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# Growth, senescence and water use efficiency of spring oilseed rape (*Brassica napus* L. cv. Mozart) grown in a factorial combination of nitrogen supply and elevated $CO_2$

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ABSTRACT

Atmospheric $CO_2$ enrichment is expected to affect the resource use efficiency of C3 plants with respect to water, nutrients and light in an interactive manner. The responses of oilseed rape (OSR) to elevated $CO_2$ have not much been addressed. Since the crop has low nitrogen use efficiency, the interactive effects of $CO_2$ enrichment and nitrogen supply deserve particular attention.

Spring OSR was grown in climate chambers simulating the seasonal increments of day length and temperature in South-Western Germany. Three levels of N fertilisation representing 75, 150 and 225 kg $ha^{-1}$ and two $CO_2$ concentrations (380 and 550 µmol $mol^{-1}$) were used to investigate changes in source–sink relationships, plant development and senescence, water use efficiency of the dry matter production ($WUE_{prod.}$), allocation patterns to different fractions, growth, yield and seed oil contents. Seven harvests were performed between 72 and 142 days after sowing (DAS).

Overall, plant performance in the chambers was comparable to the development under field conditions. While $CO_2$ responses were small in the plants receiving lowest N-levels, several significant N × $CO_2$ interactions were observed in the other treatments. Increasing the N availability resulted in longer flowering windows, which were furthermore extended at elevated $CO_2$ concentrations. Nevertheless, significantly less biomass was allocated to reproductive structures under elevated $CO_2$, while the vegetative C-storing organs continued to grow. At the final harvest shoot mass of the $CO_2$ exposed plants had increased by 9, 8 and 15% in the low, medium and high N treatments. Root growth was increased even more by 17, 43 and 33%, respectively and $WUE_{prod.}$ increased by 23, 42 and 35%. At the same time, seed oil contents were significantly reduced by $CO_2$ enrichment in the treatments with ample N supply.

Obviously, under high N-supply, the $CO_2$ fertilisation induced exaggerated growth of vegetative tissues at the expense of reproductive structures. The interruption of source–sink relationships stimulated the formation of side shoots and flowers (branching out). While direct effects of elevated $CO_2$ on flowering can be excluded, we assume that the increased growth under high N and $CO_2$ supply created nutrient imbalances which hence affected flowering and seed set.

Nevertheless, the final seed macronutrient concentrations were slightly increased by elevated $CO_2$, indicating that remobilisation of nutrients from the sources (leaves) to the sinks (seeds) remained effective. These findings were supported by the lower nitrogen concentrations in senescing leaves and probably increased N remobilisation to other plant parts under elevated concentrations of $CO_2$. All the same, $CO_2$ enrichment caused a decline in seed oil contents, which may translate into a reduced crop quality.

## 1. Introduction

Elevated atmospheric carbon dioxide has been shown to increase growth and yield in particular in $C_3$ plants since $C_3$ photosynthesis is not substrate saturated at current ambient $CO_2$ concentrations (Bowes, 1993; Long et al., 2006). At the same time, resource use efficiency is improved in $C_3$ plants with respect to water use, nutrient use and light use (Drake et al., 1997). In $C_3$ cereals which are determinate species often a faster development and an earlier onset of senescence has been observed (Sicher and Bunce, 1998; Fangmeier et al., 2000) which has been attributed to a divergence in C and N acquisition under elevated $CO_2$, and therefore a trade-off between carbon and nitrogen allocation and redistribution towards reproductive organs during grain filling.

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There is evidence from both chamber and field studies that $CO_2$ fertilisation effects on plant growth are stronger at ample availability of nutrients as compared to nutrient limited conditions (Rogers et al., 1993; Owensby et al., 1994; Wolf, 1996; Erbs et al., 2010). The supply of nutrients will therefore be an important modifier of plant responses and determine the yield stability under increasing levels of $CO_2$. Nevertheless, some basic physiological responses of $C_3$ species may not be overcome with increased fertilizer supply (Fangmeier et al., 1999). This concerns decreased concentrations of nitrogen and some other nutrients and, thus, increased nutrient use efficiency under elevated $CO_2$ which has been reported for several functional groups of $C_3$ species (Gifford et al., 2000; Yin, 2002; Marinari et al., 2007), however with a lower effect in legumes (Cotrufo et al., 1998; Taub et al., 2008). The 'dilution' of leaf N occurs mainly due to the increased photosynthetic assimilation of C and a potential decrease in Rubisco and enzymes of the photorespiratory pathway observed as a consequence of the photosynthetic acclimation to $CO_2$ enrichment (Nie et al., 1995; Stitt and Krapp, 1999; Fangmeier et al., 1999). With the decreasing N concentrations leaf density tends to be adapted (higher leaf mass per area, LMA, and lower specific leaf area, SLA), which can be understood as a response maximising the nutrient content per area (Yin, 2002; Ishizaki et al., 2003). Because sink organs are affected, too, seed N and protein concentrations may be reduced as well eventually resulting in a changed crop quality (Jablonski et al., 2002; Taub et al., 2008; Högy and Fangmeier, 2008). Besides the 'dilution' effect, another mechanism behind the reduced N concentrations is the lower mass transport of resources via the transpiration stream due to the decreased stomatal conductance observed in plants grown at elevated $CO_2$ which in turn increases the water use efficiency (WUE). Moreover, a reduced root uptake of minerals under elevated $CO_2$ (Taub and Wang, 2008) and the inhibition of nitrate assimilation into organic nitrogen compounds are being discussed (Bloom et al., 2010).

The mentioned effects are crop specific and variable for different mineral elements. Therefore it will be difficult to derive general suggestions for the adaptation of fertilisation regimes under climatic change and rising $CO_2$ concentrations (Lynch and St. Clair, 2004; Brouder and Volenec, 2008). Transcriptome studies have been initiated (Zheng, 2009) to understand the underlying molecular processes driving plant C/N balances and the involved responses to elevated $CO_2$. In order to understand $CO_2 \times N$ interactions in crops and to derive fertilisation recommendations to sustain or optimally exploit yield formation under $CO_2$ enrichment targeted experiments need to be performed in which nutrient use efficiency and allocation patterns are addressed over the entire growing cycle of the plants. Because root mass has often been shown to increase more under $CO_2$ enrichment than the shoot (Rogers et al., 1996; Jensen and Christensen, 2004; Yang et al., 2008) allocation to belowground organs must be included in such studies.

Although regarded as a terminal growth stage in the first place, senescence in crops is important for the remobilisation of nutrients and their redistribution to the grains or kernels or vegetative storage organs, such as tubers, as final sinks. Leaf senescence is a complex and highly coordinated developmental process under genetic control (Smart, 1994; Noodén et al., 1997; Buchanan-Wollaston et al., 2003) and may be regarded as a nutrient salvage mechanism to support younger sinks (Bleecker, 1998). Sink and source strength are involved in signalling during senescence. $CO_2$ enrichment affects the sink–source balance with respect to carbon on the one hand and nitrogen and other nutrients on the other hand in different directions since carbohydrate source strength increases whereas nitrogen source strength decreases. Because sugar accumulation and sugar signalling during senescence play an important role, the higher carbohydrate load and the change in C:N ratios under $CO_2$ enrichment may directly interact with the timing and progress of senescence (Wingler et al., 2006). Taylor et al. (2008) hypothesized that, with no sink limitation, photosynthesis and canopy greenness will be maintained for longer in elevated $CO_2$. Indeed, senescence was significantly delayed in perennial *Populus* tree species and some candidate genes to regulate these processes have already been identified (Rae et al., 2006). Also the timing and duration of flowering determine the remobilisation of resources between sources and sinks. In many experiments, $CO_2$ enrichment interacted with the flowering windows of plants.

Whereas cereals and protein crops such as soybean have been intensively studied for their response to $CO_2$ enrichment (e.g. Cure and Acock, 1986; Ziska and Bunce, 2007; Taub et al., 2008), only few reports exist from oilseed rape (OSR) exposure and the response to elevated $CO_2$. In contrast to $C_3$ cereals, nitrogen use efficiency in OSR must be regarded as relatively low since in early developmental stages rosette leaves are shed with still relatively high nitrogen contents of 2–2.5% of dry weight before stem elongation and long before seed filling. This nitrogen is not available for the stem and the inflorescences any more so that nutrient uptake occurs via the roots rather than from redistribution from lower (rosette) senescing leaves (Rossato et al., 2001; Malagoli et al., 2005). In consequence, plant breeders aspire to develop new OSR cultivars with a more efficient remobilization of N which will improve the seed yields and reduce environmental problems related to N leaching (Rathke et al., 2006; Schulte Auf'm Erley et al., 2007).

$CO_2$ enrichment may interact differently with the N redistribution and signalling during senescence in OSR compared to $C_3$ cereals. In addition, OSR has an indeterminate growth and is likely to show plasticity in yield responses, probably resulting in cultivar specific differences in the magnitude of $CO_2$ effects. Accordingly, the onset of leaf senescence appears to depend on the identity of cultivars since Frick et al. (1994) found a delayed senescence in $CO_2$ exposed dwarf OSR, while Johannessen et al. (2002) reported an earlier initiation of senescence and maturation in other cultivars. In growth chamber studies elevated $CO_2$ delayed the onset of flowering in *Brassica* species stimulating vegetative shoot growth mostly at the expense of seed yield at maturity (Frick et al., 1994; Johannessen et al., 2002). In a field study with OSR, however, flowering was insignificantly advanced (Franzaring et al., 2008a) and also the review of Springer and Ward (2007) suggests that most annual crop species tend to show an earlier rather than a later flowering under $CO_2$ enrichment. Underlying physiological and molecular mechanisms may be related to the excess accumulation of carbohydrates, which serve as flowering signals.

The aims of this study were to test the effects of atmospheric $CO_2$ enrichment on oilseed rape. Since we hypothesize an interaction between carbon and nitrogen availability, OSR was subjected to a combination of today's ambient and future $CO_2$ projected for the year 2050 and different nitrogen supply ranging from suboptimal to supra optimal, in a full-factorial design. In order to identify treatment effects on development and biomass acquisition and carbon allocation, frequent harvests including root mass and non-destructive assessments were performed over the entire growing cycle of OSR. Furthermore, we wanted to test whether $CO_2$ effects on water use efficiency will be modified by nitrogen supply and therefore followed water use throughout the experiment.

## 2. Materials and methods

### 2.1. Growth chambers

Experiments were performed in a system of six growth chambers (Vötsch BioLine, Balingen, Germany) equipped with 10 metal halide Osram HQI-T 400 W bulbs and 6 Krypton 100 W bulbs, respectively, to achieve photon flux densities (PFD) of up to 1000 $\mu mol\,m^{-2}\,s^{-1}$. Climatic conditions and $CO_2$ concentrations