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Biochar but not earthworms enhances rice growth through increased protein turnover

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ABSTRACT

The aim of this work was to compare the effects of biochar and earthworms on rice growth and to investigate the possible interactions between both. In addition to classic macroscopic variables we also monitored some leaf-level cellular processes involved in protein turnover. Both biochar and earthworms significantly increased shoot biomass production. However, biochar had a higher effect on the number of leaves (+87%) and earthworms on leaf area (+89%). Biochar also significantly increased the leaf turnover. At the cellular level, biochar but not earthworms enhanced protein catabolism by an increase in leaf proteolytic activities. This could be related to the increased expression of three of the six genes tested related to protein catabolism, one serine protease gene *OsSP2* (+24%), one aspartic acid protease gene, *Oryzasin* (+162%) and one cysteine protease gene *OsCatB* (+257%). Furthermore, biochar also enhanced the expression level of two genes linked to protein anabolism, coding for the small and large subunits of rubisco (+33% and +30%, for *rbcS* and *rbcL*, respectively), the most abundant protein in leaves. In conclusion, our data gives evidence that biochar increased rice biomass production through increased leaf protein turnover (both catabolism and anabolism) whereas earthworms also increased rice biomass production but not through changes in the rate of protein turnover. We hypothesize that earthworms increase nitrogen uptake at a low cost for the plant through a simultaneous increase in mineralization rate and root biomass, probably through the release in the soil of plant growth factors. This could allow plants to accumulate more biomass without an increase in nitrogen metabolism at the leaf level, and without having to support the consecutive energy cost that must bear plants in the biochar treatment.

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1. Introduction

Many soils of the lowland humid tropics are thought to be too infertile to support sustainable agriculture. One of the major problems is the rapid decomposition of organic matter (Zech et al., 1990) due to the high temperatures, intense precipitation, and the lack of stabilizing minerals. On soils with low nutrient retention capacity the strong tropical rains easily leach available and mobile mineral nutrients limiting the efficiency of conventional fertilizers. The reduction of soil content in organic matter (SOM) is causing soil degradation. The agriculture is often not sustainable without nutrient inputs beyond 3 years of cultivation (Tiessen et al., 1994). In tropical areas, the development of techniques improving soil fertility is thus a priority. The use of more stable organic matter could help to increase the sustainability of soil fertility. In this context, biochar addition to soils is a promising alternative to transfer of more easily decomposable organic matter (Zech et al., 1990; Fearnside et al., 2001). Indeed, the existence of anthropogenic biochar-enriched dark soils (*terra preta de indio*) and the fact that they have kept a high fertility for hundreds of years supports this idea. Apart from high carbon contents, the most striking feature of biochar is its capacity to retain mineral nutrients (Glaser, 2007). The fertility of *terra preta de indio* is most likely linked to an anthropogenic accumulation of phosphorus (P), calcium (Ca), and fragmented biochar.

Another sustainable way to increase tropical soil fertility is by maintaining high biomasses of earthworms (Lavelle et al., 2001). They are known to positively affect plant growth via five main mechanisms (Scheu, 2003; Brown et al., 2004): (1) an increased mineralization of soil organic matter (2) the production of plant

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growth substances via the stimulation of microbial activity; (3) the control of pests and parasites; (4) the stimulation of symbiotic microorganisms; (5) modifications of soil porosity and aggregation, which induces changes in water and oxygen availability to plant roots.

We have previously reported significant macroscopic effects of biochar and earthworms on rice growth in a greenhouse experiment using different soil types (Noguera et al., 2010). We have shown that (1) biochar and earthworms have additive positive effects on rice growth, (2) they differently influence resource allocation and (3) these effects depend on soil type. In the present article, we use the same greenhouse experiment but focus on the physicological effects of biochar and earthworms in the most fertile soil where differences between treatments were the most significant (Noguera et al., 2010). Ecological studies on plant responses to a particular soil treatment generally focus on root-level responses (Gregory, 2006). Very few studies have included measurements of leaf-level physiology (Day and Detling, 1990a, 1990b; Jaramillo and Detling, 1992a; Jaramillo and Detling, 1992b; Peek and Forseth, 2003; Blouin et al., 2005) and up to now the molecular processes underlying the observed changes in plant growth and morphology have seldom been addressed (Blouin et al., 2005; Jana et al., 2010; Endlweber et al., 2011). Studying the physiological and cellular processes occurring at the leaf-level in the presence of earthworms, biochar or both should therefore deepen our understanding on the mechanisms through which earthworms and biochar influence plant growth. To tackle these issues, in addition to macroscopic variables, we monitored some leaf-level cellular processes involved in leaf protein turnover.

Plant scientists have long recognized protein turnover as a fundamental component in plant development. Research has however traditionally focused on physiological processes relevant for agriculture and variety improvement, including the breakdown of storage proteins during seed germination, and protein remobilization upon the onset of leaf senescence, concomitant with the reallocation of N resources to reproductive organs (Huffaker, 1990). However, the proper functioning of a cell is ensured by the precise regulation of protein levels that in turn are regulated by a balance between the rates of protein synthesis and degradation. Therefore, we suggest that macroscopic treatments influencing plant growth should lead to different regulations of leaf protein synthesis and degradation.

Within plant cells, protein degradation is mediated by proteolysis (Callis, 1995; Schaller, 2004). Unlike other cellular enzymes, proteolytic enzymes (also termed proteases) do not have specific substrate targets and nomenclature is based on the amino acids present at the active site. There are mainly 4 super families of proteases assembled in the MEROPS database (Rawlings et al., 2008; http://merops.sanger.ac.uk/): aspartic acid proteases, serine proteases, cysteine proteases and metalloproteases. Since proteases can cleave more or less any available protein, they are present in specific cellular compartments, namely in lysosome-like acidic vacuoles (Callis, 1995; Vierstra, 1996). Protease activity is also under tight control, both at the expression and post-translational levels and also by specific inhibitors.

Nitrogen (N) is an essential macronutrient for plant growth, and crop production is often greatly affected by N nutrition. In rice seedlings, about 70% of N in the aboveground part is allocated to leaf blades and supports their photosynthetic function (Mae et al., 1984). Approximately 80% of total leaf N is invested in chloroplasts (Makino and Osmond, 1991). A number of proteins participate in photosynthetic reactions in chloroplasts, ribulose-1,5 – bisphosphate carboxylase/oxygenase (Rubisco) being the most abundant. Rubisco is both an enzyme of photosynthesis and the most abundant leaf protein. It accounts for 12–35 % of total leaf N in C_3 plants (Makino, 2003; Makino et al., 2003; Kumar et al., 2004). It comprises eight small subunits (*SSUs*) and eight large subunits (*LSUs*), which are products of the nuclear *rbcS* gene and the chloroplast *rbcL* gene, respectively. Rubisco is degraded during leaf senescence and its N is re-mobilized and translocated into growing organs and used for their growth. Rubisco-derived N is considered to account for about 40% of total re-mobilized N from senescing leaves in rice (Makino et al., 1984). Therefore, the turnover of Rubisco, namely, its synthesis and degradation, should closely be related to both C and N economy in plants (Imai et al., 2005).

In this context, our study aimed at testing the following hypotheses: First, since biochar and earthworms influence plant growth at least through an increase in mineral nutrient availability, they should influence nitrogen metabolism, namely protein turnover; Second, since biochar and earthworms influence plant growth through partially different mechanisms, they should affect plant physiology differently at the leaf cellular level. In order to test these hypotheses we measured some classic macroscopic parameters (shoot root and leaf biomasses, C/N.) and tried to relate them to the underlying processes related to leaf protein turnover operating at the cellular and molecular levels.

2. Materials and methods

2.1. Microcosms preparation

The soil was collected from a coffee plantation at Pescador, located in the Andean hillsides of the Cauca Department, southwestern Colombia (2° 48′ N 76° 33′ W). As previously described (Noguera et al., 2010) the Pescador soil is a moderately acid ($pH = 5.1$) Inceptisol (USDA, 1998) relatively rich in organic matter (11.5%), mineral nitrogen (12.9 mg NH_4^+–N kg^{-1}, 27 mg NO_3^-–N kg^{-1}) and with a relatively high CEC (6.0 cmol kg^{-1}). The soil was dried and sieved (2 mm mesh). Two soil treatments were implemented: soil with no addition (NB) and soil with the addition of biochar (B). Biochar has been prepared at the CIAT (Centro Internacional de Agricultura Tropical) as described previously (Rondon et al., 2007) and has been added locally around coffee plants in a long term experiment to assess biochar effect on coffee production. Our NB (B) treatment consisted in soil collected from the control (biochar) treatment of the field experiment. Taken together, the soil of our B treatment contained 25.5 g of biochar per kg of dry soil. This corresponds to 20.4 t of biochar per ha assuming that the biochar has been mixed with the first 10 cm layer of soil. Microcosm containers consisted of PVC pots of 10 cm diameter and 15 cm height. They were filled with 900 g of dry soil. The earthworm treatment consisted in the addition of five adults of *Pontoscolex corethrurus* (initial fresh weight 5 ± 0.5 g), an endogeic species common in all humid tropics (Lavelle et al., 1987).

2.2. Plant growth and experimental design

Rice plants (*Oryza sativa* cv. Linea 30) (Chatel et al., 2000) were grown in a greenhouse for three months under controlled conditions (temperature 27–29 °C, relative humidity 65–95 %, light intensity of 600 μmol m^{-2} s^{-1} and a 12-h photoperiod) as previously described (Noguera et al., 2010). Microcosms were regularly weeded during the experiment and maintained at 80% of soil field capacity (this was checked through regular weighing of the pots). Pots were arranged in a completely randomized design. Plants were submitted to four combinations of treatments: Earthworms and Biochar (EB), Biochar (B), Earthworms (E) and a Control (C) without biochar or earthworms. Five replicates were implemented per treatment.

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