1996).

The most obvious possible mechanism for avoidance of self-competition through root segregation in *F. chiloensis* is via physiological integration between connected plants due to vascular transport between stolons. It has been previously shown that maintaining physical connections between members of a plant clone can increase their performance when resources are uniform (Lovett Doust 1981; Schmid and Bazzaz 1987; de Kroon et al. 1992). This would explain why disconnecting plants reduces root segregation and in turn decreases overall plant performance. It is also consistent with the difference between clones that we found in this study. We found clear evidence for root segregation in a clone of *F. chiloensis* known to have a relatively high degree of resource sharing between connected plants (Alpert 1999) and much less indication for such segregation in a less integrated clone. If connection between plants is required for cooperation within plant clones, then the potential to avoid competition within clones is more limited in plants than in clonal animals. At least some of these animals can recognize and avoid competition even with unconnected members of the same clone (Sebens 1986; Ayre and Grosberg 1995; Ishii and Saito 1995).

One alternative mechanism for root segregation could be local depletion of soil resources combined with the well-known tendency of many plants to locate more roots where soil water or nutrient availability is higher (Caldwell et al. 1991; de Kroon and Hutchings 1995; Casper and Jackson 1997). Gersani and Sachs (1992) and Gersani et al. (1998) argue that patterns of soil resource depletion could induce root segregation in the absence of any transmission of substances between plants. However, it is not easy to see how this mechanism could account for dependence of root segregation upon connection between plants.

Another alternative mechanism for selective root segregation could be recognition between plants by means of chemicals released into the soil (Mahall and Callaway 1996; Schenk et al. 1999) or detected upon root contact (Mahall and Callaway 1991). Again, it is hard to see how this could explain an effect of connection between plants on root segregation. Moreover, in the desert shrub *Ambrosia dumosa* studied by Mahall and Callaway (1996), separate plants (ramets) generated by artificially dividing and propagating a shrub showed reduced elongation of roots after contacting each other's roots, whereas roots of the same plant showed no reduction in elongation after contacting each other. Such clonal fragments occur naturally when sections of the shrubs split apart (Schenk 1999). This may lead to a positive effect of disconnection between plants of the same clone on root segregation, instead of the negative effect seen in *F. chiloensis*.

Pot partitioning had one unexpected effect on the clone that showed avoidance of self-competition (Fig. 4a). If the sole effect of partitioning were to prevent root overlap, then pairs of plants that were unconnected and therefore subject to root overlap should perform better in partitioned than in unpartitioned pots. Instead, unconnected plants performed equally well in the two pot types. In contrast, in the clone that did not show evidence for avoidance of self-competition (Fig. 4b), effects of partitioning were consistent with the assumption that the only effect of partitioning was to prevent root competition; unconnected plants of this clone did perform better in partitioned than in unpartitioned parts. These patterns are difficult to interpret. One notion is that the well-integrated clone did not place roots selectively under the specific experimental conditions. To maintain symmetry between plant placement in the two treatments, plants in partitioned pots were placed such that they were closer to the partition than to the side of the pot, creating a smaller rooting volume towards than away from the partition. Under such conditions root placement directed towards the partition could lead to crowding and therefore to relative low efficiency of resource uptake (see McConnaughay and Bazzaz 1991). That this happened only with the well-integrated clone is consistent with suggestions that strong integration between ramets should dampen plastic responses to local conditions by individual ramets (Hutchings and Price 1993; Dong 1995). However, there has been very little work on differences between plant clones within species in regard to plasticity. On the other hand, the lower than expected performance of well integrated ramet pairs in divided soil volumes suggests that actual root contact is needed for coordinated root growth. The underlying mechanisms for such a scenario are not yet known, but may suggest active communication among roots as it has been demonstrated for roots of a desert shrub (Mahall and Callaway 1991). In that study, specific root growth responses have been found only after roots of neighboring plants actually touched each other.

In sum, it appears that the ability to avoid self-competition between plants of the same clone via root segregation could be a hitherto unrecognized consequence of clonal growth in some clones in some species. Because many clonal species form large groups of connected, closely spaced, vegetative offspring (e.g., Herben and Hara 1997), "root cooperation" within clones could significantly increase the fitness of these clones in natural populations.

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