Soil Biology & Biochemistry 115 (2017) 415–422

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Soil respiration declines with increasing nitrogen fertilization and is not related to productivity in long-term grassland experiments

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ARTICLE INFO

Article history:
Received 6 September 2016
Received in revised form
10 August 2017
Accepted 24 August 2017
Available online 18 September 2017

Keywords:
Fertilizer
Nitrogen
Phosphorus
Potassium
Soil CO_2-C respiration
Soil fertility

ABSTRACT

Soil respiration is often used as an index of fertility because the majority of nutrients are cycled through the microbial biomass. We assessed the role of soil respiration as a measure of resource productivity in three long-term grassland experiments near Pietermaritzburg, South Africa. All of these experiments have shown significant changes in grass species composition and productivity. An ongoing Veld (=field) Fertilizer Experiment (VFE) that manipulated the level of nitrogen fertilizer, phosphorus and lime has been running since 1951. A Burning and Mowing Experiment (BME) has been running since 1950. The third experiment is part of the Nutrient Network (NutNet), a global fertilizer experiment that has been manipulating nitrogen, phosphorus, potassium and micronutrients and has been running since 2009. We found that longer-term experiments were more likely to show significant effects on soil respiration. We found several significant effects in the VFE but no significant differences in soil respiration among fertilization treatments in the shortest-term experiment (NutNet). In the VFE, we found significant differences in soil respiration due to levels of nitrogen fertilizer, form of nitrogen fertilizer (limestone ammonium nitrate and ammonium sulphate), phosphorus and lime. We found no significant relationship between above-ground net primary productivity and soil respiration despite the frequent detection of such a pattern due to the link between soil respiration, soil fertility and productivity. We found that, while there was a consistent increase in total soil nitrogen with increasing levels of nitrogen fertilizer applied, there was a consistent decrease in soil microbial respiration. There was a significant positive correlation between soil respiration and pH. Possible mechanisms behind this are unclear but may involve changes in dominant enzymes and possibly switches between dominance of bacteria and fungi. We also found significant effects of the timing of burning in the BME, but not due to the frequency of burning or the occurrence of mowing. Our results suggest that studies may need to be long-term, for example here at least 10 years, before key functional relationships with soil fertility can be reliably understood.

1. Introduction

Considerable evidence shows a strong role for bottom-up or nutrient control of grasslands (Adler et al., 2011; Harpole et al., 2011; Borer et al., 2014). We attempted to assess the role of bottom-up control by measuring soil respiration in three adjacent long-term grassland experiments near Pietermaritzburg, South Africa. Soil respiration is an important aspect of soil quality and is often used as an indicator of soil fertility (Groffman et al., 1996; Haney et al., 2008a). A number of soil studies have shown the utility of testing soil CO_2 respiration as a means to gauge active soil carbon (C) and soil microbial biomass, as well as potential release of nutrients for crop production (Groffman et al., 1996; Robertson et al., 1999; Fierer and Schimel, 2003; Haney et al., 2008a, 2008b).

Interpreting the effects of changes in soil fertility due to disturbance may best be achieved by examining long-term experiments rather than short-term experiments because of the transient nature of the initial species' responses (Tilman, 1988; Tilman and Wedin, 1991). That is, interpreting the results of short-term experiments may be limited because of potential priority effects

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http://dx.doi.org/10.1016/j.soilbio.2017.08.035
0038-0717/

(i.e., the effect of particular species on community development due to arriving earliest at a site) (Davis and Pelsor, 2001; Fukami et al., 2005; Kardol et al., 2013). Other important reasons for establishing long-term experiments include studying the manifold relationships of nutrient availability and biodiversity (Crawley et al., 2005), the functional stability of soils to perturbation (Griffiths et al., 2001), and because the processes of soil development and change are slow and take time to occur (Silvertown et al., 2006).

Current long-term grassland trials conducted at Ukulinga, the University of KwaZulu-Natal research farm just outside Pietermaritzburg in KwaZulu-Natal, are among the longest-running field experiments in Africa (cf. Swift et al., 1994; Morris and Fynn, 2001; Fynn and O'Connor, 2005; Fynn et al., 2004, 2005; Tsvuura and Kirkman, 2013). Two of the ongoing experiments at Ukulinga, the Burning and Mowing Experiment (BME) and the Veld Fertilizer Experiment (VFE), were initiated in 1950 and 1951, respectively. Treatments in the BME were designed to determine the yield and quality of hay in moist tall grassland due to removal by burning or mowing. The VFE was designed to examine possible ways of increasing the yield of grassland (termed “veld” in South Africa) by fertilizing (Morris and Fynn, 2001). An additional experiment, termed Nutrient Network (NutNet), was started in 2009, and is part of a global network of more than 90 grassland sites worldwide (www.nutnet.org), using nutrient (and herbivore) manipulations. The range of treatments (and their combinations) applied to these three long-term grasslands allow for an examination of some relevant ecological questions such as productivity-diversity of species along nutrient gradients and the interactive effects of mowing and burning season and frequency on community composition and productivity. A further advantage is that treatments are replicated within an appropriate statistical design (Morris and Fynn, 2001; Fynn and O'Connor, 2005; Adler et al., 2011).

We wished to determine in these adjacent grassland experiments what the importance of soil respiration was to soil fertility and productivity. We made the following hypotheses regarding changes in soil microbial respiration in these long-term experiments:

(1). There would be greater effects on microbial respiration in the long-term fertilization experiment (VFE) than the shorter-term experiment (NutNet) with the long-term effects of fertilization and concomitantly greater observed changes in plant-species composition. There should also be increased soil respiration with increased nitrogen (N) fertilization and significant interaction effects between N fertilizer and lime.

(2). Frequent burning would lead to decreases in soil microbial respiration due to the diminished amount of C and N in the soil and the volatilization of N compounds.

(3). Removal of biomass, such as by mowing, should cause a peak in microbial biomass due to the combined, stimulatory effects of increases in the supply of labile C and other nutrients, through defoliation-induced root exudation and changes in root turnover.

2. Materials and methods

2.1. Study area

The BME, VFE and NutNet experiments are situated at Ukulinga, a research farm of the University of KwaZulu-Natal, Pietermaritzburg, South Africa (29° 24′E, 30° 24′S). The experiments were all situated on top of a small escarpment, ranging in altitude between 838 and 847 m, within ca. 100 m of one another. Soils are fine-textured and derived from shales and were classified as Westleigh forms (Soil Classification Working Group, 1991) or Plinthic Acrisols (FAO). The vegetation of the area is classified at a large spatial scale as KwaZulu-Natal hinterland thornveld (Mucina and Rutherford, 2006), which is an open savanna of *Acacia* (also known as *Vachellia*) *sieberiana* (Burtt Davy) Kyal. & Boatwr. trees and *Hyparrhenia hirta* (L.) Stapf, *Aristida junciformis* Trin. & Rupr., *Themeda triandra* Forssk. and other grass species. At a smaller spatial scale (as on the escarpment of Ukulinga), the vegetation is tall grassveld (Acocks, 1953). With regular burning, trees are sparse and *T. triandra* is the dominant grass, with *Tristachya leucothrix* Trin. ex Nees and *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult. also being common (Morris and Fynn, 2001). Together these grass species account for much of the herbaceous above-ground net primary production (ANPP) at Ukulinga (Fynn et al., 2004). The native grass species in the locality all use the C_4 photosynthetic pathway (Fynn et al., 2004).

The mean annual precipitation in the locality is 790 mm (32-year mean); about 80% of this falls during summer as convective storms (October-April). Mean monthly maximum and minimum temperatures range from 26.4 °C in February to 8.8 °C in July, respectively. Winters are mild with a mean maximum of 13.2 °C in July (43-year mean), with occasional frost. There has been no grazing on the experimental sites for >60 yrs.

2.2. Experimental design

2.2.1. Veld fertilization experiment (VFE)

A full description of the Veld Fertilization Experiment (VFE), which was established in 1951 on virgin native grassland, is given elsewhere (Le Roux and Mentis, 1986; Tsvuura and Kirkman, 2013). This experiment was replicated in three blocks of 32 plots each, giving a 4×2^3 factorial design, although some second-order and third-order interactions did not occur (Fynn and O'Connor, 2005). Individual plots measured 9.0 × 2.7 m, with 1 m spacing between plots (Le Roux and Mentis, 1986). Four levels of N fertilizer were applied in this experiment, viz. (0 (i.e. control), 7.1, 14.1 and 21.2 g m^{-2}), with the same amount being applied in both the limestone ammonium nitrate (LAN) and ammonium-sulphate treatments (Fynn and O'Connor, 2005). Each form of N was not applied in combination with the other, but only with P and lime. Phosphorus (P) was applied annually as super-phosphate at two levels (0 (control) and 33.6 g m^{-2}). Lime treatments were applied every 5 years at two levels (0 (control) and 225 g m^{-2}). The details of the VFE are to be found in Supplementary Information.

2.2.2. Nutrient Network fertilization experiment

This is part of an international grassland experiment, termed Nutrient Network (NutNet), that manipulates the levels of N, phosphorus (P) and potassium (K), as well as micronutrients applied to the K-fertilizer plots only. N, P, and K are applied at 10 g m^{-2} y^{-1} by elemental mass, before the growing season of each treatment year. This experiment was started in 2009. N is applied as 60–90 day time-release urea, P is applied as ‘triple super phosphate’ (P_2O_5) and K as potassium sulphate (K_2SO_4). The micronutrient mix (‘MicroMax’) was applied at the first treatment application into K-treatment plots only (Adler et al., 2011). The ‘MicroMax’ mix contains the following elements: Ca (6%), Mg (3%), S (12%), B (0.10%), Cu (1%), Fe (17%), Mn (2.50%), Mo (0.05%), and Zn (1%), and is applied at 100 g m^{-2} y^{-1} fertilizer. Each plot is 25 m^2 in size and there are 10 plots per treatment combination (three replicates of each of the four fertilizer treatments on their own, each of these in two and three-way combinations plus one extra control and one extra NPK + micronutrients per replicate = 30 plots total).