



Effects of nitrogen on plant-microorganism interaction

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Abstract

The rhizosphere is a biologically active zone in the soil around the roots of plants. Root-microorganism interaction in the rhizosphere can be both beneficial to the plant, the microorganisms or to neither of them. Which factors affect the interactions between plants and microorganisms within this crowded rhizosphere? In order to investigate their interaction, contrasted tests were carried out. The plants across the nitrogen gradient were incubated with and without microorganisms. Results showed that nitrogen might play an active role in root-microorganism communication, and thus have an important effect on plant growth. With no nitrogen nutrient medium, microorganisms did not affect the plants growth obviously and the statistical interaction intensity of plant-microorganism approached zero. However, with a low level of nitrogen nutrient medium and an optimal nitrogen nutrient medium, plant biomass in sterile soil was more than plant biomass in non-sterile soil. The interaction intensity of plant-microorganism appeared negative. With a high level of nitrogen nutrient medium, plants grown in a non-sterile soil had better growth than plants grown in sterile soil. The interaction intensity of plant-microorganism appeared positive. Additionally, plant growth significantly increased the microorganism biomass both in the sterile soil and non-sterile soil.

Keywords: Interaction, nitrogen, plant-microorganism, rhizosphere, soil.

Qiu M, Zhang H, Wang G, Liu Z (2008) Effects of nitrogen on plant-microorganism interaction. *EurAsia J BioSci* 2, 4, 34-42.
www.ejobios.com/content/2/4/34-42

INTRODUCTION

The soil environment includes physical, chemical and biological factors that can affect plant growth. Much of the interaction between plants and soil microorganisms occurs in the rhizosphere or, in the case of symbioses, it is initiated in the rhizosphere. In simple terms, the rhizosphere is the zone of soil adjacent to and influenced by plant roots. The surface of the root is known as the rhizoplane, although it is often difficult to distinguish between rhizoplane and rhizosphere in terms of microbial ecology (Bolton et al. 1993). The rhizosphere is inhabited by a diverse range of microorganisms. Soil microorganisms that are adapted to competitive colonization of the rhizosphere and the root are called rhizobacteria (Schroth and Hancock 1982).

During recent decades, there has been an increasing interest in the role of soil microorganisms. Studies on the interaction between plants and microorganisms in the rhizosphere are important for understanding a range of processes, such as nutrient cycling, ecosystem functioning and carbon sequestration. Soil microorganisms have profound effects on plants through pathogenic effects, root-fungus mutualisms and by driving the nutrient cycles on which plants depend (Brundrett 1991, Crowley et al. 1991, Newsham et al. 1994, Van der Putten et al. 2001, Mitchell and Power 2003). On the basis of our current knowledge, plant-microorganism interactions can be classified

Received: January 2008
Received in revised form: April, 2008
Accepted: May, 2008
Printed: July, 2008

into three basic groups: (1) negative (pathogenic) interaction; (2) positive interaction, in which both partners derive benefits from close association (symbiosis), both partners derive benefits from loose association or only one partner derives benefits without harming the other (associative) and (3) neutral interaction, where none of the partners derive a direct benefit from interaction and in which neither is harmed.

Plant-microorganism interactions contribute to two contrasting types of feedback between plants and the microorganism communities that develop around their roots. Positive feedback occurs when plant species accumulate microorganisms near their roots that have beneficial effects on the plants that cultivate them, such as mycorrhizal fungi and nitrogen fixers. Positive feedback is thought to lead to a loss of local community diversity (Bever et al. 1994, Bever 2002). Negative feedback occurs when plant species accumulate pathogenic microorganisms in their rhizospheres, creating conditions that are increasingly hostile to the plants that cultivate the pathogens (Van der Putten et al. 1993, Bever 1994, Klironomos 2002). Negative feedback is thought to enhance community diversity by increasing species turnover rates.

Which factors affect the interactions between plants and microorganisms within this crowded rhizosphere? Some evidence suggests that root exudates might initiate and manipulate biological and physical interactions between roots and soil microorganisms, and thus play an active role in root-root and root-microorganism communication (Harsh et al. 2004). However, when environmental conditions change, the kind and the number of root exudates change (McCreary and Tecklin 1997). Environmental conditions may change the flow of interaction types between plants and microorganisms. Hence, plant-microorganism interaction is also highly influenced by environmental conditions. How do plant-microorganism interactions change when environmental conditions change? Under the effect of limiting factors, deficient or excessive mineral nutrition elements in particular, a situation can arise when the

rhizosphere microorganisms actually compete with the plant roots for the mineral nutrition elements (Jingguo and Bakken 1997). This may substantially reduce the stimulating effect of rhizosphere microorganisms or retard growth processes in plants. The interrelation of plant with microorganism will change when the plant nutrition changes from infertile to fertile (Gifford 1995). Nitrogen is the primary limiting nutrient in most terrestrial ecosystems (Vitousek and Howarth 1991). Competition between plants and microorganisms for this nutrient is believed to be intense (Jackson et al. 1989, Jingguo and Bakken 1997). In this paper, the contrasted tests were carried out. Plants across a nitrogen gradient were incubated with and without microorganism. The results of the test should contribute to finding out how the plant biomass changes across the nitrogen gradient and how the interaction intensity of plant-microorganism changes across the nitrogen gradient.

MATERIAL AND METHODS

Soils and plant materials

The soils for these studies were obtained from a forested area near Zhejiang University at Hangzhou (In China) with no cropping and pesticide application history. Soil testing results showed a pH at (1:1water) 5.8; organic matter (OM) content at 2.4% and the cation exchange capacity (CEC) at 4.89 cmol/kg.

Soil samples were air-dried, sieved (3 mm) and placed in plastic pots 10 cm in diameter and with a soil depth of 10 cm. Half the soil samples was treated at 125°C for one hour to kill soil microorganisms. The sterilized soils were used to assess the impact of nitrogen concentration on plant growth in the absence of microorganisms.

Arabidopsis seeds supplied by the Institute of Ecology (Zhejiang University, China) were used in the tests. Half of these seeds were surface-sterilized for 5 minutes with ethanol and a 3% solution of hydrogen peroxide at ratio of 1:1.

Experimental design

Preliminary experiments were conducted to estimate the effect of nitrogen concentration

on plant growth. The *Arabidopsis* seeds were grown across different levels of nitrogen concentration (0 g.L⁻¹, 0.032g.L⁻¹, 0.063 g.L⁻¹, 0.189 g.L⁻¹, 0.378 g.L⁻¹, 0.756 g.L⁻¹ and 1.512 g.L⁻¹ nitrogen level) and placed in the growth chambers for 45 days. Then, the plant biomass was measured in all replicates of the experiment. As compared to the control plants, with the level of nitrogen at 0.063 g.L⁻¹, plant biomass was the most prevalent. With the level of nitrogen 0.756 g.L⁻¹, plant growth was obviously inhibited compared to the control plants. With the level of nitrogen at 1.512 g.L⁻¹, plants appeared dead. These preliminary experiments established the range level of nitrogen for the main experiment. So, in this test, 0g.L⁻¹, 0.032g.L⁻¹, 0.063 g.L⁻¹, 0.189 g.L⁻¹, 0.378 g.L⁻¹, 0.756 g.L⁻¹ and 1.26 g.L⁻¹ nitrogen levels were chosen as the nitrogen gradient.

There were two treatments, in order to assess the impact of soil microorganisms on plant growth, ten sterile and ten non-sterile *Arabidopsis* seeds were respectively sown into the sterile soils and into the non-sterile soils. In order to investigate the effects of nitrogen on plant-microorganism interaction, seven levels of nitrogen (0g.L⁻¹, 0.032 g.L⁻¹, 0.063 g.L⁻¹, 0.189 g.L⁻¹, 0.378 g.L⁻¹, 0.756 g.L⁻¹ or 1.26 g.L⁻¹ nitrogen level) were used for each treatment, with six replicates for each.

Before sowing, the sterilized nutrient solution with a nitrogen gradient were added to each pot with the soil moisture level at 30 ± 5% field water content (FWC).

Sterile seeds and non-sterile seeds were equably sown in pot with sterile soils or non-sterile soils. All seeds were grown in auto-control growth chambers. The growth chamber temperature was maintained at 25 ± 2°C, and the light regime was a 16/8h day/night cycle, with a photosynthetic photon flux rate of 200 μmol.m⁻².s⁻¹ from metal halide bulbs. The relative humidity in the chambers was set at 70 ± 5%. Sterile Hoagland's nutrient solution (Murashige and Skoog, 1962) was added all pots resulting in a nitrogen gradient (0g.L⁻¹, 0.032g.L⁻¹, 0.063 g.L⁻¹, 0.189 g.L⁻¹, 0.378 g.L⁻¹, 0.756 g.L⁻¹ or

1.26g.L⁻¹ nitrogen level).

Hoagland's nutrient medium contains 0.493g.L⁻¹ MgSO₄.7H₂O, 0.35 g.L⁻¹ CaSO₄, 0.0138 g.L⁻¹ FeSO₄.7H₂O, 0.00186g.L⁻¹ NaEDTA.2H₂O, 0.34 g.L⁻¹ KH₂PO₄, 0.0868 g.L⁻¹ H₃BO₄, 0.0025g.L⁻¹ CuSO₄.5H₂O, 0.001452 g.L⁻¹ Na₂MoO₄.2H₂O, 0.04202 g.L⁻¹ MnCl₂.H₂O, 0.00575 g.L⁻¹ ZnSO₄.7H₂O and 4.76 × 10⁻⁵ g.L⁻¹ CoCl₂.6H₂O. The pH was adjusted to 5.7 with (1 + 1) sulphuric acid.

To standardize the experiment conditions, the position of the pots was interchanged every two days.

Harvest and analyses

The experiment time from sowing to harvesting was 45 days. At harvest, the rhizosphere microorganism biomass in the soil, plant biomass and the nitrogen content in the shoots were measured.

Plants were separated from the soil by shaking. Plant biomass weights are reported on a dry weight basis. Plants were dried for 48h at a temperature of 75°C. Results are represented by mean arithmetic values.

In this experiment, plant growth conditions were kept the same except for with microorganisms or without microorganisms. Therefore, soil microorganisms were the main factor of impact on plant growth. Interaction intensity among plant and microorganism could be assessed by the change of the plant biomass of the plants grown in sterile soil and the plants grown in non-sterile soil.

In this paper, ΔM is used as the interaction intensity where ΔM = M₁ - M₂. ΔM is an estimation of the change in plant biomass between plants grown in sterile soil and plants grown in non-sterile soil. M₁ is an estimation of plant biomass grown in non-sterile soil and M₂ is estimation of plant biomass grown in sterile soil. The interaction intensity (ΔM) with positive values indicates facilitation and a positive effect. The interaction intensity (ΔM) with negative values indicates a negative effect.

To determine the rhizosphere microorganism biomass, the roots were washed in a glass with a measured amount of phosphate buffer with a pH of 5.8, and the

solution was diluted serially. The roots were then homogenized, serially diluted and inoculated on meat-peptone agar (MPA) and on a mineral medium with glucose for rhizosphere microorganisms. The microorganism biomass was calculated on a dry biomass basis (Cheng and Coleman 1989, Cheng and Virginia 1993). And they were dried for 48h at 75°C.

The nitrogen content in the shoot was analyzed in the laboratory using EPA-approved methods (Anonymous 1992).

Statistical analyses of data

All experiments were performed at least six times and each value was presented as mean + or - standard error (S.E.). The data was statistically analyzed by two-way ANOVA using SPSS statistical software (SPSS for Windows, Release 10) to evaluate whether the means were significantly different, taking $P < 0.05$ as significant.

RESULTS

Plant biomass assays

At the first week of the experiment, it was observed that plants in all treatments began to grow. Later, plant growth began to appear different across the nitrogen gradient. At 45 days, plant biomass across the different levels of nitrogen treatment is shown in Fig. 1. It indicates that the level of nitrogen had an important effect on plant growth. With a low nitrogen nutrient medium and high nitrogen nutrient medium, plant growth was retarded and plant biomass was low. With level of nitrogen at 0.063 g.L⁻¹, plants grew well. This level of nitrogen is the optimal growth condition for Arabidopsis. With a high nitrogen nutrient medium, plants grown in non-sterile soil had better growth than plants grown in sterile soil. With a low nitrogen nutrient medium and an optimal nitrogen nutrient medium, plant biomass grown in sterile soil was more than plant biomass in non-sterile soil. Microorganisms have an important impact on plant growth. In Fig.1, it can also be seen that the rhizosphere microorganisms did not affect the growth obviously of plants with no nitrogen medium. But, with the low nitrogen nutrient medium or

optimal nitrogen nutrient medium, rhizosphere microorganisms were found to be harmful to plant growth. With a high nitrogen nutrient medium, rhizosphere microorganisms were beneficial to plant growth.

Effects of nitrogen concentration on plant-microorganism interaction

The interaction intensity of plant-microorganism across the nitrogen gradient after 45 days of plant growth is shown in Fig. 2. It indicates that the level of nitrogen had an important effect on the interaction intensity of plant-microorganism. With no nitrogen nutrient medium, the interaction intensity of plant-microorganism approached zero. Between nitrogen levels of 0 g.L⁻¹ and 0.063 g.L⁻¹, the interaction intensity of plant-microorganisms began to appear negative and the interaction intensity (negative effect) increased bit by bit with the level of increasing nitrogen. However, between nitrogen levels of 0.063 g.L⁻¹ and 1.26 g.L⁻¹, the interaction intensity of plant-microorganism changes from negative to positive. With the level of nitrogen increasing, the negative effect of plant-microorganisms became weak and the positive effect of plant-microorganisms became strong. At last, with a high nitrogen nutrient medium, the interaction intensity of plant-microorganisms appeared positive.

Nitrogen content in the shoot assays

With no nitrogen nutrient medium, the amount of organic nitrogen in the shoot was similar in sterile soil and in non-sterile soil. With a low nitrogen nutrient medium or optimal nitrogen nutrient medium, the total nitrogen content in the shoot was identical in sterile soil and non-sterile soil, yet the amount of organic nitrogen of plants in the non-sterile soil was more than that of the plants in sterile soil. Plants in a non-sterile soil were better in transforming the nitrogen of nitrates into the organic matter of the plant. Plants in sterile soil had more nitrate nitrogen in the shoot. With a high nitrogen nutrient medium, the total nitrogen content in the shoot was identical in sterile soil and non-sterile soil, yet the amount of organic nitrogen of the plants in sterile soil was more than the plants in non-sterile soil.

Rhizosphere microorganism assays

Soil microorganism biomass at the end of experiment is shown in Fig. 3. It indicates that the soil microorganism biomass in the sterile soil slightly increased compared to the initial soil microorganism biomass. Between nitrogen level of 0 g.L⁻¹ and 0.063 g.L⁻¹, with the level of nitrogen increasing, the soil microorganism biomass also increased. Between nitrogen level of 0.063 g.L⁻¹ and 1.26g.L⁻¹, the level of nitrogen increased, and the soil microorganism biomass decreased slowly.

DISCUSSION

Plant growth depends on light, moisture and available nutrients. The nutrient availability in the rhizosphere may be influenced by plant roots directly. The mechanisms include changes in rhizosphere pH induced by root metabolism, and it is assumed that organic acids and non-protein amino acids in root exudates directly contribute to plant element uptake by chelating trace elements such as Fe, Mn and Zn (Freckman 1982). In this paper, plant growth conditions were the same except for the level of nitrogen. Therefore, the level of nitrogen seems to play a crucial role in the maintenance of the balance in the interaction between microorganisms and plants.

Nitrogen is the primary limiting nutrient in plant growth in this experiment. After a week of growth, environmental nitrogen concentration started to show up in plant growth. Low nitrogen nutrient medium or high nitrogen nutrient medium caused retarded plant growth. Arabidopsis grew best with the level of nitrogen at 0.063 g.L⁻¹.

It is difficult to assess the direct interactions between plants and microorganisms for soil nitrogen because (1) there are multiple loops and pathways through which nitrogen cycles at variable rates and in varying amounts between different pools, and (2) some plants and some fungi in any ecosystem will be in a mycorrhizal symbiosis, providing an additional pathway for nitrogen movement. The use of ¹⁵N-pool-dilution techniques has helped to resolve many

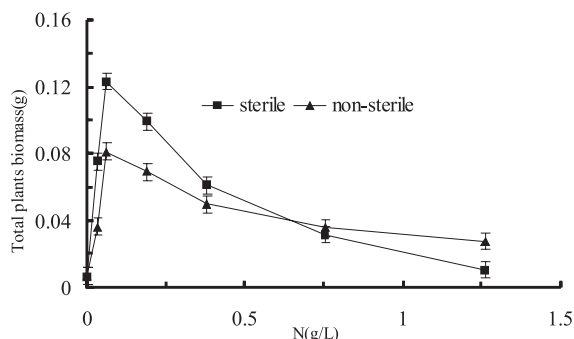


Fig. 1. At 45 days, the total plants biomass grown in non-sterilized soil and sterilized soil across the nitrogen gradient treatments. Vertical lines in each point show + or - S.E. (n=6) (P<0.05).

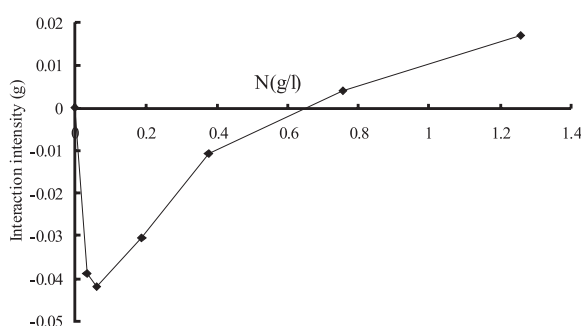


Fig. 2. Effects of nitrogen concentration on the plant-microorganism interaction intensity at 45 days.

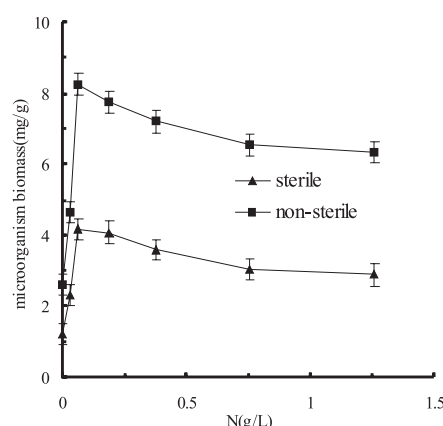


Fig. 3. The biomass of rhizosphere microorganism in non-sterilized soil and sterilized soil across the nitrogen gradient at 45 days. Vertical lines in each point show + or - S.E. (n=6) (P<0.05).

uncertainties about N-pool fluxes. For example, ¹⁵N-labelling of the NH₄⁺ and NO₃⁻ pools of a grassland soil revealed that, even

though the NH_4^+ pool was always moderately large, it was extremely dynamic and had a turnover time of one day. The NO_3^- pool was even more dynamic, being consumed as rapidly as it was produced (Jackson et al. 1989). Similarly, the mean residence time of small amounts of NO_3^- in undisturbed coniferous forests was only 15 hours (Stark and Hart 1997), indicating intense microorganism activity. On a longer timescale, pulses of NH_4^+ in an acid woodland soil were short-lived persisting for a few weeks (Farley and Fitter 1999).

With no nitrogen nutrient medium, plant growth is retarded seriously. It cannot be ruled out that soil microorganisms could fix atmospheric nitrogen, however, soil microorganisms did not affect the plant growth. The plant biomass increased mainly owing to the internal supply of nitrogen in the seed (Somova et al. 1997).

With a low nitrogen medium or optimal nitrogen medium, plant growth is limited by low nitrogen. Soil microorganisms could obtain their energy from the oxidation of inorganic nitrogen compounds (NO_3^-). On a short time scale, soil microorganisms do compete better than plants for NO_3^- . The NO_3^- uptake rate by microorganisms could have been double than that of plants (Jackson et al. 1989). It was also assumed that soil microorganisms are superior competitors for this nitrogen because of their major role in the mineralization process, large surface-area, volume ratios and rapid growth rates compared with plant roots (Rosswall 1982). Hence, soil microorganisms may compete with plants for nitrogen and lead to nitrogen deficiency. Plant biomass in sterile soil was more than the plant biomass in non-sterile soil. The interaction intensity of plant-microorganism appeared negative. Microorganisms were harmful for plant growth.

With a high nitrogen nutrient medium, plant growth was retarded by excessive nitrogen (nitrogen in this high content is harmful for plant growth). Soil microorganisms could capture some nitrogen

for their metabolism and cause a loss of NO_3^- by denitrification (Michael et al. 2000). Soil microorganisms may hence decrease the nitrogen level in the soil. This could have been of benefit to plant growth. Hence, soil microorganisms may promote plant growth and interaction intensity of plant-microorganism is positive.

With high nitrogen concentration, the plants in non-sterile soil had more nitrate nitrogen in the shoot. Appropriate rhizospheric microorganisms could have reduced the nitrate content in the shoot.

Microorganism activity in the soil is generally thought to be limited by the availability of carbon (Anderson and Domsch 1978), except in the rhizosphere where there is a constant supply of readily available carbon sources to the heterotrophic microflora (Cheng et al. 1993, Cheng et al. 1996). Due to the excess carbon supply, microorganism activity and biomass in the rhizosphere of plants differ considerably from non-rhizosphere soil.

In addition to the compounds that roots synthesize and accumulate (Flores 1999), a remarkable diversity of micro-molecular metabolites is also secreted into the rhizosphere as root exudates (Bais et al. 2001).

Microorganism biomass increased both in sterile soil and in non-sterile soil in 45 days. The increase of microorganism biomass in sterile soil could be a result of proliferation in the previously non-culturable organisms stimulated by the favorable environment in the growth chambers and or some level of contamination during the growing period. Additionally, planting significantly increased the microorganism biomass in both the non-sterile soil and sterile soil. Microorganisms could receive ample quantity of carbon from root exudates (Harsh et al. 2004).

The positive correlation observed between plant biomass and the biomass of microorganisms in the soil could be indicative of the proliferation of microorganism stimulated by the greater supply of nutrients from a vigorous plant.

CONCLUSIONS

(1) Nitrogen may play an active role in root-microorganism communication, and thus have an important effect on plant growth.

(2) With a high nitrogen nutrient medium, the interaction intensity of plant-microorganism appears positive. Microorganisms are beneficial to plant growth.

(3) With a low nitrogen nutrient medium and an optimal nitrogen nutrient medium, the interaction of plant-microorganism appears negative. Microorganisms are harmful for

plant growth.

(4) With no nitrogen nutrient medium, microorganisms did not affect plant growth obviously, and the interaction intensity of plant-microorganisms approached zero.

(5) Plant growth increased significantly the microorganism biomass both in the sterile soil and in non-sterile soil.

ACKNOWLEDGEMENTS

The study was supported by the Key Item of Zhejiang Province (2005C23082)

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Azotun Bitki-mikroorganizma Etkilesimine Etkileri

Ozet

Kok bolgesi, bitki koklerini cevreyeyen topraklarda yer alan biyolojik acidan aktif bir bolgedir. Rizosferdeki kok-mikroorgaizma etkilesimi bitki ve mikroorganizmanın her ikisi icin faydali olabilecegi gibi, hic faydasi da olmayabilir. Bitki ve mikroorganizma arasindaki etkilesimi etkileyen faktorler nelerdir? Etkilesimi incelemek amaciyla capraz testler yapildi. Azot gradyanti boyunca bitkiler mikroorganizmalarla incube edildi. Bir kısmi incube edilmeden birakildi. Sonuclar, azotun kok-mikroorganizma iletisiminde aktif bir rol oynayabilecegini ve bitki buyumesinde onemli bir etkisi olabilecegini gostermistir. Azot icermeyen ortamda, mikroorganizmalar bitki buyumesini etkilememistir ve istatistiksel bitki-mikroorganizma etkilesim yogunlugu sifira yaklasmistir. Ancak, dusuk azotlu ve optimum azotlu ortamlarda, steril topraktaki bitki biyokutlesi steril olmayan topraktakinden daha fazlaydi. Bitki-mikroorganizma etkilesim yogunlugu negatifti. Yuksek azot icerikli ortamlarda, steril olmayan topraklardaki bitkiler steril topraklardaki bitkilere gore daha iyi buyumuslerdir. Bitki-mikroorganizma etkilesim yogunlugu pozitif. Ek olarak, bitki buyumesi, hem steril hem de steril olmayan topraklarda mikroorganizma biyokutlesini onemli olcude artirmistir.

Anahtar Kelimeler: Azot, bitki-mikroorganizma, etkilesim, rizosfer, toprak.