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The effects of temporal variation in soil carbon inputs on resource allocation in an annual plant

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Abstract

Aims

Resource allocation in plants can be strongly affected by competition. Besides plant–plant interactions, terrestrial plants compete with the soil bacterial community over nutrients. Since the bacterial communities cannot synthesize their own energy sources, they are dependent on external carbon sources. Unlike the effect of overall amounts of carbon (added to the soil) on plant performance, the effect of fine scale temporal variation in soil carbon inputs on the bacterial biomass and its cascading effects on plant growth are largely unknown. We hypothesize that continuous carbon supply (small temporal variance) will result in a relatively constant bacterial biomass that will effectively compete with plants for nutrients. On the other hand, carbon pulses (large temporal variance) are expected to cause oscillations in bacterial biomass, enabling plants temporal escape from competition and possibly enabling increased growth. We thus predicted that continuous carbon supply would increase root allocation at the expense of decreased reproductive output. We also expected this effect to be noticeable only when sufficient nutrients were present in the soil.

Methods

Wheat plants were grown for 64 days in pots containing either sterilized or inoculated soils, with or without slow-release fertilizer, subjected to one of the following six carbon treatments: daily (1.5 mg glucose), every other day (3 mg glucose), 4 days (6 mg glucose), 8 days (12 mg glucose), 16 days (24 mg glucose) and no carbon control.

Important Findings

Remarkably, carbon pulses (every 2–16 days) led to increased reproductive allocation at the expense of decreased root allocation in plants growing in inoculated soils. Consistent with our prediction, these effects were noticeable only when sufficient nutrients were present in the soil. Furthermore, soil inoculation in plants subjected to low nutrient availability resulted in decreased total plant biomass. We interpret this to mean that when the amount of available nutrients is low, these nutrients are mainly used by the bacterial community. Our results show that temporal variation in soil carbon inputs may play an important role in aboveground–belowground interactions, affecting plant resource allocation.

Keywords: resource allocation, temporal variation, soil carbon inputs, immobilization, microbial loop, *Triticum*

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INTRODUCTION

Plant–plant competition is an inevitable way of life for many plant species. It is therefore not surprising that a substantial amount of research has been devoted to its effect on plant growth, resource allocation and community structure (e.g. Casper and Jackson, 1997; Goldberg, 1990; Goldberg and Barton, 1992; Wilson and Tilman, 1992). However, a plant in the field also engages in competition with the soil microorganisms in its vicinity (e.g. Chapin *et al.*, 1986; Harte and Kinzig, 1993; Kaye and Hart, 1997; Marion *et al.*, 1982; Schmidt *et al.*, 1997a). Although receiving less attention than plant–plant competition, such competitive interactions can have significant effects on plant performance (Hodge *et al.*, 2000; Inselsbacher *et al.*, 2010; Kaye and Hart, 1997; Schmidt *et al.*, 1997b), resulting in decreased biomass (Eschen *et al.*,

2006; Jonasson *et al.*, 1996a, 1996b; Schmidt *et al.*, 1997b), as well as in changes in resource allocation (Eschen *et al.*, 2006; Schmidt *et al.*, 1997b).

Plant root exudation is an important belowground process that can mediate the interaction between plants and soil microorganisms (Jones *et al.*, 2004; Wang *et al.*, 2012). Plants have been shown to exudate a highly diverse array of substances into the rhizosphere (Bertin *et al.*, 2003; Farrar *et al.*, 2003; Uren, 2007). Such root exudation has been shown to account for a significant fraction of plant fixed carbon, ranging from minute amounts (Farrar *et al.*, 2003; Jones *et al.*, 2004) up to significant carbon costs, which can be as high as 40% of the dry matter produced by plants (Lynch and Whipps, 1990). This substantial voluntary contribution of carbon into the soil is especially interesting considering the nature of the interaction between plants and their associated bacterial community (Keurentjes *et al.*, 2011). While both need energy and nutrients in order to grow, each is dependent on the other to supply one of these requirements. On the one hand, while plants can produce their own energy by photosynthesis, they are unable to mineralize soil organic matter (SOM), which is the main source of nutrients in the soil, and are dependent on the bacterial community's ability to do so. On the other hand, most of the soil bacterial community is dependent on plants as the main suppliers of external energy sources, in the form of carbon compounds found in leaf litter (Bowman *et al.*, 2004), dead root material (Griffin *et al.*, 1976) and in root exudates (Meier *et al.*, 2009).

Plant originated carbon inputs have been shown to cause significant changes in a variety of soil processes part of which can directly and indirectly influence nutrient availability (Cheng *et al.*, 2014). Nutrient immobilization by the bacterial community is a possible outcome of fresh carbon inputs into the soil and one of the main avenues by which the bacterial community can restrict plant growth (e.g. Schmidt *et al.*, 1997b). Due to their highly efficient nutrient uptake abilities, the bacterial community is able to quickly and efficiently uptake large quantities of nutrients (Jonasson *et al.*, 1999). However, the fact that plants manage to grow in a great variety of habitats indicates that the bacterial uptake efficiency is not absolute. Spatial variability in nutrient availability can create nutrient gradients, which plant roots should be able to intercept (Schimel *et al.*, 2004). This ability is enhanced due to the longevity of plant roots compared to soil microbes, which have relatively a short turnover rate (Jonasson *et al.*, 1999), enabling plants to accumulate nutrients slowly over relatively long time periods (Schimel and Bennett, 2004).

The negative effects that carbon exudates can have on plant growth contrast with an opposite role that they have also been shown to play. Specifically, according to the 'microbial loop' hypothesis (Clarholm, 1985), plants release carbon into the rooting zone to stimulate the growth of the bacterial community. During this period of bacterial growth, large amounts of nitrogen (N) from organic matter are mineralized (a process plants cannot perform on their own) and immobilized by bacteria. This increase in SOM decomposition as a result of plant originated carbon has been termed 'priming effect' (Blagodatskaya and Kuzyakov, 2008; Cheng *et al.*, 2014; Fontaine *et al.*, 2003, 2011; Kuzyakov *et al.*, 2000; Perveen *et al.*, 2014; Shahzad *et al.*, 2015). The mineralized N is later liberated from the microbes and made locally available for uptake by plants due to the strong top-down regulation inflicted upon the bacterial community by bacterial predators, therefore resulting in a net positive effect on plant growth.

The fact that soil carbon inputs can have both negative and positive effects on plant growth suggests that there might be another important factor at play here. Since soil carbon availability is one of the main determinates of bacterial biomass, it is possible that temporal variation in soil carbon inputs will result in significant changes in the bacterial biomass, altering their competition with plants over nutrients. One possible mechanism generating temporal variability in soil carbon inputs is the increase in rhizodeposition following defoliation/grazing (Hamilton and Frank, 2001; Paterson and Sim, 1999). Notably, these facilitating effects of defoliation on rhizospheric processes can positively affect soil inorganic N pools, plant N uptake, leaf N content and photosynthesis (Hamilton and Frank, 2001). Unlike the effect of overall amounts of carbon added to the soil on plant performance, the effect of fine scale variability in soil carbon inputs has received limited attention (but see Schmidt *et al.*, 1997b).

We hypothesize that continuous carbon supply (small temporal variance) should retain a relatively constant bacterial biomass, leaving fewer nutrients for plant uptake, thus restricting plant growth. In contrast, soil carbon pulses (large temporal variance) can result in significant bacterial biomass oscillations. During the phases of bacterial biomass decline, large amounts of nutrients should be liberated and are expected to increase plant nutrient availability (Jonasson *et al.*, 1996a).

In this study, we manipulated the temporal pattern of soil carbon input (continuous vs. pulse) for wheat plants growing in sterilized and non-sterilized SOM poor soils and subjected to varying levels of nutrient availability. Since plants tend to increase their root allocation under nutrient shortage, we predicted that continuous carbon supply should increase root allocation at the expense of decreased reproductive output due to high nutrient immobilization. In contrast, we posited that carbon pulses should bring about an increase in reproductive allocation at the expense of decreased root allocation, owing to the increased nutrient availability associated with bacterial biomass decline. We expected these effects to be noticeable only when sufficient nutrients are present in the soil. This is because under severe lack of nutrients, the response of the bacterial community to the added carbon will be limited (Rosswall, 1982). To the best of our knowledge, this is the first attempt to test the effect of small scale temporal variation in the soil carbon inputs on plant performance and allocation.

MATERIALS AND METHODS

Pot preparation

Potting material was composed of four parts of washed dune (31°06′N, 34°49′E; for a chemical description of the soil, see Singer, 2007) and one part of Loess soil collected from the hills outside Be'er Sheva, Israel (31°16′N, 34°50′E; for a chemical description of the soil, see Singer, 2007). A SOM poor potting material was used in order to enable a low nutrient treatment, high nutrient availability was created using fertilizer (see below). Moist potting material was put into autoclave bags and was sterilized at 120°C. The bags were kept closed and were sterilized again a week later. Plastic pots (10×10×15 cm) were filled with 280 ml of the above-described potting material. The soil pH was 7.76 and electrical conductivity was 2.02 mS following 1:1 w/w water extraction (CyberScan pH 11, Thermo Fisher Scientific Inc.; Soil and Plant Analysis Council Inc. 1999). The soil bulk density was 1.512 g cm^{-3}. All pots were placed in a tub with shallow water until they reached field capacity. The pots were placed in a growth room with a 12/12 light/dark cycle and were kept at 24°C with 40–60% relative humidity. Pots were placed on elevated nets in order to avoid drainage of water from one pot to the next. Light intensity at pot level was 121.28±20.9 (μE m^{-2} s^{-1} ± SD).

Soil inoculation

Half of the pots were inoculated using 25 ml of unsterilized potting material. The other half received the same volume of sterilized potting material.

Germination

Seeds of cultivated wheat (*Triticum aestivum*, Yuval variety) were soaked in water for 24 h, after which two seeds were sown in each pot. Sowing took place 2 days after the second sterilization round. One week after sowing, seedlings were thinned to one seedling per pot and the carbon treatments were initiated.

Carbon treatment

Carbon treatments were executed every 24 h for 64 days. Every pot was assigned to one of the following six carbon treatments: daily (1.5 mg glucose), every other day (3 mg glucose), 4 days (6 mg glucose), 8 days (12 mg glucose), 16 days (24 mg glucose) and no carbon control. In all these treatments, except for the control, the cumulative amount of carbon added to each pot throughout the experiment was the same (96 mg glucose). This amount of glucose equaled ~12 and 4% of the final total plant biomass of the low and high nutrient treatments, respectively. Such values fall within the range of previously recorded values of rhizodeposition (e.g. Farrar *et al.*, 2003; Paterson and Sim, 1999). The carbon was given as glucose powder mixed in 4.5 ml of water. Glucose has been previously shown to invoke significant changes in bacterial biomass (e.g. Blagodatskaya and Kuzyakov, 2008). Although often containing glucose, root exudates contain many other C-compounds that are likely to affect the soil bacterial community in different ways. We deliberately chose to use glucose because it is a simple sugar, used by many bacterial species.

Plants not receiving carbon on a certain date received 4.5 ml of plain water instead. Besides this water, each plant received an extra 4.5–30 ml of water after the carbon addition in order to maintain pot moisture (the amount of water increased as the season progressed but was consistent among all pots).

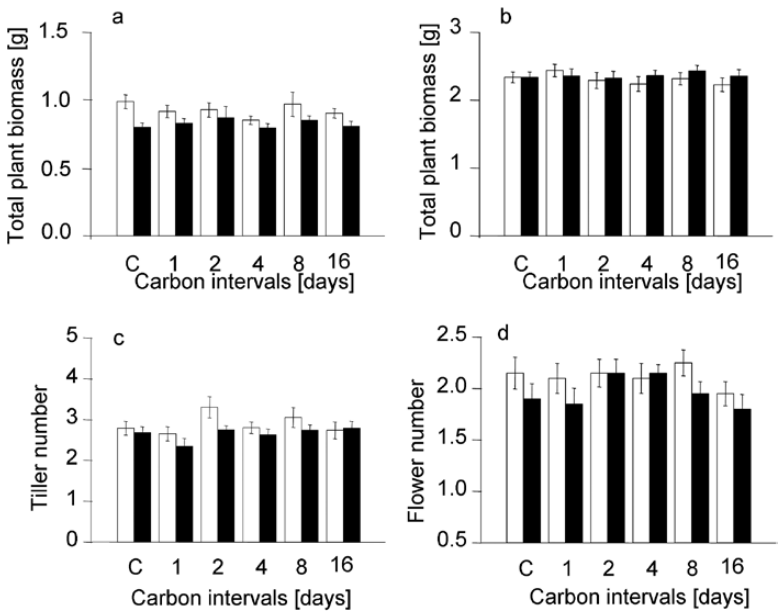

Figure 1: the effect of both carbon additions (C—no carbon control) and soil sterilization (inoculated soil: dark bars, sterilized soil: empty bars) on total plant biomass of plants experiencing either low (**a**) or high (**b**) nutrient availability. Tiller number (**c**) and flower number (**d**) are presented only for the high nutrient levels (see Materials and Methods for additional information). Data are mean ± 1 SE.

Since plant exudation was probably taking place during the experiment, our setup was only able to test the net effect of the exogenous glucose.

Nutrients

Nutrients were added to half of the pots in the form of slow-release fertilizer. Two and a half grams of Osmocot-controlled release fertilizer (15% N, 9% P_2O_5, 10% K_2O; Scotts®, Geldermalsen, The Netherlands) were thoroughly mixed into the top three centimeters of the soil of each pot.

Antibiotics

Antibiotics were given to the sterilized pots every 12 days (Thiele-Bruhn, 2003) in order to repress bacterial growth and minimize the effect of possible contamination. Each plant received 4.5 ml of antibiotics solution (biological industries, Israel, *Pen-Strep*, 0.3 g l^{-1}). Plants growing on unsterilized soil received an equivalent amount of water. Clearly, this treatment in itself is not able to eliminate all soil bacteria and it was used only as a second line of defense after the soil was autoclaved twice.

The above-mentioned full-factorial design resulted in 24 treatment combinations that were each replicated 20 times, resulting in 480 pots all together.

Plant harvest

Sixty-four days after the initiation of the carbon treatments, all plants were harvested. The root system of each plant was carefully washed and the plants were dismantled into roots, vegetative shoots and reproductive parts. The number of inflorescences and tillers was also recorded. All plant parts were oven dried at 60°C for 72 h. Dry biomass was determined using an analytical scale (CP224S, Sartorius AG, Goettingen, Germany; accurate to 0.1 mg). Root and reproductive allocation were calculated by dividing the root and reproductive biomass by the total plant mass, respectively.

Statistical analysis

We first analyzed the following response variables: total plant biomass, shoot biomass and allocation, root biomass and allocation, flower number and tiller number, using three-way analyses of variance (ANOVAs), with carbon treatment, soil sterilization and nutrient addition as explanatory variables. However, owing to the large size differences between the two nutrient levels, we had to analyze the data for each nutrient level separately (i.e. two-way ANOVAs with carbon treatment and soil sterilization as explanatory variables). In order to minimize mean proportional variance differences, all mass and number data were log transformed. An angular transformation ($\arcsin\left(\sqrt[3]{p}\right)$) was used when analyzing proportions such as root and reproductive allocations. All presented data are non-transformed. Because of the high number of possible pair-wise comparisons (most of which are not applicable to our research question), we calculated, for each level of carbon treatment within each block, the difference between the inoculated and sterilized soils ($y_{\text{inoculated soil}} - y_{\text{sterilized soil}}$) with

Table 1: the effects of carbon and soil sterilization treatments on various size and architectural variables in plants experiencing low nutrient availability

		Total plant biomass		Shoot biomass		Root biomass		Reproductive biomass		Tiller number		Reproductive allocation		Root allocation	
Low nutrients	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Carbon	5	0.782	ns	0.652	ns	0.832	ns	1.298	ns	1.324	ns	1.267	ns	0.721	ns
Soil sterilization	1	16.811	***	10.999	**	6.119	*	16.928	***	0.106	ns	0.971	ns	0.020	ns
Carbon × soil sterilization	5	0.474	ns	1.188	ns	0.470	ns	0.741	ns	1.301	ns	1.238	ns	0.986	ns
Error	225			226		226		225		216		225		225	

ANOVA. ns—$P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. df = degrees of freedom.

respect to each response variable and did the following three carbon treatment contrasts: (i) no carbon control versus daily carbon supply, (ii) no carbon control versus carbon pulses (every 2, 4, 8 and 16 days), (iii) daily carbon supply versus carbon pulses. In all ANOVAs of data collected from plants experiencing *low nutrient availability*, neither the carbon treatment nor carbon × soil sterilization interaction was significant. We thus present contrasts only for the data collected from plants experiencing high nutrient availability. In addition, all plants in the low nutrient treatment had one inflorescence, except for one plant that had two and another that did not have any. Due to this lack of variance, flower number was not analyzed for the low nutrient group. All analyses were conducted using SYSTAT 11 (Systat Software, Inc., Chicago, IL, USA).

RESULTS

Total plant biomass was significantly affected by nutrient availability ($F_{1,473}$ = 2331.8, P < 0.001). Plants receiving fertilizer were 170% larger than plants growing without nutrient addition (Fig. 1a and b). Due to these large size differences, we next present the results for each nutrient level separately.

Low nutrients

Total plant mass in the inoculated soil was 11% lower than that of the sterilized soil (Fig. 1 and Table 1, P < 0.001) but was not significantly affected by carbon treatment (P > 0.05; Table 1). Similar patterns were evident when examining the shoot, root and reproductive biomasses (Fig. 2 and Table 1). We could not detect any significant effects of the two treatments on root or reproductive allocation, nor were there any significant interactions (P > 0.05; Fig. 2 and Table 1).

High nutrients

Neither the soil sterilization nor carbon treatments had any significant effect on either total plant (Fig. 1) or shoot biomasses (P > 0.05; Table 2). Similarly, none of the carbon treatment contrasts, of the difference in total plant or shoot biomass between the inoculated and sterilized soils, were significant (P > 0.05; Table 3). Root biomass was 17% higher in the sterilized soil than in the inoculated soil (Fig. 3a, P < 0.01), but there was no significant carbon effect (P > 0.05; Table 2), and all three carbon treatment contrasts were not significant (P > 0.05; Table 3). Reproductive biomass showed the opposite pattern, with inoculated soil resulting in 9% higher reproductive output (Fig. 3c and Table 2, P < 0.05). Furthermore, these differences in reproductive biomass were significantly larger in plants subjected to carbon pulses than in those receiving a daily carbon supply or those in the control group (Fig. 3c and Table 3, P < 0.01 and P < 0.05, respectively).

The effect of the carbon treatment on root allocation was not consistent among the two levels of the soil sterilization treatment (significant soil sterilization × carbon interaction; P < 0.05; Fig. 3b and Table 2). Specifically, root allocation of plants subjected to carbon pulses was significantly lower in the inoculated than in the sterilized soil. However, no such effect was evident in plants receiving a daily carbon supply (Fig. 4b and Table 3, P < 0.05). The reproductive allocation showed an opposite trend, being higher in the inoculated soils subjected to carbon pulses (Fig. 4a and Tables 2 and 3, P < 0.01).

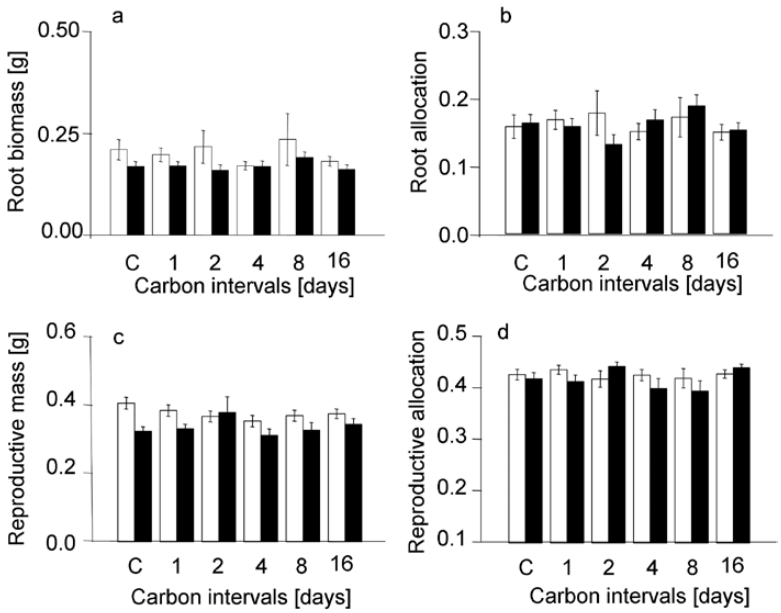

Figure 2: the effect of both carbon additions (C—no carbon control) and soil sterilization (inoculated soil: dark bars, sterilized soil: empty bars) on root biomass (**a**), root allocation (**b**), reproductive biomass (**c**) and reproductive allocation (**d**). Data presented are for plants experiencing low nutrient availability. Data are mean ± 1 SE.

Table 2: the effects of carbon and soil sterilization treatments on various size and architectural variables in plants experiencing high nutrient availability

		Total plant biomass		Shoot biomass		Root biomass		Reproductive biomass		Tiller number		Flower number		Root allocation		Reproductive allocation	
High nutrients	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Carbon	5	0.521	ns	0.973	ns	1.717	ns	1.128	ns	2.390	*	1.429	ns	3.058	*	2.536	*
Soil sterilization	1	1.163	ns	0.605	ns	11.455	**	5.268	*	3.328	ns	3.458	ns	30.233	***	10.445	**
Carbon × soil sterilization	5	0.455	ns	0.022	ns	0.870	ns	1.699	ns	0.728	ns	0.749	ns	2.695	*	2.413	*
Error	226			228		228		228		220		228		226		223	

ANOVA. ns—$P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. df = degrees of freedom.

While plants receiving carbon daily developed the smallest number of tillers, plants receiving carbon every other day developed 17% more tillers and displayed the largest tiller number among all carbon levels (Fig. 1c and Table 2; $P < 0.05$); however, none of the three carbon treatment contrasts was significant ($P > 0.05$; Table 3). Flower number was not affected by any of the treatments ($P > 0.05$; Fig. 1d and Table 2).

DISCUSSION

We hypothesized that different patterns of soil carbon input (i.e. pulse vs. continuous) should generate either nutrient enrichment or shortage, which in turn should reduce or enhance plant root allocation, respectively (Bloom *et al.*, 1985). The temporal variation in soil carbon input was found to interact with soil sterilization treatment in its effect on both root and reproductive biomasses and allocations. Specifically, the difference in reproductive biomass and reproductive allocation, between the inoculated and sterilized soils, was significantly larger in plants subjected to carbon pulses (every 2–16 days) than in those receiving a daily carbon supply. The opposite pattern was evident for root allocation, being lower in plants grown in inoculated soils and subjected to carbon pulses. In accord with our prediction, these effects were noticeable only when sufficient nutrients were present in the soil. Furthermore, soil inoculation in plants subjected to low nutrient availability resulted in decreased total plant biomass. We interpret this to mean that when the amount of available nutrients is low, they are mainly dominated by the bacterial community (Rosswall, 1982). The observed allocation shift from root to reproduction is a common response to enhanced nutrient availability (e.g. Jongejans *et al.*, 2006), suggesting that carbon pulses might have increased nutrient availability.

The fact that the differences in root and reproductive allocation were evident only under high nutrient availability might have at least partially resulted from the SOM poor potting material used. With little organic matter and low nutrient availability, the bacterial community might have been restricted in its ability to respond to the carbon dynamics, due to the N limitation (Fontaine and Barot, 2005; Fontaine *et al.*, 2003; Kuzyakov *et al.*, 2000). Hodge *et al.* (2000) argued that microbes–plant competition can be intense even in N-rich soil since the rate at which new roots can be produced will never match the turnover rates of the bacterial cells. Accordingly, plant–bacterial competition was found to be significant even when nutrients were supplied in mineral form, which can be directly absorbed by the plants (e.g. Schmidt *et al.*, 1997a).

Although no changes were evident in total plant biomass, temporal variation in soil carbon input had a significant effect on plant architecture. Tiller number is a good indicator of the way the plant perceives its environment (Novoplansky, 1998). Generally, plants perceiving the environment as harsh and unpredictable tend to produce fewer branches, minimizing their risks and channeling their resources into a small

Table 3: summary of the three carbon treatment contrasts for data collected from plants experiencing high nutrient availability: (i) no carbon control versus daily carbon supply, (ii) no carbon control versus carbon pulses (every 2, 4, 8 and 16 days) and (iii) daily carbon supply versus carbon pulses

	Carbon treatment contrasts		
Response variable	No carbon control versus daily carbon supply	No carbon control versus carbon pulses	Daily carbon supply versus carbon pulses
Total plant biomass	$F_{1,93} = 0.237$; $P = 0.627$	$F_{1,93} = 1.067$; $P = 0.304$	$F_{1,93} = 2.718$; $P = 0.103$
Shoot biomass	$F_{1,93} = 0.101$; $P = 0.751$	$F_{1,93} = 0.001$; $P = 0.971$	$F_{1,93} = 0.134$; $P = 0.715$
Root biomass	$F_{1,93} = 0.007$; $P = 0.936$	$F_{1,93} = 1.104$; $P = 0.296$	$F_{1,93} = 1.329$; $P = 0.252$
Reproductive biomass	$F_{1,93} = 1.017$; $P = 0.316$	$F_{1,93} = 4.139$; $P =$ **0.045**	$F_{1,93} = 10.955$; $P =$ **0.001**
Tiller number	$F_{1,87} = 0.602$; $P = 0.440$	$F_{1,87} = 0.560$; $P = 0.457$	$F_{1,87} = 0.051$; $P = 0.822$
Flower number	$F_{1,93} = 0.000$; $P = 1.000$	$F_{1,93} = 0.709$; $P = 0.402$	$F_{1,93} = 0.709$; $P = 0.402$
Root allocation	$F_{1,93} = 0.095$; $P = 0.759$	$F_{1,93} = 3.642$; $P =$ *0.059*	$F_{1,93} = 5.279$; $P =$ **0.024**
Reproductive allocation	$F_{1,93} = 0.782$; $P = 0.379$	$F_{1,93} = 2.359$; $P = 0.128$	$F_{1,93} = 7.047$; $P =$ **0.009**

Contrasts were done on the difference in plant performance between the inoculated and sterilized soils ($y_{\text{inoculated soil}} - y_{\text{sterilized}}$), calculated for each level of carbon treatment within each block. Significant and marginally non-significant values are marked in bold and italic, respectively.

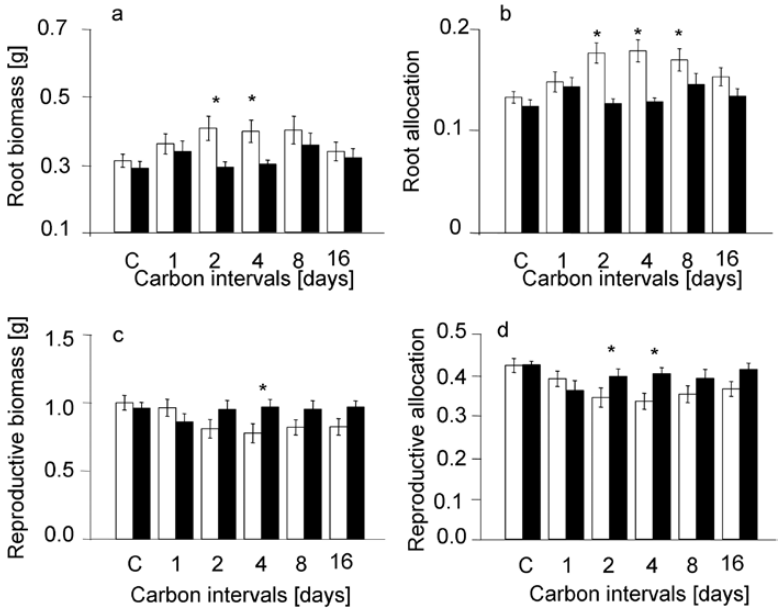

Figure 3: the effect of both carbon additions (C—no carbon control) and soil sterilization (inoculated soil: dark bars, sterilized soil: empty bars) on root biomass (**a**), root allocation (**b**), reproductive biomass (**c**) and reproductive allocation (**d**). Data presented are for plants experiencing high nutrient availability. Data are mean ± 1 SE. Planned comparisons testing for the effect of soil sterilization in each of the carbon treatment levels; *$0.01 < P < 0.05$.

number of vegetative and reproductive organs (Shemesh *et al.*, 2012). Plants receiving carbon continuously and every other day produced the smallest and largest number of tillers, respectively. This supports our hypothesis that continuous carbon supply creates unfavorable growth conditions.

Although the carbon in our experiment was externally manipulated, temporal variability in soil carbon input in natural settings might be generated by plant root exudation (Farrar *et al.*, 2003; Jones *et al.*, 2004; Lynch and Whipps, 1990). In light of the competitive interaction between plants and soil microbes, the adaptive role of rhizodeposition has been puzzling scientists for the last few decades (Bais *et al.*, 2006; Berendsen *et al.*, 2012; Bowman *et al.*, 2004; Clarholm, 1985; de Kroon *et al.*, 2012; Hamilton and Frank, 2001; Jones *et al.*, 2004; Klironomos, 2002; Kuzyakov and Cheng, 2001; Wang *et al.*, 2012). Bowman *et al.* (2004) hypothesized that plants that can survive in low nutrient conditions may exude carbon compounds to sustain the bacterial community, causing prolonged nutrient immobilization and assisting slow-growing plants to reduce the soil nutrient level below a critical value, under which certain fast-growing species cannot establish or survive (Bowman *et al.*, 2004).

According to the 'microbial loop' hypothesis (Clarholm, 1985), plant carbon inputs generate positive priming effect, leading to increased mineralization of nutrients that are made

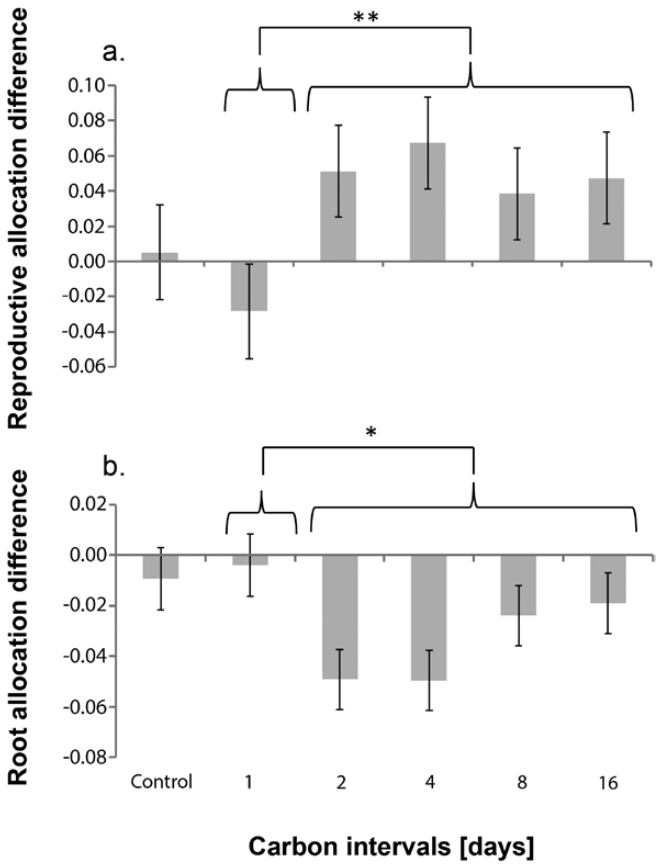

Figure 4: the effect of carbon additions on the difference in reproductive (**a**) and root (**b**) allocations between the inoculated and sterilized soils ($y_{\text{inoculated soil}} - y_{\text{sterilized}}$). Data were calculated for each level of carbon treatment within each block. Data presented are for plants experiencing high nutrient availability. Data are mean ± 1 SE. Carbon treatment contrasts; *$0.01 < P < 0.05$, **$0.001 < P < 0.01$.

locally available for uptake by plants, owing to the strong top-down regulation inflicted upon the bacterial community by their predators (Blagodatskaya and Kuzyakov, 2008; Fontaine *et al.*, 2011; Kuzyakov *et al.*, 2000). While both theories predict nutrient immobilization, they differ in the time scales over which immobilization occurs. While the 'microbial loop' assumes fast bacterial turnover and nutrient liberation, the 'nutrient immobilization' assumes long-term immobilization. A mechanistic explanation reconciling these two theories has not yet been suggested. Kuzyakov (2010) suggested that the temporal dynamics of soil carbon might play an important role in the mineralization of SOM and soil nutrient availability. However, the empirical support for this hypothesis is limited (but see Chigineva *et al.*, 2009; Hamer and Marschner, 2005). We suggest that the 'microbial loop' and 'immobilization' hypotheses might be reconciled when considering the temporal aspect of soil carbon inputs.

Although the importance of temporal variability has long been acknowledged (Levins, 1968), it is only recently that pulse dynamics have come to receive significant attention (Chesson *et al.*, 2004; Schwinning and Sala, 2004; Sher *et al.*, 2004). While not undisputedly supporting our mechanistic hypothesis, our bioassay results show that temporal variation in soil carbon inputs affect plant allocation and branching. This initial support of our hypothesis sets the stage for future experiments that should explicitly examine how carbon pulses affect the bacterial community and how such changes cascade up to affect soil nutrient dynamics, plant and bacterial uptake and possibly the fine scale temporal dynamics of root exudation. Since we used an organic poor soil, we decreased the ability of soil microorganisms to mine nutrients out of SOM. Future studies should examine all these processes also in SOM-rich soils in order to establish more ecologically sound conclusions regarding their role in natural settings. A mechanistic understanding of the link between temporal variation in soil carbon inputs and nutrient cycling can set the stage for future anthropogenic manipulations of soil resources, using harmless substances such as simple sugars.

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