Europ. J. Agronomy 63 (2015) 36–46

Contents lists available at ScienceDirect

European Journal of Agronomy

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

Effects of free air CO_2 enrichment on root growth of barley, sugar beet and wheat grown in a rotation under different nitrogen supply

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ARTICLE INFO

Article history:
Received 1 February 2014
Received in revised form 27 October 2014
Accepted 28 October 2014
Available online 28 November 2014

Keywords:
Free air carbon dioxide enrichment
Winter wheat
Winter barley
Root dry weight
Root length density
Shoot root ratio
CN ratio
N supply

ABSTRACT

Elevated atmospheric CO_2 concentrations [CO_2] are known to change plant growth by stimulation of C_3 photosynthesis and by reduction of transpiration of both C_3 and C_4 crops. In comparison to the information on above ground plant responses only limited knowledge exists on the response of root growth of arable crops to elevated [CO_2] which is particularly true for temperate crop species under real field conditions. A free air CO_2 enrichment (FACE) study (550 ppm at daylight hours) was carried out in a crop rotation of winter barley, sugar beet and winter wheat repeated twice in the course of six years on a sandy loam soil at Braunschweig, Northern Germany. Winter barley and sugar beet were included for the first time in a FACE study. A possible interaction with restricted nitrogen (N) supply was studied by fertilizing the CO_2 treatment plots with adequate and 50% of adequate N supply. Fine root samples were taken in the plough layer and below at 3–4 sampling dates during the vegetation period and root dry matter (excluding sugar beet storage root), shoot root ratio, root length density, specific root length and root tissue composition (CN ratio) were determined. Main effects of elevated [CO_2] on the investigated variables were slightly significant. Significant CO_2 effects were observed in interaction with the sampling date. In most cases elevated [CO_2] increased root dry matter early in the vegetation period with a maximum growth stimulation of up to 54% as compared to ambient [CO_2]. Concomitantly, root length densities were increased in both winter wheat and sugar beet. For winter barley also a significant decrease in root dry weight and significant increase of shoot root ratio was detected at final harvest while such an effect was not significant for sugar beet. Specific root length as an indicator of root morphology was mainly influenced by crop species. As a result, there was no consistent overall effect of elevated [CO_2] on biomass partitioning in this study as changes in shoot root ratio only occurred at specific sampling dates indicating a similar stimulation of roots and above-ground biomass due to elevated [CO_2]. Nitrogen supply did not alter the effect of elevated [CO_2] on any of the root variables apart from CN ratios. A significant increase of root CN ratios in wheat and sugar beet was observed under elevated [CO_2], but this effect was much smaller than the effect of N supply.

1. Introduction

The rapidly increasing atmospheric CO_2 concentrations [CO_2] are considered as the key driver of global climate change and an increase of [CO_2] to about 550 ppm is expected for the middle of the 21st century (Meehl et al., 2007). Apart from its physical effect on the global radiation balance and thus global temperature, elevated [CO_2] exerts direct effects on plant and crop growth. Photosynthesis and consequently growth of C_3 crop species are known to be positively affected by elevated [CO_2] which mostly goes along with modified water and nutrient turnover in the plants (Ainsworth and Long, 2005; Kimball et al., 2002). For C_4 crops beneficial growth effects of elevated [CO_2] seem to result solely from an improved water economy of the plants (Leakey et al., 2009; Manderscheid et al., 2014). Driven by concerns about potential effects of climate change on global food security most studies on effects of elevated [CO_2] have focussed on above-ground biomass growth and yields of agricultural crops with the majority of studies conducted under artificial growth conditions of e.g. growth chambers, field

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http://dx.doi.org/10.1016/j.eja.2014.10.005
1161-0301/

tunnels and greenhouses mostly using potted-plants (Ainsworth and McGrath, 2010). However, the limitations of such experiments for realistic assessments of the size of elevated [CO_2] effects have recently been discussed (Leakey et al., 2006; Long et al., 2006). Free air CO_2 enrichment (FACE) techniques have thus been developed (Hendrey and Miglietta, 2006; McLeod and Long, 1999) and applied in experiments with important staple crops (wheat, rice, soybean, barley, sugar beet) in China, Japan, USA and Germany (Kim et al., 2003; Kimball et al., 2002; Long et al., 2005; Ma et al., 2007; Weigel and Manderscheid, 2012). FACE systems leave the natural environment of a crop plot nearly fully undisturbed during the CO_2 exposure and allow the investigation of *in-situ* water and nutrient turnover at the agro-ecosystem level. Collectively, these FACE studies point to lower crop growth and yield stimulations by elevated CO_2 levels as compared to chamber studies (Long et al., 2006).

In contrast to the amount of information available on effects of elevated [CO_2] on above-ground crop growth, effects on the soil root systems have been studied less intensively (Kimball et al., 2002; Madhu and Hatfield, 2013). According to Kimball et al. (2002) elevated [CO_2] can result in a stimulation of root growth and root length density in excess of the stimulation of above-ground biomass. From earlier studies (summarized e.g. by Rogers et al., 1994), there is evidence, although highly variable, that elevated [CO_2] may stimulate total root biomass and lead to changes in root structural characteristics. However, much of this previous information results from studies where root growth was observed under non-natural soil conditions and where measurements were performed only at a single point in time. Such single point measurements do not consider transient changes in carbon allocation pattern between above- and below-ground structures in the course of the plant's ontogeny (Gregory et al., 1997). For example, root growth of most annual crops shows a strong seasonal dynamics. It has been observed in earlier studies that elevated CO_2 may stimulate root growth to a larger extent at the vigorous early vegetative growth stages than in the phase between the beginning of the vegetation period and stem elongation (Madhu and Hatfield, 2013; Pritchard et al., 2006). The few more recent FACE studies with C_3 crops where root growth has been assessed were limited to one study with paddy rice (Ma et al., 2007) and two wheat studies (spring wheat, Wall et al., 2006; Wechsung et al., 1999; winter wheat, Ma et al., 2007). For both crops significantly increased root biomass and root growth rates were observed under elevated [CO_2], with maximum increases of 37% for spring wheat (550 ppm CO_2), 75% for winter wheat (590 ppm) and 68% for paddy rice (590 ppm), respectively. There is no such field information available for important temperate crops like winter barley or sugar beet.

Effects of elevated [CO_2] on root characteristics such as total root dry matter, root length density or stem-root ratio may have strong repercussions on total crop growth and adaptation mechanisms and on carbon (C) and nutrient turnover in the agro-ecosystem. Moreover, along with an improved soil water status by reduced transpiration under elevated [CO_2] (Burkart et al., 2011) a deeper and denser root system may further improve water availability for crop growth (Wechsung et al., 1999). Changes in above-ground plant tissue composition, e.g. increased CN ratios in crop residues, have frequently been observed under elevated CO_2 conditions (Loladze, 2002, 2014; Taub et al., 2008). If this holds true for crop roots, it may have effects on nitrogen turnover and availability in agro-ecosystems. Therefore, the quantification of root growth and quality under elevated CO_2 is of general importance particularly for the modelling of overall climate change effects on agricultural crop production and agro-ecosystem properties. For example, in most models partitioning of carbon between different sink pools is one of the most important features of total crop development (Brisson et al., 2006) which also applies to the distribution of nitrogen (N) within the plant. Effects of elevated [CO_2] are mostly modified by the nutrient availability to a crop, which is particularly true for nitrogen. A number of studies have shown $CO_2 \times N$ interactions (Stitt and Krapp, 1999; Kimball et al., 2002) and a common presumption assumes that N deficiency acts as a growth inhibitory factor which may decrease the relative response to elevated [CO_2] (Ainsworth and Long, 2005). Nitrogen deficits are known to decrease the shoot root ratio (Gastal and Lemaire, 2002) and exploration of the soil can extent faster to deeper soil layers than under sufficient N supply (Svoboda and Haberle, 2006). Hence, it is important to test whether elevated [CO_2] particularly stimulates root growth under limited N supply as observed in earlier studies (Stulen and den Hertog, 1993).

The aim of the present study was to investigate the seasonal fine root growth dynamics of winter barley, sugar beet (excluding storage root) and winter wheat grown in a crop rotation in Central Europe repeated twice over a total period of six years under FACE conditions with adequate and growth limiting N fertilization. We addressed the following questions: (i) to what extent is root growth stimulated by elevated [CO_2] under the conditions of the crop rotation? (ii) do the crop species behave differently with respect to elevated [CO_2]?, (iii) how is the seasonal time course of CO_2 effects on root growth? and (iv) are relative CO_2 effects on root growth particularly evident under limited N supply and are there interactive effects of elevated [CO_2] and different levels of N supply on functional root variables such as specific root length?

To our knowledge this is the first experiment reporting on effects of elevated [CO_2] on root growth of sugar beet and winter barley under real agronomic growth conditions. With respect to root growth of winter wheat it is the first FACE study under growth conditions of central Europe.

2. Materials and methods

2.1. Experimental site

The 22-ha experimental field was located at the Thuenen Institute (TI) in Braunschweig, south-east Lower Saxony, Germany (52°18′ N, 10°26′ E, 79 m a.s.l.). The soil is a luvisol of a loamy sand texture (69% sand, 24% silt, 7% clay) in the plough horizon. The profile has a depth of about 0.6 m (0–0.3 m plough horizon, 0.3–0.45 m Eb clay eluviation layer, 0.45–0.6 m Bt clay illuviation layer, >0.6–0.7 m CII, secondary parent material). The lower layers, in particular >0.7 m, are characterized by a coarser soil texture (almost pure sand) and are structured by the succession of thin silt/clay layers. The plough layer has a pH of 6.5 and a mean organic matter content of 1.4%. The soil has a volumetric plant available water content of ca. 18% in the plough layer, which decreases slightly with increasing soil depth. Overall, the soil is of low to intermediate fertility and provides a comparatively shallow effective rooting zone (0–0.6 m).

2.2. Crop management

The FACE experiment was carried out in a typical North German crop rotation consisting of winter barley, ryegrass as a cover crop, sugar beet and winter wheat (Table 1). The rotation cycle was repeated twice, resulting in two growing seasons for winter barley (*Hordeum vulgare* cv. 'Theresa' 1999/2000 and 2002/2003), sugar beet (*Beta vulgaris* cv. "Wiebke" 2001 and cv. 'Impuls' 2004) and winter wheat (*Triticum aestivum* cv. "Batis" 2001/2002 and 2004/2005). The winter cereals were spaced in rows of 0.12 m distance while distance between sugar beet rows was 0.45 m. Agricultural management measures were carried out according to local farm practices. Amounts of added mineral nutrients were based on analysis of soil nutrient contents (K, Mg, N, P, S) determined in early