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RESEARCH ARTICLE

Low soil water content during plant growth influences soil respiration and microbial biomass after plant removal and rewetting

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Abstract

The aim of this experiment was to study the effect of previous water content in planted and unplanted soil on microbial biomass and nutrient availability after plant removal and rewetting. A silt loam was maintained 10-50% of water holding capacity (WHC) and planted with wheat or left unplanted. After four weeks, plants were removed and soils were kept atthe same water content as in the pots (original) or rewetted to 50% WHC (rewet). Then, soil respiration was measured continuously for 20 days, available N and P and microbial biomass C, N and P were measured on days 5, 10 and 20. In original soil, cumulative respiration, MBC and MBN decreased with water content in planted soil and were higher in planted than unplanted soil only at 30-50% WHC. Available N was up to 3-fold higher in un-planted than planted soil at 30-50% WHC. Only in planted soil, available N increased with decreasing water content. Rewetting increased cumulative respiration and MBN only in soil that had been at 10-20% WHC. In rewet soil, the previous water content had no effect on cumulative respiration, MBC and MBN in unplanted soil. In planted soil, cumulative respiration, MBC and MBN remained lower in soil that was at 10% WHC previously compared to that at 50% WHC. It is concluded that the effect of low water content on soil microbes is exacerbated by reduced plant growth and the reduced C input, even if soils are rewet.

Keywords: Microbial biomass, respiration, planted, soil water content

1. Introduction

Low soil water content is known to reduce plant growth and soil microbial activity due to low water availability and nutrient diffusion (Drenovsky *et al.* 2004; Rodrigues *et al.* 1995). The direct effect of low soil water content on plants and soil microbes has been studied extensively (Schimel *et al.*, 2007). Further, rewetting of dry soil is known to induce a short-term flush of respiration and nutrient availability (Sø-

rensen, 1974; Cui and Caldwell, 1997). With respect to previous water content, Cavagnaro (2016) found that low previous water content reduced subsequent mycorrhizal colonization, but did not influence mycorrhizal responsiveness after rewetting of soil.

Less is known about how previous water content with or without plants influences microbial activity, biomass and nutrient availability. In planted soil, the effect of the previous water content is likely due to its effect on plant growth, i.e. nutrient uptake and C input via exudates and senescent roots. Thus, the effect of previous water content may be greater in planted than unplanted soil. On the other hand, C input by the plants may reduce the impact of previous water content by improving substrate availability to microbes.

We hypothesised that (i) the effect of low water content on soil respiration and microbial biomass will be greater in planted than in unplanted soil, and (ii) recovery of soil respiration and microbial biomass after rewetting from low water content will be greater in planted than unplanted soil.

2. Materials and Methods

2.1. Soil

The silt loam soil for this study was collected on the Waite Campus of the University of Adelaide (Longitude 138˚38´3.2˝ E, Latitude 34˚58´0.2˝ S) at 0-10 cm depth. The soil has the following properties: 22% sand, 60% silt, 18% clay, maximum water capacity (WHC) 371 g kg^{-1}, pH (1:5) 5.6, EC (1:5) 0.1 dS m^{-1}, total organic C 17 g kg^{-1}, total organic N 1.5 g kg^{-1}, bulk density 1.3 g cm^{-1}, available P 10 mg P kg^{-1} and available N 15 mg N kg^{-1}. Several samples were collected randomly across the plot and then pooled. The site has Mediterranean climate with a hot, dry summer and cool, wet winter. The soil is classified as Rhodoxeralf according to US Soil Taxonomy. After removal of stones and litter, the soil was dried at 40 °C and then sieved through a 2 mm sieve.

2.2. Experimental design

The soil was adjusted to 10, 20, 30, 40 or 50% WHC(these water contents correspond to water potentials of -1.7, -0.7, -0.32, -0.16, -0.078 MPa) and then 400 g dry soil equivalent was filled into 40 pots (9.5 × 8.5 ×10 cm, 8 pots for each soil water content). To obtain planted soil, twenty of the pots (4 pots of each soil water content) were densely planted with pre-germinated wheat (*Triticum aestivum* L. cv. Krichauff) seeds (20 per pot). The other twenty pots remained unplanted. The pots were placed in a glasshouse with natural light and watered three times a day to maintain constant soil water content throughout plant growth. Any weeds germinating in the unplanted pots were removed. Four weeks after planting, when a dense plant cover was established in the planted pots, roots and shoots were collected. All soil in the planted pots was considered to be planted soil because the root density was high. Although roots were carefully removed, the planted soil may contain small root fragments.

The soils were separated into two experimental groups, one remained at the water content it had previously (termed original) and the other was rewetted to 50% WHC (referred to as rewet). Then, 30 g soil (dry weight equivalent) of each group and water content treatment was placed into PVC cores (height 5 cm and diameter 3.7 cm with a nylon base). Soil bulk density was adjusted to 1.3 g cm^{-3} by packing the soil in the cores to the required height. Then the cores were transferred into glass

jars and kept at 20-23 °C in the dark. The desired water content was maintained by weight every two days. Soil respiration was measured continuously for 20 days. Cores were destructively sampled on days 5, 10 and 20 with four replicates at each harvest for determination of available N and P, microbial biomass C, N and P and water extractable organic C.

2.3. Analyses

Soil texture was determined using the hydrometer method (Bowman *et al.*, 2002). Soil maximum water holding capacity was measured using a sintered glass funnel (Haines, 1930). Soil pH and EC were measured in a 1:5 (w/v) soil to reverse osmosis (RO) water ratio after 1 h end-over-end shaking. Soil total organic C was determined after Walkley and Black (1934). Soil total N was measured using the Kjeldahl method (McKenzie and Wallace, 1954). Shoot and root biomass were determined after oven dried to constant weight.

Soil respiration was measured daily by quantifying the CO_2-C concentration of in the headspace of the jars using a Servomex 1450 infra-red analyzer (Servomex Group, Crowborough, UK) as described in Setia *et al.*(2011). After each measurement, the jars were vented using a fan to refresh the headspace and then resealed for measurement on the following day. The CO_2 evolved during a given interval was calculated as the difference in CO_2 concentration between measured and ambient CO_2 concentration. Linear regression based on injection of known amounts of CO_2 into empty jars of similar size was used to define the relationship between CO_2 concentration and detector reading.

Microbial biomass C (MBC) was determined by chloroform fumigation followed by extraction with 0.5 M K_2SO_4 at a 1:4 soil to extractant ratio (Vance *et al.*, 1987). The organic C concentration in the filtered extract was measured by titration with 0.033 M acidified $(NH_4)_2Fe(SO_4)_2.6H_2O$ after dichromate oxidation (Anderson and Ingram, 1993). The chloroform-labile C concentration is the difference between fumigated and un-fumigated soil which was multiplied by 2.64 to calculate microbial biomass C (Vance *et al.*, 1987). For microbial biomass N (MBN), the ammonium concentration in the K_2SO_4 extract was determined (Moore *et al.*, 2000) as described below for available ammonium. The difference between fumigated and un-fumigated soil was multiplied by 1.75 to calculate microbial biomass N (Moore *et al.*, 2000). For determining soil available N (ammonium + nitrate), soil was extracted with 2 M KCl at a 1:5 soil to extractant ratio on a horizontal shaker at 80 rpm for one hour. Ammonium-N in the filtered extracts was measured afterWillis *et al.* (1996). Nitrate-N was determined as described in Cavagnaro *et al.* (2006). Available and microbial biomass P (MBP) were determined using anion exchange resin following Kouno *et al.* (1995). For MBP, 1 ml hexanol was added. The P concentration in the extracts was determined colorimentrically according to Murphy and Riley (1962). Microbial biomass P is the difference between fumigated and un-fumigated extracts. The recovery of a P spike in this soil was 98% (Butterly *et al.*, 2010). Therefore no correction factor was used. Water extractable organic C (WEOC) was extracted at a 1:5 soil:water ratio. After 1h end over end shaking, organic C was measured as described above for MBC.

2.4. Statistical analysis

The experiment was arranged in a complete randomized block design with 2 soil treatments (planted and un-planted soil) × 5 water contents

×3 sampling times and 4 replicates for each sampling time of original and rewet treatment. One-way ANOVA was used to test the effect of soil water content on shoot and root biomass. Repeated measures ANOVA was performed separately within each group (original and rewet) to test the effect of soil treatment and soil water content over time using time as repeated measure. The interaction between sampling time and experimental treatments was significant. Therefore, data of cumulative respiration, available N, P, WEOC, MBC, MBN and MBP per sampling time were subjected to two-way ANOVA (treatment × water content) for each group and sampling time separately. Average values were compared using post-hoc Tukey test. All analyses were carried out with Genstat software (GenStat® for Windows, 18th edition, 2015; VSN International Ltd, Hemel Hempstead, UK). Only significant differences are mentioned in the text ($p < 0.05$).

3. Results

Shoot and root biomass were higher at 30-50% WHC than at 10 and 20% WHC (Figure 1). The decrease in biomass from 50 to 10% WHC was greater in shoots (75% lower at 10% WHC) than roots (25% lower). Therefore, shoot biomass was about 30% higher than root biomass at 40 and 50%, but it was two-thirds lower at 10%. The shoot/root ratio was > 1 at 40 and 50% WHC, but only 0.3 at 10% WHC.

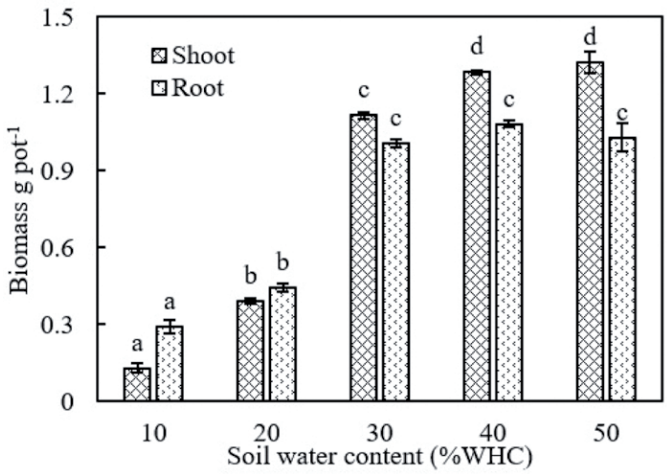

Figure 1. Shoot and root biomass after 4-week with 10-50% of water holding capacity. Vertical lines at the top of the bars indicate standard error, different letter of shoot or root biomass indicate significant differences ($P < 0.05$, n=4).

Cumulative respiration after 20 days was 2 to 2.5 fold higher in planted than unplanted soil at 30-50% WHC (Figure 2). But at 10 and 20% WHC, cumulative respiration in planted soil was only 25% higher than un-planted soil in original soil and there was no difference between planted and un-planted soil in rewet soil. Soil water content had a stronger effect on cumulative respiration in planted than un-planted soil. In the original treatment, cumulative respiration in planted soil at 40 and 50% WHC was four to five-fold higher than at 10 and 20% WHC whereas it was only about two-fold higher in un-planted soil. In the rewet treatment, cumulative respiration in planted soil that had been at 30-50% WHC was about 40% higher than in soil that had been at 10 and 20% WHC. In rewet un-planted soil, cumulative respiration was about 25% higher in soil that had been at 10 and 20% WHC than in soil that previously had 40 and 50% WHC. Rewetting increased cumulative respiration at 10 and 20% WHC, but did not influence respiration at 40 and 50% WHC.

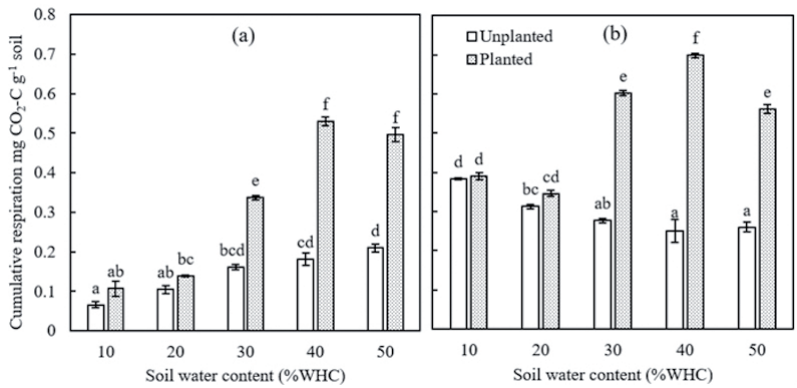

Figure 2. Cumulative respiration after 20 days in original (a) and rewet (b) unplanted and planted soil.Vertical lines at the top of the bars indicate standard error, different letter of original or rewet soil indicate significant differences ($P < 0.05$, n=4).

On days 5 and 10 in original soil, MBC was 25-80% higher in planted than un-planted soil at 30-50% WHC, but at lower water contents there was either no difference between planted and un-plantedsoil or MBC was lower in planted soil (Figure 3 a, c). In the original treatment, water content influenced MBC only in planted soil. On day 5, MBC in planted soil decreased in the following order 50>40, 30>20, 10. On day 10, MBC was higher at 30-50% WHC than at the lower water contents (Figure 3 a, c). Water content did not influence MBC in un-planted soil. Rewetting had no consistent effect on MBC. In rewet soil, MBC generally did not differ between planted and un-planted soil. Only on day 20, MBC in rewet planted soil was higher in soil that had previously been at 50% WHC than in soil with 10% WHC. This was also the case on days 10 and 20 for rewetted un-planted soil (Figure 3 d, f).

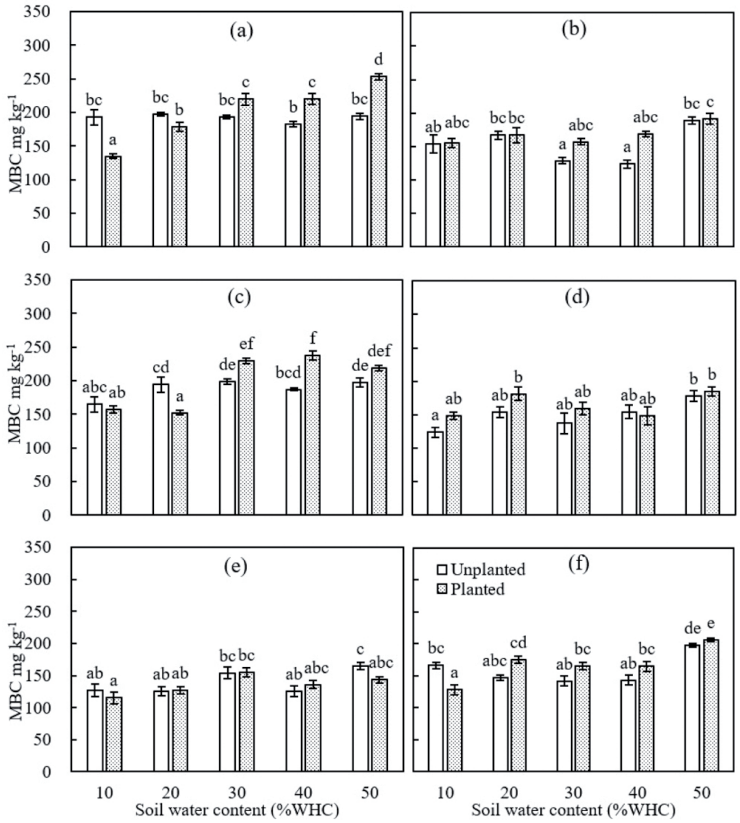

Figure 3. Microbial biomass carbon concentrations on days 5 (a, b), 10 (c, d) (e, f) and 20 (e, f) in original (a, c, e) and rewet (b, d, f) unplanted and planted soil. Vertical lines at the top of the bars indicate standard error, different letter of original or rewet soil on the same day indicate significant differences ($P < 0.05$, n=4).

At all sampling dates, MBN in original planted soil was four to six-fold higher at 40 and 50% WHC than at 10 and 20% WHC (Figure 4 a, c, e). In original soil, MBN was lower on day 20 than days 5 and 10 at 20, 30 and 50% WHC whereas MBN did not change over time in rewet soils (Figure 4 b, d, f). Compared to original soil, rewetting increased MBN only at 10 and 20% WHC. At most sampling times(except day 10 in the rewet treatment),MBN in planted soil decreased in the following order: 50> 40, 30> 20, 10% WHC. In original planted soil, MBN at 50% WHC was up to ten-fold higher than at 10% whereas in rewet soil it was only about two-fold higher at 50% than at 10% WHC. At 30-50% WHC, MBN in planted soil was up to two-fold higher than in un-planted soil, but there was no consistent difference between planted and un-planted soil at the lower water contents. In original un-planted soil, MBN at 50% WHC was three to four-fold higher than at 10 and 20% WHC, but differences among water contents were smaller than in planted soil. In the rewet treatments, MBN was higher in planted than un-planted soil only when the soil had been at 40 and 50% WHC (Figure 4, b, d, f). The previous water content had no consistent effect on MBN in rewet un-planted soil.

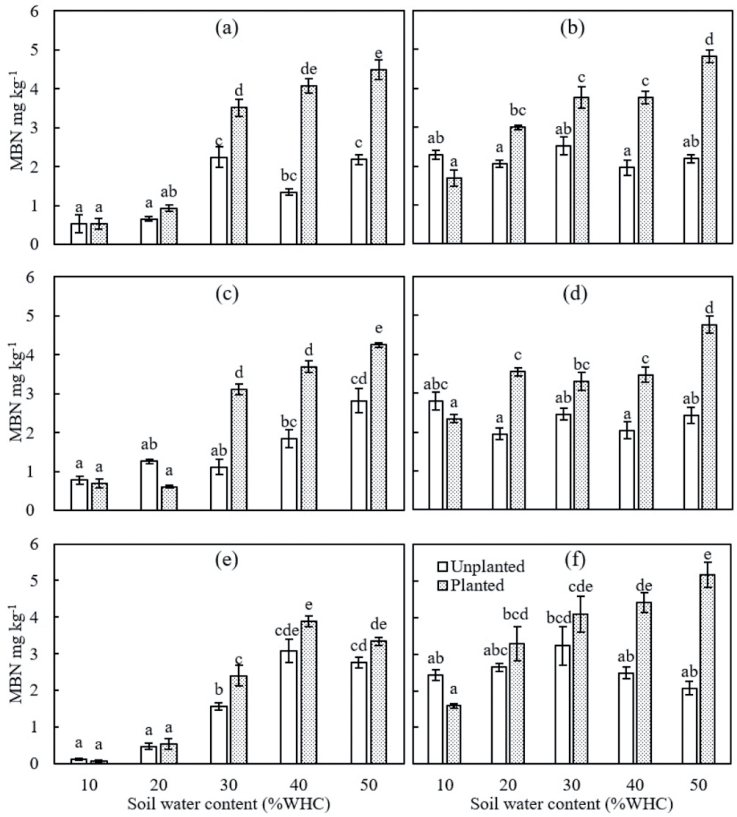

Figure 4. Microbial biomass nitrogen concentrations on days 5 (a, b), 10 (c, d) (e, f) and 20 (e, f) in original (a, c, e) and rewet (b, d, f) unplanted and planted soil. Vertical lines at the top of the bars indicate standard error, different letter of original or rewet soil on the same day indicate significant differences ($P < 0.05$, n=4).

In the original treatment, MBP was similar in plant-edand un-planted soil at most sampling times except day 20 when it was up to two-fold higher in planted than un-planted soil at 30-50% WHC . In both planted and un-planted soil MBP on days 5 and 10 was higher at 50% WHC than at 10 and 20% WHC. Rewetting had little effect on MBP compared to original soil. In rewet planted soil, MBP was about 20% higher in soil that had been at 50% WHC than soil previously maintained at 10 or 20% WHC. In rewet un-planted soil this was only the case on day 10 whereas on the other sampling days, MBP was not influenced by the previous water content.

In original and rewet soils, WEOC was higher in planted than un-planted soil at 40 and 50% WHC, but not at the lower water contents. In planted soil, WEOC at 40 and 50% WHC was higher on day 5 than day 20, but WEOC changed little over time at the other water contents and in un-planted soil. Rewetting did not influence WEOC compared to original soil.

In both original and rewet soil, available N was up to three-fold higher in un-planted than planted soil at 30-50% WHC whereas there was little difference between un-planted and planted at lower water contents (Figure 5). In planted soil, available N was lower at 30-50% WHC than at lower water contents, but water

content had little effect on available N in un-planted soil. Available N did not change over time at 10 and 20% WHC, but was lower on day 5 than days 10 and 20 at the higher water contents. Rewetting had little effect on available N.

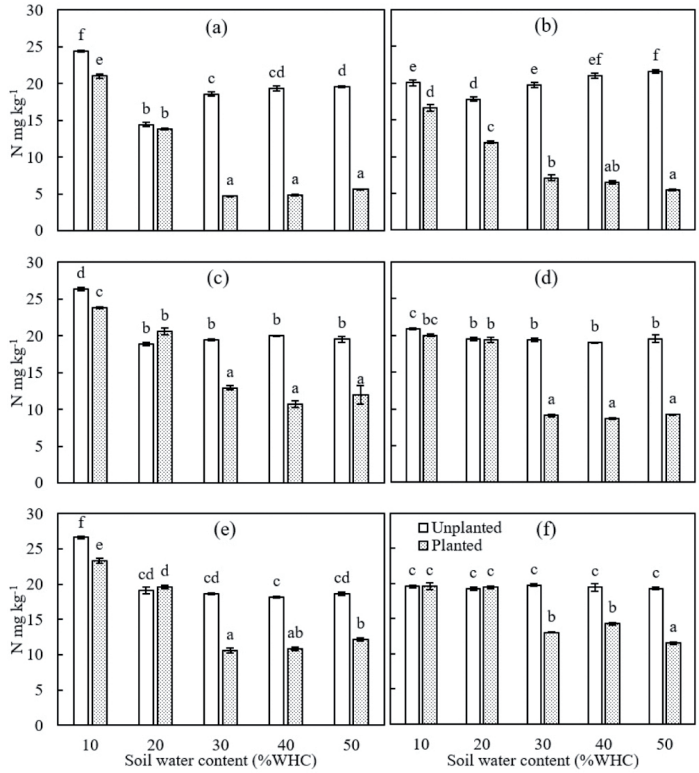

Figure 5. Available nitrogen concentrations on days 5 (a, b), 10 (c, d) (e, f) and 20 (e, f) in original (a, c, e) and rewet (b, d, f) unplanted and planted soil. Vertical lines at the top of the bars indicate standard error, different letter of original or rewet soil on the same day indicate significant differences ($P < 0.05$, n=4).

Available P on days 5 and 20 was lower in planted than un-planted soil at 30-50% WHC, but not at lower water contents. Rewetting had no consistent effect on available P and available P did not change over time. In original planted soil, available P was higher at 10% than at 50% WHC on days 5 and 10, but not on day 20. In original un-planted soil, water content did not consistently affect available P. In rewet soil, available P tended to be lowest in soil previously kept at 30% WHC.

4. Discussion

This experiment showed that the effect of low water content on microbial biomass, soil respiration and nutrient availability differs between planted and unplant-

ed soil even after the soil is rewetted to optimal water content. The negative effect of low water content on soil respiration and microbial growth was stronger in planted than unplanted soil which can be explained by the poor plant growth at low water content.Thus, we can confirm the first hypothesis (the effect of low water content on soil respiration and microbial biomass will be greater in planted than in unplanted soil).

As expected from previous studies (Nobel *et al.*, 1989), shoot and root biomass were lower at 10 and 20% WHC than at the higher water contents. Also in agreement with previous studies (Matsui and Singh, 2003; Asch *et al.*, 2005), the reduction at low water content was greater for shoots than roots because plants invest relatively more into roots than shoots when water availability is low to access the remaining water. The poor plant growth at 10 and 20% WHC is also reflected in the available N concentration in planted soil. At 30-50% WHC, available N on day 5 was about three times lower in planted than unplanted soil due to plant N uptake. But at 10 and 20% WHC, available N was similar in planted and unplanted soil because the small plants took up little N. Due to the low plant biomass at 10 and 20% WHC, the C input by the plant into the soil in form of roots and exudates can be assumed to be lower than at 30-50% WHC.

4.1. Original treatment

When the soil was incubated at the same water content as in the pots (original soil), cumulative respiration was higher at 40 and 50% WHC than at 10 and 20% WHC. The difference between water contents was much greater in planted than unplanted soil. In both planted and unplanted soil, this can be explained by the direct effect of low water availability on microbes including reduced substrate and enzyme diffusion, reduced water uptake and possibly even loss of water from cells (Ilstedt *et al.*, 2000, Guntinas *et al*., 2013). In planted soil, this effect of low water availability is exacerbated by poor plant growth, thus C input into the soil. In planted soil, MBC on days 5 and 10 was also higher at 30-50% WHC than at 10 and 20% WHC, but the differences were less pronounced than for cumulative respiration, indicating that microbial activity is more strongly influenced by low water availability than microbial growth. Microbial biomass was not influenced by water content in unplanted soil which suggests that the effect in planted soil was related to plant growth rather than soil water content. The reduction in MBN at low (10 and 20% WHC) compared to high water content (40 and 50% WHC) was much greater than for MBC and occurred in both planted and unplanted soil. This indicates that microbial N uptake was strongly reduced at low water content. Organic N mineralization did not appear to be reduced because available N concentration was either similar or higher at low compared to high water content. However, this may be an analytical artifact. Addition of KCl to dry soil for inorganic N determination may release inorganic N that would not be available in dry soil, e.g. by breaking up aggregatesand soil colloids (Bremner, 1965; Wang *et al.*, 2014). The low MBN at 10 and 20% WHC may also be related to microbial demand. At low water content, microbes were likely in stationary growth or even dormant. Cells in stationary phase have lowera N requirement than those in exponential growth (Kolter *et al.*, 1993). The higher MBN in planted than unplanted soil at 30-50% WHC can be explained by the improved substrate supply by roots which increased microbial growth and N mineralization. However, at 10 and 20% WHC, MBN did no differ between planted and unplanted soil, likely because the plants were too small to provide sufficient substrate.

Available N was higher at 10% WHC than at the other water contents in both planted and unplanted soil. Although the N mineralization rate was probably low

at 10% WHC, it could accumulate during the plant growth period and incubation because of the lack of microbial uptake and in planted soil, low plant N uptake.

4.2. Rewet treatment

In planted soil, the effect of water content during plant growth on cumulative respiration, MBC, MBN and available N and P in rewet soil was similar as in the original treatment. Cumulative respiration, MBC and MBN were higher at 50% WHC than at 10% WHC whereas available N and P were lower. However, the differences in cumulative respiration and MBC between water contents were smaller than in the original treatment because rewetting increased respiration and MBC in soil that was previously at 10 and 20% WHC, but had no effect at the higher water contents. Rewetting of dry soil may have released substrates that were previously not available through aggregate breakdown or release of bound organic matter (Turner and Haygarth, 2003; Peltovuori and Soinne, 2005).

In unplanted soil however, the previous water content had no effect on the measured parameters suggesting rapid recovery of microbes when dry soil is rewet. But respiration and microbial biomass were lower than in planted soil indicating that microbes were limited by substrate availability in unplanted soil.

Rewetting increased cumulative respiration and microbial biomass to a similar extent in unplanted and planted soil. Therefore, we have to decline the second hypothesis (recovery of soil respiration and microbial biomass after rewetting from low water content will be greater in planted than unplanted soil). Likely because substrate input into the soil was low at 10 and 20% WHC due to poor plant growth. Thus at 10 and 20% WHC,microbes in planted and unplanted soil had similar substrate supply after rewetting. Further, the previous water content influenced soil respiration and microbial biomass only in planted soil because of differences in plant growth. This suggests that substrate input by plants plays an important role in the effect of the previous water content on soil respiration and microbial biomass after rewetting of dry soil.

5. Conclusion

After rewetting, the previous water content influenced soil respiration, microbial biomass and nutrient availability in planted soil, but had little effect in unplanted soil. This suggests that differences in C input and nutrient availability induced by plants play an important role in soils that undergo changes in water content. Therefore, low water content has a direct negative effect on soil microbes which is exacerbated by reduced plant growth even after the soil is rewet.

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