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Soil and rhizosphere microorganisms have the same Q_{10} for respiration in a model system

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Abstract

We compared the Q_{10} relationship for root-derived respiration (including respiration due to the root, external mycorrhizal mycelium and rhizosphere microorganisms) with that of mainly external ectomycorrhizal mycelium and that of bulk soil microorganisms without any roots present. This was studied in a microcosm consisting of an ectomycorrhizal *Pinus muricata* seedling growing in a sandy soil, and where roots were allow to colonize one soil compartment, mycorrhizal mycelium another compartment, and the last compartment consisted of root- and mycorrhiza-free soil. The respiration rate in the bulk soil compartment was 30 times lower than in the root compartment, while that in the mycorrhizal compartment was six times lower. There were no differences in Q_{10} (for 5–15 °C) between the different compartments, indicating that there were no differences in the temperature relationship between root-associated and non-root-associated organisms. Thus, there are no indications that different Q_{10} values should be used for different soil organism, bulk soil or rhizosphere-associated microorganisms when modelling the effects of global climate change.

Keywords: mycorrhiza, Q_{10}, respiration, rhizosphere, soil, temperature

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Introduction

Root respiration and respiration driven by the plant (due to mycorrhiza and rhizosphere microorganisms) can make up a large proportion of the total carbon dioxide evolution both from agricultural (Kuzyakov & Cheng, 2001) and forest soil (Epron *et al.*, 2001; Högberg *et al.*, 2001). This proportion will, however, change due to environmental conditions that affect root-dependent and soil organic matter-dependent respiration differently. Such a differential effect was reported for temperature by Boone *et al.* (1998). In a field study of a mixed-hardwood forest stand, they found that Q_{10} (the ratio of the respiration at two different temperatures with a 10° difference) was higher for root-derived respiration (4.6) than for soil-derived respiration without any roots present (2.3–2.5). Similar results were later reported by Epron *et al.* (2001) in a beech forest. Since Q_{10} for root respiration *per se* (that is, without any associated microorganisms) is usually reported to vary between 2 and 3 (Lawrence & Oechel, 1983; Burton *et al.*, 1996; Ryan *et al.*, 1996; Zogg *et al.*, 1996; Bouma *et al.*, 1997), Boone *et al.* (1998) suggested that 'the temperature sensitivity and Q_{10} values for the mycorrhizae and rhizosphere heterotrophs together must be much higher than 2–3' to account for this difference between root- and soil-derived respiration. However, soil microorganisms have usually been reported to have Q_{10} values of around 2–3 in the temperature range studied (4–21 °C), and it is usually only at lower temperatures that Q_{10} becomes higher (Díaz-Raviña *et al.*, 1994; Kirschbaum, 1995).

Although field studies have the advantage of being more realistic than laboratory studies involving microcosms, they have the disadvantage of it being difficult to make clear-cut conclusions regarding cause and relationship. Many variables can co-vary with temperature, and there is always a potential risk of confounding factors. We therefore tried to compare the temperature relationship of root-dependent respiration with that of the mycorrhizal mycelium and that of non-root-associated soil microorganisms in a model system consisting of pine trees and ectomycorrhizal fungi growing in a sandy soil.

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Materials and methods

Microcosms

We used a set-up similar to that used by Bidartondo *et al.* (2001). Ectomycorrhizal association was synthesized according to Finlay *et al.* (1988) using *Pinus muricata* seedlings and either *Rhizopogon* 2272 (species group I in Kretzer *et al.*, 2000) or *Rhizopogon* 378 (species group IV in Kretzer *et al.*, 2000) as ectomycorrhizal fungi. Mycorrhizal seedlings were transferred to transparent polystyrene microcosms (Fig. 1) made from TC dishes $245 \times 245 \times 25$ mm (Nunc A/S, Roskilde, Denmark). Sandy soil collected from a *Pinus sylvestris* stand (Ek *et al.*, 1994) served as a substrate. Before use, the soil was microwaved at 90 °C twice with a 2- to 3-day interval to kill mycorrhizal fungal propagules. The microcosms were provided with 1 cm wide Plexiglas barriers in order to obtain three different compartments; one (the root compartment) with the plant root and rhizosphere-associated microorganism (including the external mycorrhizal mycelium and bulk soil microorganisms), and two with only microorganisms (the root was excluded by the barriers). Three holes (1.5 mm wide) drilled through one of the barriers allowed the mycorrhizal mycelium to grow into one of these two compartments (the mycelial compartment), while the other compartment contained only bulk soil microorganisms (the bulk soil compartment). Once the fungi had grown through one hole, the other two were sealed. Roots trying to grow through the holes were cut. The microcosms were wrapped in an aluminium foil, placed inside a ventilated plastic bag and maintained at 15 °C in a growth chamber until the mycelium had colonized a large part of the mycelial compartment (approximately 8 months). Light conditions (PAR) were maintained at 200 μmol $m^{-2} s^{-1}$ and soil moisture was kept constant by watering if needed. At the start of the experiment, the shoot length was approximately 15 cm.

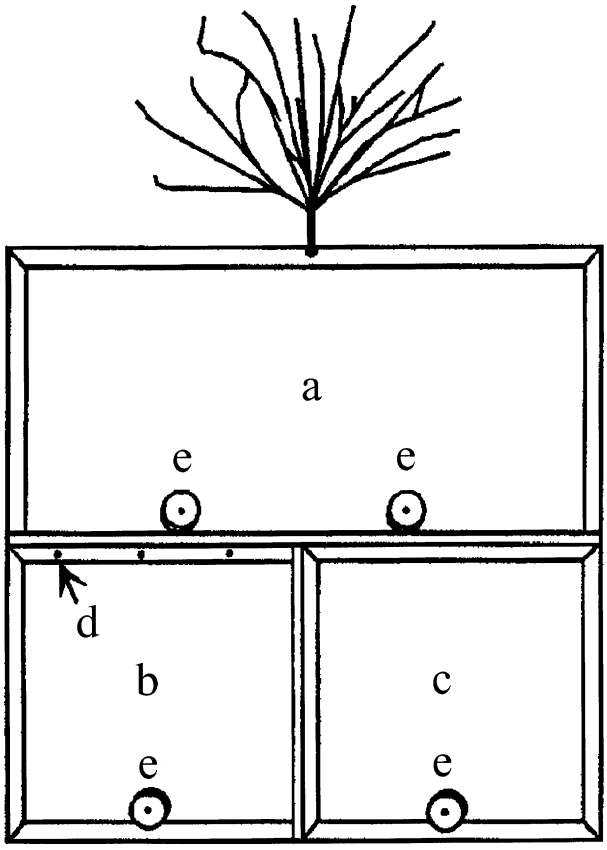

Fig. 1 Design of the microcosm unit: (a) root compartment, (b) mycelial compartment, (c) bulk soil compartment, (d) 1.5 mm perforation through barrier, (e) CO_2 traps with perforation through the lid. The total microcosm unit was $245 \times 245 \times 25$ mm.

Experimental conditions

During the experiment, the temperature in the growth chamber was first reduced to 5 °C and after one day at this temperature (to allow the plants to acclimate), CO_2 measurements began (see below). The temperature was thereafter raised to 15 °C and then to 22 °C and CO_2 measurements were performed at each temperature. The temperature was again reduced to 5 °C and CO_2 measurements were repeated at this temperature after giving the plants one day to acclimate. No difference was observed in the respiration rate on the two occasions at 5 °C, and a mean value was used in further calculations. We chose to have a short acclimation time, in order not to allow microorganisms to grow too much during this period. One day might, however, be a short period for total acclimation of the plant.

CO_2 measurements

A 1.5 mL plastic container was placed in each compartment. The compartments were then sealed with Terostat VII Sealing Profile (Terosan AG, Heidelberg, Germany), so that each compartment was gas tight with regard to the others. The plastic containers were then filled with 1.0 mL 1.5 M NaOH solution using a syringe through a 2 mm perforation, sealed with Terostat just before the microcosm was placed in the desired temperature environment. The NaOH solution was removed with a syringe after an appropriate time (4 days at 5 °C, 3 days at 15 °C, and 1 day at 22 °C), and fresh NaOH was added before incubation of the microcosms at a new temperature. The collected NaOH was immediately injected into a 15-mL N_2-flushed vial containing 5 ml 1.5 M H_2SO_4. The vials were equili-

brated for at least 24 h before analysing the CO_2 in the headspace using gas chromatography.

Results and discussion

The respiration rate at 15 °C was lowest in the bulk soil compartment, while the mycelial compartment exhibited six times higher respiration rate (0.18 ± 0.039 and 1.08 ± 0.24 μmol CO_2 h^{-1} g^{-1} soil, respectively). Thus, the respiration rate measured in the mycelial compartment was, to a large extent, due to the external mycorrhizal mycelium colonizing this compartment, and thus the Q_{10} values calculated for this compartment (see below) will be mainly due to the fungal mycelium. In the root compartment, the mean respiration rate (5.79 ± 1.27 μmol CO_2 h^{-1} g^{-1} soil) was 5 times higher than in the mycelial compartment. This higher respiration rate could be due to root respiration and respiration from rhizosphere microorganisms, and also partly due to respiration from the fungal mycelium, since the colonization in the root compartment was higher than in the mycelial compartment. The respiration due to bulk soil microorganisms would only constitute a minor part (3%) of the respiration rate measured in the root compartment. Thus, the respiration in the three compartments of the microcosms indicates respiration from non-root-associated microorganisms (bulk soil compartment), mainly external ectomycorrhizal mycelium (mycelial compartment) and root + root-associated respiration (root compartment). The activity in the two latter compartments would be mainly driven by plant-derived energy.

There was no difference between the Q_{10} values of the different mycorrhizal fungi used, and the data were therefore analysed together. The Q_{10} values for the three different compartments did not differ significantly (ANOVA) for 5–15 °C (Fig. 2) and were between 2.2 and 2.4, irrespective of compartment, neither did the relative respiration for 15–22 °C differ significantly (ANOVA) between the root and mycorrhizal compartments, although it was higher (although not significant) in the bulk soil compartment. Recalculation of the 7 °C difference between 15 °C and 22 °C to Q_{10} values gave values for the root and mycorrhizal compartment of around 2.3 and for the bulk soil compartment around 3.5. Thus, there were no indications of higher Q_{10} values in root-associated than in non-root-associated organisms (comparing the root and bulk soil compartments) or between external mycorrhizal mycelium and non-root-associated mycelium (comparing the mycelial and bulk soil compartments), despite the large differences in the absolute respiration rates (see above).

Our results therefore apparently contradict the results of Boone *et al.* (1998) and Epron *et al.* (2001).

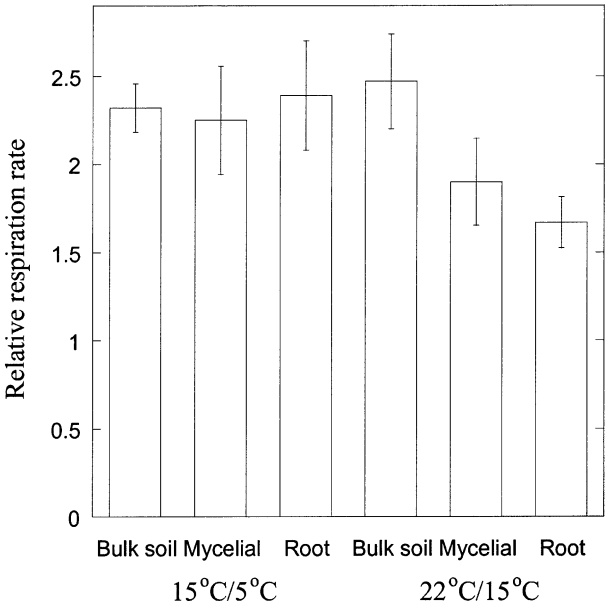

Fig. 2 Relative respiration rate for the root ($n = 7$), mycelial ($n = 8$) and bulk soil ($n = 5$) compartments of the microcosm unit. 15 °C/5 °C is the ratio of the respiration rate at 15 °C and 5 °C (= Q_{10}), while 22 °C/15 °C is the ratio of the respiration rate at 22 °C and 15 °C. Error bars indicate SE.

The probable reason for this is that their studies were field studies, while our study was a more controlled microcosm set-up. There might have been an environmental factor affecting soil organism respiration that co-varied with temperature in the field measurements. One such factor is light. It is well known that rhizosphere respiration is affected by light, in that more photosynthate is transported to the root and rhizosphere organisms if the light conditions are good, resulting in high rhizosphere respiration (Kuzyakov & Cheng, 2001). During summer, the temperature will be higher and light conditions better, boosting root respiration and root-associated respiration, while in the winter both low temperature and poorer light conditions will lead to low respiration rates. In our laboratory study, the light conditions were the same for all temperature measurements, and no confounding effect was introduced. Thus, all compartments had the same Q_{10} relationships.

The importance of light was also suggested in a recent field study of seasonal changes in soil respiration after girdling of a boreal Scots pine forest (Bhupinderpal -Singh *et al.*, 2003). During a 20-day-long 6 °C decline in soil temperature in the middle of the summer (that is, during a period of similar light conditions), they could not find higher Q_{10} values for root-associated respiration (nongirdled plots) than for non-root-associated respiration (in girdled plots).

Kuzyakov & Cheng (2001) reported that diurnal variation in root-derived CO_2 efflux from spring wheat was coupled to the plants' photosynthetic cycle. Davidson *et al*. (1998) cited a personal communication of Eric Sundquist and coworkers, that there were differences in soil respiration on clear and cloudy days in a hardwood forest. These two studies thus also indicate the importance of light conditions in determining the respiration rate and apparent Q_{10} temperature relationships in the field.

Beside changes in light conditions, changes in root biomass over time will also affect the respiration rate. This was acknowledged by Boone *et al*. (1998) and Epron *et al*. (2001), since the high Q_{10} values found for rhizosphere respiration by them were explained as a combination of temperature and changes in root biomass and root and shoot activities over the year (root phenology). The Q_{10} values reported by them are therefore relevant under the present environmental conditions. However, when predicting the effects of long-term climatic changes in temperature, it is important to differentiate between the direct effect of temperature and the effect of other conditions (e.g. light) co-varying with temperature over the year. An increase in temperature due to global warming will not necessarily be accompanied by more intense light conditions. Thus, there are no indications that different Q_{10} values should be used for different soil organism compartments, bulk soil or rhizosphere-associated microorganisms when modelling the effects of global climate change, as suggested by Boone *et al*. (1998).

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