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Research article

Effect of elevated CO_2 and nitrogen levels on lentil growth and nodulation

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Abstract – Global carbon dioxide levels are rising, and could reach levels of 815 μmol mol^{-1} by the year 2100. Since photosynthetic rate in C_3 species under the current levels of ambient CO_2 is still below physiological saturation levels, it is anticipated that photosynthesis and consequently productivity for most crops should be stimulated by the higher levels of atmospheric CO_2. A stronger response is expected in legumes as nitrogen is not considered as a limiting factor for growth. This study investigates the effect of elevated CO_2 and different nitrogen fertilizer levels on the growth and nodulation of lentils. Syrian lentil was grown under ambient CO_2 concentration of 400 μmol mol^{-1}, and under elevated CO_2 concentration of 700 μmol mol^{-1}, at five nitrogen levels equivalent to 5, 25, 50, 75 and 100 kg N ha^{-1}. Five harvests were conducted over the growth period and measurements of leaf area index (LAI), biomass dry weight, nodule number, and seed yield at the final harvest were recorded. The results showed that, compared to the ambient control, elevated CO_2 led to a significant increase in LAI after flowering (+20–30%), biomass dry weight (+35%) and seed yield: +60% from 1292.74 kg ha^{-1} to 2639.55 kg ha^{-1} at the lowest and highest N levels respectively. Moreover these values increased with increasing levels of nitrogen. Nodule number also increased under elevated CO_2 and the highest nodule number was observed at the nitrogen level equivalent to 50 kg N ha^{-1} under ambient and 75 kg N ha^{-1} under elevated CO_2. The average increase of nodule number for all treatments under elevated CO_2 was +52%. Examination of total nitrogen and phosphorus concentrations in the dry matter showed that the total uptake was higher under elevated CO_2 but due to the increases in biomass concentration levels were slightly lower. For all parameters, no significant interaction between CO_2 and nitrogen treatment was recorded.

1. INTRODUCTION

Global carbon dioxide levels are rising, and it is anticipated that by the year 2100 these levels under high emissions of CO_2 could reach 815 μmol mol^{-1} (UKCIP, 2002). Since photosynthetic rate in C3 species under the current levels of ambient CO_2 is still below physiological saturation levels, it is anticipated that photosynthesis should be stimulated by the higher levels of atmospheric carbon dioxide (Allen, 1998). As a consequence it is expected that primary productivity for most crops will increase under the increased levels of CO_2 (White, 2001), and a large number of experiments have shown that doubling CO_2 levels leads to an average increase in productivity of agricultural and horticultural crops of about 33% (Kimball, 1983). Whilst plant responses to elevated CO_2 are species dependent they can be limited by other factors such as light, temperature, water and nutrients (Patterson and Flint, 1990).

Under drought conditions however, whilst drought can reduce the overall yield of crops, the response to elevated CO_2 can mitigate this somewhat through improved water-use efficiency (Kaddour and Fuller, 2004; Manderscheid and Weigel, 2007). The demand for nutrients is increased as growth increases (Stitt and Krapp, 1999), and over time nutrient limitation, particularly nitrogen, will increasingly restrict production under high levels of CO_2 (Newton, 1991; Bazzaz, 1990). It is therefore believed that nitrogen fixing species can have a stronger response to elevated CO_2 than non- fixing species as N is reduced as a limiting factor (Soussana and Hartwig, 1996; Reich et al., 2001) since root nodules provide a large source of nitrogen (Soussana and Hartwig, 1996). Schenk et al. (1996) reported that in a perennial ryegrass/white clover sward mixture, the response in yield to high levels of CO_2 was an increase of 16 to 42% in white clover, while the response of ryegrass yield ranged between −33 and +9 % depending on N supply, mixture and year. It is also suggested that the increased growth of legumes will lead to increased nitrogen fixation as the demand for nitrogen from the plant increases (Soussana and Hartwig, 1996).

The interaction between elevated carbon dioxide and nitrogen supply has been studied in different crop species such as winter wheat (Wolf, 1993), rice (Bannayan et al., 2005)

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soybean (Sims et al., 1998), and others. No work, however has been reported on the legume crop lentils (*Lens culinaris* Medic), which is one of the most important food crops in the semi-arid regions of the world especially in the Indian Subcontinent and in dry areas of the Middle East (Muehlbauer et al., 1985). The seeds of lentils are a valuable human food product containing a high amount of protein (22–34.5%) and carbohydrate (65%) (Muehlbauer et al., 1985), and in many countries, lentils are used as meat substitutes (Duke, 1981). The work reported here is the initial investigation of the effect of elevated CO_2 and different levels of nitrogen on the growth and nodulation of this crop.

2. MATERIALS AND METHODS

Syrian lentil cultivar ILL6995, commonly known as Idlib 3, was grown under ambient (400 μmol mol^{-1}) and elevated (700 μmol mol^{-1}) CO_2 at five nitrogen levels equivalent to 5, 25, 50, 75 and 100 kg N ha^{-1}. The plants were grown in tightly sealed ventilated chambers (60 × 60 × 80 cm) within a glasshouse located at the University of Plymouth, UK. Two replicate chambers were supplied with elevated CO_2 and two with ambient air, and 25 pots (5 replicates pots of each the five nitrogen levels) were placed at random in each chamber. One pot per chamber was destructively sampled on each of 5 occasions. Carbon dioxide supplementation was achieved using cylinders of compressed CO_2 (BOC gases) coupled to an IRGA Eurotherm^{TM} controller which constantly coupled the air in the chamber and pulsed $CO_2$from the bottled gas to a set point of 750 μmol mol^{-1} (twice ambient) in a pre-mix chamber prior to flowing into the growing chambers. Telaire^{TM} monitors were used to measure CO_2 and temperature in each chamber at 15 minute intervals, and data logged to Hobo^{TM} dataloggers. From these data, daily average CO_2 and temperature were calculated. Empirical adjustment showed that a setpoint of 750 μmol mol^{-1} in the pre-mix chamber led to an actual concentration in the growing chambers of 700 μmol mol^{-1}.

The seeds were inoculated with *Rhizobium leguminosarum* bacteria (Soya UK Ltd) immediately before sowing into medium-grade horticultural perlite growth medium, which facilitated easy root system recovery. Three seeds were sown in each pot (constructed from cylindrical polypropylene pipe 30 cm high × 10 cm diameter), and thinned to two plants after establishment. A complete Hoagland's solution minus nitrogen was irrigated every 10–14 days (100–150 mL), and similar amounts of tap water supplied in between according to demand. Nitrogen (NH_4NO_3) was added in the first week and in three subsequent doses 18–20 days apart to give fertilization rates equivalent to 5, 25, 50, 75 and 100 kg ha^{-1}.

Five destructive harvests were conducted after 30, 52, 72, 86, and 103 days from sowing. Measurements of leaf area were taken using a Delta-T Image Analysis System (type DIAS^{TM}) and LAI calculated. Above and below ground dry weight (after 48 h at 80 °C in a Gallenkamp 250 ^{o}C drying oven), nodule number, and seed yield (final harvest only) were also recorded. At the end of the experiment, the pots were soaked in water overnight, drained and washed with fresh water and samples of the solutions collected and later analysed for N, P, using Bran and Luebbe Autoanalyser 3 (flow injection analyser), and K analysed using Atomic Absorption Spectrometer (Varian – Model SpetrAA-600) .

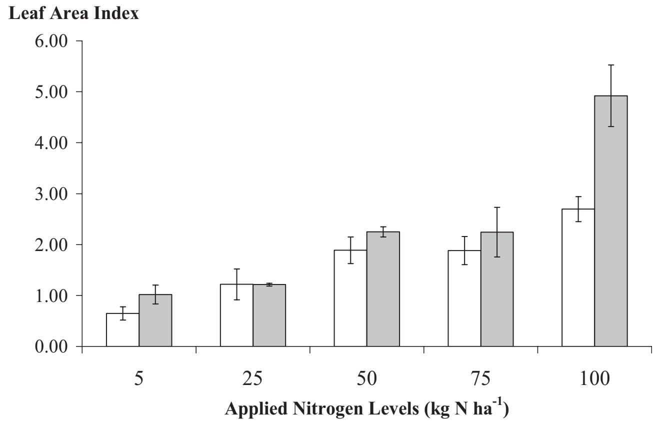

Figure 1. Increases in leaf area index (LAI) caused by elevated CO_2 at various levels of Nitrogen fertilisation in lentil (cv. Idlib 3) at 72 days after sowing. (vertical bars are +/−1 se) (open columns: ambient CO_2, closed columns: elevated CO_2).

Dried plant material was subsequently analysed for total nitrogen by Kjeldhal analysis according to Cerdà et al. (1997) using a digestion block instead of a microwave. Phosphorus was analysed according to Murphy and Riley (1962) using a Bran and Luebbe Autoanalyser 3 (flow injection analyser).

Nodule numbers per plant were obtained by counting active nodules identified by their pink, red and sometimes light brown colour showing leghaemoglobin activity (Somasegaran and Hoben, 1994). Data were analysed using Minitab 13.1, Analysis of Variance (Balanced ANOVA with interaction).

3. RESULTS AND DISCUSSION

3.1. Leaf area index (LAI), dry weight, and seed yield

Leaf area continued to increase up to and after anthesis, which was first recorded at 50 days after sowing. Maximum values of leaf area were observed in the third harvest (72 days after sowing). Elevated CO_2 significantly increased LAI by the third harvest ($P = 0.027$). The LAI increased with increasing inputs of nitrogen ($P < 0.001$) with the higher values always recorded under elevated CO_2 (Fig. 1). LAI at the third harvest ranged between 0.65 and 4.90 under the different treatments, and these LAI's compare favourably with field measurements for lentils of 1.5 to 5.5 (Wall, 1996).

Above ground dry weight showed a significant increase under elevated CO_2 at all nitrogen levels and was up to 76% higher than at ambient CO_2 (Tab. I, Figs 2, 3), and the higher the nitrogen input the higher the value. Root dry weight was also significantly ($P \leqslant 0.001$) increased under elevated CO_2, however, the root/shoot ratios were only slightly, and not significantly increased. Similarly, elevated CO_2 significantly increased the average pod number per plant, which ranged

Table I. Percent increases of above ground dry weight under elevated CO_2 compared to ambient CO_2 over the growth period of lentil (cv. Idlib 3) at different Nitrogen levels.

Harvest (days from sowing)	5 kg N ha^{-1}	25 N ha^{-1}	50 N ha^{-1}	75 N ha^{-1}	100 N ha^{-1}
30	60	7	18	47	47
52	66	−3	14	14	−9
72	67	16	43	48	63
86	−28	42	31	76	41
103	66	21	25	39	53

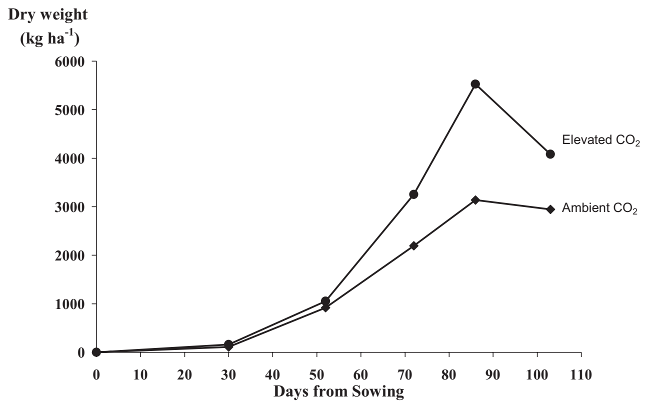

Figure 2. Increases in above ground dry weight caused by elevated CO_2 at 75 kg N ha^{-1} Nitrogen fertilisation in lentil (cv. Idlib 3). (square symbols: ambient CO_2, circle symbols: elevated CO_2).

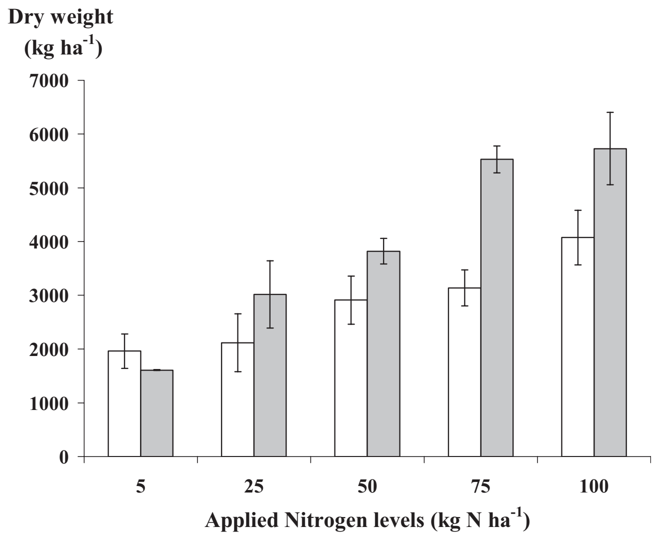

Figure 3. Increases in above ground dry weight 86 days after sowing caused by elevated CO_2 at varying Nitrogen fertilisation in lentil (cv. Idlib 3). (vertical bars are +/ − 1 se) (open columns: ambient CO_2, closed columns: elevated CO_2).

between 7.00 and 23.25, with the highest value recorded under the highest level of nitrogen. Seed yield under all nitrogen treatments was higher under elevated carbon dioxide than under ambient and this increase was more obvious at the high levels of nitrogen (equivalent to 75 and 100 kg ha^{-1}) (Fig. 4). In fact, the seed yield under both ambient and elevated CO_2

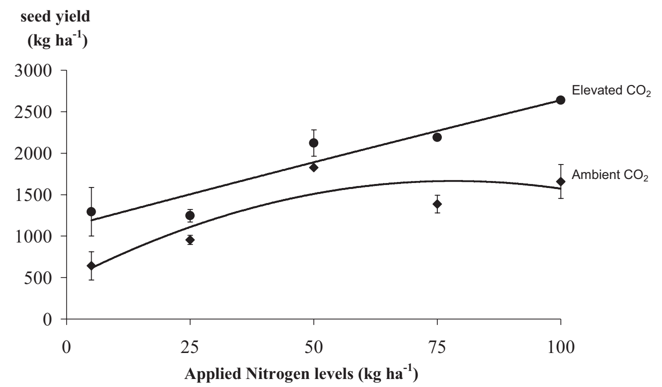

Figure 4. Increases in seed yield caused by elevated CO_2 in response to Nitrogen fertilisation in lentil (cv. Idlib 3). (square symbols: ambient CO_2 $y = -0.1957x^2 + 30.637x + 465.68$, $R^2 = 0.7822$; circle symbols: elevated CO_2 $y = -0.0061x^2 + 15.878x + 1111.3$, $R^2 = 0.9071$).

increased steadily with the increasing inputs of nitrogen up to 50 kg N ha^{-1}. There was then a slight decrease under ambient with the higher levels of nitrogen (75, 100 kg N ha^{-1}), whereas, under elevated carbon dioxide, the seed yield continued to increase.

3.2. Nodule number

Over the growth period, and under both ambient and elevated carbon dioxide, active nodule number per plant increased steadily up until the third harvest (72 days after sowing), but decreased rapidly thereafter (Tab. II).

Nodule number was significantly increased under elevated CO_2 ($P = 0.009$), whereas there was no overall significant difference between the different nitrogen levels ($P = 0.106$). The lowest nodule numbers were found under the highest nitrogen treatment which also showed a slower increase in numbers during early plant growth. Interestingly the lowest (5 kg N ha^{-1}) nitrogen level also showed relatively low nodule numbers.

3.3. Nutrient content

The total amount of nitrogen absorbed by the above ground dry matter increased incrementally throughout the growth cycle of the plants and also increased significantly ($P \leqslant 0.001$) with increasing inputs of nitrogen. Nitrogen concentration

Table II. Increased root nodule number caused by elevated CO_2 at different Nitrogen levels in lentil (cv. Idlib 3).

Days from sowing	5 kg N ha^{-1}		25 kg N ha^{-1}		50 kg N ha^{-1}		75 kg N ha^{-1}		100 N kg ha^{-1}	
	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
30	16.5	34.5	20.3	27.0	16.8	36.0	12.3	42.5	11.8	19.3
52	65.3	98.8	97.0	104.0	86.3	106.8	71.3	102.5	35.3	58.5
72	63.3	42.8	74.3	123.5	107.8	121.3	84.0	133.5	87.5	90.0
86	27.8	35.0	20.8	20.3	16.8	41.0	21.3	26.3	21.8	11.5
103	5.3	1.3	3.3	2.0	2.3	3.3	0.0	0.5	2.8	1.5

Table III. Decreased levels of nitrogen concentration (g 100 g^{-1}) in dry matter caused by elevated CO_2 at different N levels in lentil (cv. Idlib 3).

Harvests (days from sowing)	5 kg N ha^{-1}		25 kg N ha^{-1}		50 kg N ha^{-1}		75 kg N ha^{-1}		100 kg N ha^{-1}	
	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
30	1.615	2.461	1.750	3.531	2.158	1.735	2.888	1.929	2.100	1.940
52	1.074	1.000	1.312	1.275	1.844	2.353	2.180	2.363	2.944	2.708
72	0.761	0.915	0.834	0.859	0.852	1.265	2.405	2.024	1.990	2.203
86	1.053	0.833	1.738	2.228	2.357	2.370	2.708	2.327	2.222	2.091
103	2.686	2.692	3.103	3.970	4.447	4.076	4.358	4.023	4.513	4.227

however, was lower, but not always significantly so under the lower input levels, elevated CO_2 had no effect on nitrogen content of the plants (Tab. III) so the greater uptake observed was a result of increased biomass. Protein content in the seeds varied between 13.30–24.30% and similarly elevated CO_2 had no effect on the concentrations which increased with the higher levels of nitrogen inputs.

Phosphorus uptake was similar to nitrogen being significantly greater ($P < 0.001$) under higher levels of nitrogen inputs and with increases in total uptake where biomass increased but the concentration tended to be lower wherever biomass was increased, although these differences were not always significant.

The residual nutrient concentrations in the perlite at the end of the experiment were always higher in the ambient CO_2 treatment reflecting the greater uptake by the improved biomass production under elevated CO_2.

This investigation confirmed that lentils responded positively to elevated CO_2 in a manner similar to other crops and plants. The leaf area at all nitrogen levels increased under elevated CO_2 by 20–30% after flowering, and maximum LAI was achieved after flowering as previously reported in winter sown lentil in the field (Saxena and Hawtin, 1981). Increased leaf area under elevated CO_2 is commonly reported (Newton, 1991) and is an essential aspect of the crops physiological response to the increased availability of a limiting factor.

Nitrogen availability is essential to increase both leaf area and to maintain leaf longevity which combines to improve light interception (Grindlay, 1997), and in this experiment LAI increased proportionally with the increased inputs of nitrogen under both ambient and elevated CO_2 treatment.

Aboveground dry weight was increased under elevated carbon dioxide by up to 76%, and increased with the higher levels of nitrogen. Dry weights were up to two to three times higher under the highest nitrogen level compared to the lowest. Elevated CO_2 also led to a significant increase in root dry weight, but the root/shoot ratios which ranged between 0.06 and 0.14 were not significantly affected. Increased root biomass under elevated CO_2 has been previously reported in other species (Rogers et al., 1994), and little change, or even a reduced root to shoot ratio, has also been recorded (Norby, 1994; Gavito, 2000). The increases in biomass were always associated with increases in pod number and thereby seed yield (Fig. 3). Productivity for different crops, especially C3 plants, increases under elevated CO_2 as a result of increased net assimilation rate due to the increased carboxylation to oxygenation rate of ribulose bis phosphate carboxylase/ oxygenase (Rubisco) (Stitt, 1991); the subsequent increase in carbohydrate production increases biomass and seed yield (Fuller and Jellings, 2003). The response shown here for lentils is similar to that for other legumes, for example seed yield in soybean increased by 32% when grown under carbon dioxide concentration of 630 μmol mol^{-1} whilst that of cowpeas was reported to be about 78% (Allen, 1998). In fact, the yield of many crops has been reported to increase under even higher concentrations of CO_2, and levels of about 1000 μmol mol $^{-1}$ are exploitable in practice in glasshouse production of tomato and cucumber, leading to a noticeable rise in yield (Wittwer, 1986).

In the current investigation, the response of seed yield to the higher levels of nitrogen inputs was more obvious under elevated CO_2 compared to that at ambient conditions. This can be attributed to increased atmospheric carbon dioxide concentration, an improved assimilation rate and hence growth rate increases, which results in increased demand for nitrogen. Therefore, increased nitrogen availability can support increased growth under elevated CO_2. At ambient conditions the higher inputs of nitrogen increase the productivity, but since photosynthetic rate is below saturation level, the benefit is not as big. Data collected from different experiments conducted on different crops such as rice, cotton, and tobacco, showed that when grown at varying levels of nitrogen fertiliser, elevated CO_2 led to a greater increase in biomass at the higher levels

Table IV. Decreased levels of phosphorous concentration (mg 100 g^{-1}) in dry matter caused by elevated CO_2 at different N levels in lentil (cv. Idlib 3).

Harvests (days	5 kg N ha^{-1}		25 kg N ha^{-1}		50 kg N ha^{-1}		75 kg N ha^{-1}		100 kg N ha^{-1}	
from sowing)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
30	414.0	163.5	422.9	255.2	427.9	525.4	407.2	539.9	496.4	735.7
52	317.8	420.0	398.1	414.0	400.5	467.0	428.0	367.1	387.8	377.9
72	405.3	412.9	347.7	345.0	308.5	312.5	340.0	255.7	266.8	194.8
86	373.2	338.6	365.6	310.7	282.0	267.2	269.8	189.5	258.4	161.5
103	866.9	683.8	751.7	800.0	569.1	537.8	655.3	531.0	567.9	424.8

of nitrogen, whereas the increase was often small at the moderate levels, with little or no effect at the lowest N level (Stitt and Krapp, 1999).

It is not unusual that legume species respond positively to elevated availability of mineral nitrogen since nitrogen fixation has a metabolic cost to the plant. It was clear in this investigation that lentils are no different in this respect and maximum yields were always obtained under moderate to high levels of N inputs. Nodulation was not greatly depressed by the availability of N fertilizer, only really being restricted by the highest N level (100 kg N ha^{-1}). Nodule number was also increased by elevated CO_2, which may be a response to the larger source of extra carbohydrate in the plants caused by the increased photosynthetic rates (Arnone and Gordon, 1990). Wilson (1940) indicated that the inhibitory effect of NO_3^- can be decreased by adding sugars to the growth media or by increasing photosynthesis with increased light or carbon dioxide levels. In general, if there are adequate amounts of nitrogen available, the nitrogen uptake can be increased under elevated CO_2 (Stitt and Krapp, 1999) and this is supported by the results of this investigation. By an analysis of the nitrogen budget (data not shown), it was concluded that there was a significant increase in symbiotic N-fixation under elevated CO_2 and this agrees with previous reports that elevated CO_2 usually increases total N_2 fixation due to increased nodule weight and/or activity (Díaz, 1996). Soussana and Hartwig (1996) also showed that in pure and mixed clover swards using a ^{15}N isotope dilution technique, the nitrogen derived from nitrogen fixation was significantly higher under elevated carbon dioxide.

Despite the significant increase in biomass under elevated CO_2 in this experiment, the dilution effect on nitrogen concentration was not significant. Generally, the concentration of nitrogen (and other minerals) is reduced in plants grown under elevated CO_2 (Wong, 1979). However, Lüscher et al. (1996) indicated that in white clover there was only a slight decrease in nitrogen concentration despite a clear increase in biomass. Similarly, the phosphorus concentration of biomass was also reduced under elevated CO_2 but not significantly, and this indicates that the amount of phosphorus in the feeding solution was adequate for plant needs even with the additional growth observed under increased CO_2.

The results from this study are from a chamber based pot experiment, and there is a question as to whether the results can be considered robust enough to reflect actual field conditions. In this experiment, the use of perlite in small pots allowed the supply of sufficient amounts of nutrients which can be much more limited under field conditions. The sterile perlite provided good conditions for root growth with a medium free of soil borne diseases and pests to remove limitations and potentially enhance the response to CO_2 enrichment but at the same time, the small size of the pots can restrict the root growth and present some limitations to the benefits of CO_2 fertilization. Furthermore, under field conditions many different strains of rhizobium bacteria exist in the soil, from which some strains may be more responsive to elevated CO_2 than the strain used in this experiment. In fact, it is very difficult to compare conditions of that of enclosed chambers with that in the field and plants have the potential to respond differently under each set of conditions. Nevertheless, Kimball et al. (2002) compared results from free air CO_2 enrichment (FACE) experiments under field conditions with previous chamber based experiments and concluded that for CO_2 enrichment there is a high degree of consistency of responses and this gives confidence to the conclusions obtained from each approach. However, some argue that the results obtained from enclosed CO_2 enrichment experiments are over estimated by about 50% compared to that from FACE experiments (Long et al., 2006). It was also reported by Idso and Idso (1997) that under the conditions of resource limitation and environmental stress of the natural ecosystem, it is expected the percentage growth response to elevated CO_2 could be greater than that of managed agricultural and horticultural systems. It can be predicted therefore that similar results to those presented here for lentils under controlled conditions can be expected under field conditions although the degree of response may be somewhat less.

4. CONCLUSION

Lentils are responsive to elevated CO_2 and biomass and seed yields can increase by an average of 35% and 53% respectively under CO_2 levels of 700 μmol mol^{-1}. Yield response to elevated CO_2 is maximised by raising the availability of exogenous nitrogen which does not have an undue detrimental effect on the levels of nitrogen fixation as nodule number continued to increase under higher levels of nitrogen, up to 75 kg N ha^{-1}. The implications of these findings are that higher yield potentials can be expected from field grown lentils as atmospheric levels of CO_2 rise but higher fertilizer inputs will need to be adopted in order to realise this potential.

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