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Soil compaction effects on growth and root traits of tobacco depend on light, water regime and mechanical stress

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ABSTRACT

Soil compaction can strongly affect plant performance as many other stress factors. In nature, many combinations of different stress factors may be found. We expect that the effects of soil compaction may be different depending of the occurrence of other stress. This has not been fully investigated; most studies have included only one stress factor together with soil compaction. In this study, we combine soil compaction with the interaction of shade, low water availability and mechanical stress. We use as a model system tobacco plants (*Nicotiana tabacum*), in which the effects of the combination of these factors in a greenhouse experiment were studied on their growth, biomass allocation, root morphology and anatomy. Soil compaction effects on growth and root traits depended strongly on the other factors. In unstressed conditions, plant growth increased with compaction up to 1.4 g cm^{-3} bulk density and then declined. However, at low water and under mechanical stress plant growth declined monotonically with compaction, while under shade, soil compaction had no effect on growth. Soil compaction reduced fine root proportion in all treatments except in shade condition, while it increased root diameter and xylem area only under mechanical stress. These results indicate that analyses of soil compaction effects on plant performance should take the levels of other stress factors into account. More generally, they illustrate the difficulty of interpreting effects of a given stress factor on plants as these effects tend to interact with presence of other stressors.

1. Introduction

Soil compaction is commonly considered to have a negative effect on plant growth and agricultural yields (Wolkowski, 1990; Hansen, 1996; Kozlowski, 1999). It is also considered to be an ecological factor that for instance plays a role in hampering forest succession after land clearance for pasture use (Small and McCarthy, 2002; Lawrence, 2003) while in (semi)arid regions it may aggravate the impact of overgrazing and contribute to desertification (Rietkerk et al., 2000, 2004; Castellano and Valone, 2007).

The direct impact of soil compaction is an increase of the mechanical resistance to root penetration, which makes it more difficult for plants to exploit a large soil volume. However, a major complication in understanding the effects of compaction is that its occurrence tends to be correlated with the presence of other environmental factors with which it may interact. For example, it may decrease (more negative) the soil matric potential (Whalley et al., 2006), thus reducing water availability to plants, and can thus aggravate the effects of drought (Taylor and Ratliff, 1969). Soil compaction also tends to increase under grazing (Drewry et al., 2008), logging in forests (Small and McCarthy, 2002) or tillage in agricultural systems (Diaz-Zorita et al., 2002), all of which tend to increase light availability as well wind exposure, while grazing is also associated with mechanical stress through trampling. Agricultural and silvicultural treatments entail disturbances whereby a set of factors that can influence plant growth occur simultaneously (changes in soil compaction, light and water availability, wind, etc.) (Godefroid and Koedam, 2008). Overall this raises the question to what extent the effects of soil compaction depend on light and water availability and on the magnitude of mechanical stress (i.e. wind or trampling) to which plants are exposed.

Light is probably the most important factor affecting plant growth as it supplies the energy for photosynthesis. High light availability tends to increase the demand of plants for soil resources, so plants at high light availability could be more susceptible to changes in soil compaction, due to its key role in root–soil interaction.

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On the other hand, in many environments plant growth is limited by water availability, which is strongly determined by the soil physical characteristics. However, under natural conditions it may be difficult to separate the effects of water limitations from other physical factors affecting root growth (Cortina et al., 2008). Soil compaction entails changes in various soil properties such as penetration resistance, porosity and bulk density. Since these properties have different and interactive effects on plants, controlled greenhouse and lab experiments are needed in which they can be quantified separately.

Mechanical stress is another stress factor affecting plant growth. Plants typically respond to mechanical stress through reduced stem elongation and increased allocation to root growth, a set of responses commonly denoted as thigmomorphogenesis (Jaffe and Forbes, 1993; Anten et al., 2005). It has also been suggested that responses to soil compaction (i.e., mechanical impediment to root growth) and externally applied mechanical force (wind, flexing or rubbing) on the plant shoot involve at least partly the same signal transduction pathway (Anten et al., 2006). It could thus be hypothesized that externally applied mechanical stress may aggravate the effects of soil compaction.

Plant responses to soil compaction are probably in the first place mediated by changes in root traits and functioning. Yet studies that combine growth analysis and measurements of root anatomy and morphology in this respect are rare. It is commonly reported that specific root length (SRL; root length per unit root mass) decreases with soil compaction (Bengough and Mullins, 1990). The activity of the phytohormones ABA and ethylene seems to be involved in regulating the responses to compaction (Hussain et al., 1999; Roberts et al., 2002; Anten et al., 2006; Whalley et al., 2006), having two main effects: changes in root morphology and shoot growth inhibition. Although plants are able to regulate shoot growth in response to a mechanical impedance signal, it is difficult to avoid side effects on water uptake. Due to compaction, root length and the amount of fine roots are reduced, while soil matric potential is decreased (more negative); both of which reduce the ability of plants to take up water. A decrease in root diameter has been suggested (Hund et al., 2009) in response to water stress. This is coherent with the theoretical considerations about hydraulic conductivity and resistance (Steudle, 2000), which assumes that roots with a smaller cortex width have lower resistances for water transport from soil to xylem vessels. Xylem vessel diameter may also decrease in order to maximize hydraulic conductivity under safety margins (Martinez-Vilalta et al., 2002). Therefore, we would expect two types of root anatomy changes in response to water stress: a cortex reduction and xylem vessels diameter reduction. Iijima and Kato (2007) addressed the difficulty to distinguish soil compaction and water stress effects on root anatomical changes because of their high interdependence and the specific response of the species studied.

In this paper we address the following questions: (i) what are the effects of soil compaction on plant performance in terms of growth, (ii) to what extent do these effects depend on light and water availability and on the degree of mechanical stress to which plants are exposed and (iii) to what extent can the effects on growth be explained by changes in root characteristics? To this end we exposed tobacco plants (*Nicotiana tabacum* L.), as a model system, to a continuous range of soil compaction together with four different conditions: control, shade, low water availability and mechanical stress. Tobacco is an extensively cultivated species with a high economic value. Soil compaction is an important factor reducing yield in this species (Tursic et al., 2008). This work attempts to use tobacco as a model system in order to describe the interaction between soil compaction and other environmental factors (light, water and mechanical stress) under an ecophysiological point of view.

2. Materials and methods

2.1. Growth facility and plant material

This experiment was carried out in a greenhouse at Utrecht University (The Netherlands; 52° 30′ N, 5° 45′ E) between June and August of 2009. We used the annual plant, tobacco (*N. tabacum* L., cv. Samson N × N), this particular cultivar reaching a maximum height of about 2.5 m. On May 18th, seeds were sown in trays in a mixture of sand and potting soil. Seedlings were grown at 30% of natural daylight, a level achieved with neutral-density shade cloth and shading by the greenhouse roof. When plants reached a fresh mass of 1.4 ± 0.6 g, they were fresh weighed and transplanted into pots. These were PVC tubes of 30 cm in height and 10.5 cm in diameter, whose base was drilled to get a good drainage of the irrigation water. At the same time, a subsample of plants ($n = 10$) were harvested, fresh weighed, dried out at 70 °C for at least three days and the dry mass was obtained. Initial dry mass ratio was calculated as the ratio of dry and fresh mass to be used to estimate the dry mass of each seedling (see Section 2.4). For the description of soil type and soil compaction treatment see Section 2.3.

The day/night temperatures in the greenhouse were set to 22 and 18 °C, respectively. For the control plants (CO) the light and water availability was the following. The light level during the experiment was 50% of natural day light and was created by the shading of the greenhouse roof. Watering was done by hand using 100 ml each time and 3 times a week for a total of 2900 ml during the experiment. This irrigation system forces plants to use soil water reserve as a function of soil compaction treatment.

2.2. Experimental design: water, light and mechanical treatments

The experiment was set up as an incomplete factorial design focusing in soil compaction as main factor, thus only compaction × other stress factors (shade; low water; mechanical stress) interactions were studied. This allows to answer our questions keeping the number of replicates under a reasonable number. Soil compaction treatments were made in order to create a continuous range of bulk density (see Section 2.3). A total amount of 15 plants, covering the whole range, were assigned to each treatment: control (CO), shade conditions (SH), low water (LW) and mechanical stress (MS). For the control treatment the plants were grown in optimal conditions of light, water (see Section 2.1) and without mechanical stress. The shade treatment was created using a cloth which transmitted just 10% of total day light. The low water treatment was established by applying 40% less water than under optimal conditions (60 ml 3 times a week). The mechanical stress treatment consisted of gently grasping the plants at the base and flexing them no more than 45° for a total of 50 flexures (see Anten et al., 2005). This treatment was done daily during the last 30 days prior to the final harvest.

2.3. Soil compaction treatments

The soil substrate was a mixture of sand, silt and gravel in a proportion 3:2:1 resulting in a sandy soil texture. This type of soil was chosen as it is most easily compacted. We added a 7% of NPK fertilizer (7:7:7) to each pot to avoid nutritional deficiencies. Different levels of soil compaction were made considering three bulk density ranges having as reference the increment of soil mass per volume unit (a cylindrical pot of 10.5 cm in diameter and a known soil height). No compaction treatment (NC) was made just filling the whole volume of the pot with soil without compacting. For the other two compaction levels, we used an electric hammer (GSH 11 E, Bosch, Germany) with a modified piston to compact with the purpose of being able to increase the soil mass per