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Elevated carbon dioxide and nitrogen supply affect photosynthesis and nitrogen partitioning of two wheat varieties

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ABSTRACT
The response of wheat to elevated carbon dioxide concentration (e[CO_2]) is likely to be dependent on nitrogen supply. To investigate the underlying mechanism of growth response to e[CO_2], two wheat cultivars were grown under different carbon dioxide concentration [CO_2] in a chamber experimental facility. The changes in leaf photosynthesis, C and N concentration, and biomass were investigated under different [CO_2] and N supply. The result showed an increase in photosynthesis under e[CO_2] at all N level except the one with the lowest N supply. Furthermore, a significant decrease in g_s and Tr for both the cultivars was also observed under e[CO_2] at all N levels. A considerable increase in WUEi was observed for both the cultivars under e[CO_2] at all N levels except for the lowest concentration one. Therefore, the study shows that a stimulation of plant growth under e[CO_2] to be marginal at higher N supply.

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KEYWORDS
C and N concentrations; elevated CO_2 concentration; nitrogen; photosynthesis; wheat

Introduction

Since the industrial revolution, the atmospheric carbon dioxide concentration (a[CO_2]) has increased by more than 40% (IPCC 2013) and it is projected to exceed 700 µmol mol^{-1} by the end of the 21st century (Pachauri et al. 2014). Increase in a [CO_2] directly and indirectly affects growth and development of plants (Seneweera and Conroy 2005). For example, the growth response to elevated carbon dioxide concentration (e[CO_2]) (550 µmol mol^{-1})for wheat illustrates the increase in the order of 5–40% (Ainsworth and Long 2004; Weigel and Manderscheid 2012; O'Leary et al. 2015). Studies show increase in root biomass and root growth rates with a maximum increase of 37% in spring wheat (Thilakarathne et al. 2015) and 75% in winter wheat (Ma et al. 2007) under e[CO_2] (550 µmol mol^{-1}). CO_2 fertilization effect may be limited by the low supply of nitrogen (N). Some studies argued that low soil N fertilization constrained the positive response of plant biomass and yield for majority of the crops to e[CO_2] (Seneweera et al. 2005; Langley and Megonigal 2010; McCarthy et al. 2010; Larsen et al. 2011; Inauen, Korner, and Hiltbrunner 2012; Reich and Hobbie 2013).

The majority of plant species including wheat (*Triticum aestivum)* shows an increase in growth and yield under rising [CO_2] mainly due to increased photosynthesis rate (Carlisle et al. 2012). While the long-term exposure of plants to e[CO_2] may reduce photosynthetic capacity introducing photosynthetic acclimation for most C_3 plants (Long et al. 2004). There are several factors for

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explaining this phenomenon: (1) limitation by nitrogen (N) supply (Seneweera et al. 2002; Sanz-Sáez et al. 2010), (2) insufficient capacity of sink organs (Aranjuelo et al. 2011; Ruizvera et al. 2017), (3) the downregulation of photosynthetic genes by carbohydrates (Vicente et al. 2017). But according to Farage, McKee, and Long (1998), no acclimation was observed under e[CO_2] in wheat plants, while other studies showed strong acclimation in wheat plants at elevated [CO_2] (700 µmol mol^{-1}) (Pérez et al. 2005; Aranjuelo et al. 2011). Many studies in wheat and other species also show a decline in leaf N concentration accentuating photosynthetic acclimation under e[CO_2] (Bloom et al. 2010, 2014; Aranjuelo et al. 2011; Pleijel and Uddling 2012; Lekshmy et al. 2013; Zhang, Yu, and Ma 2013). Elevated CO_2-induced photosynthetic acclimation was predominating in N-limited plantscompared to well-fertilized ones (Seneweera et al. 2002; Sanz-Sáez et al. 2010; Vicente et al. 2015a).

Some studies show decrease in tissue N concentrations of crop and non-crop species ranging from 4.9 to 19% under e[CO_2] (Ainsworth and Long 2004; Weigel and Manderscheid 2012; McGrath and Lobell 2013; Bloom et al. 2014; Vicente et al. 2016; Dier et al. 2018). Explanations for this reduction include: (1) increasing plant biomass, the so-called "dilution effect" (Reich et al. 2006); (2) reducing mass flow of nutrients through the soil to plant due to decreased stomatal conductance and transpiration (Mcgrath and Lobell 2013); (3) decreasing the prevalent protein Rubisco concentrations (Long et al. 2004); (4) inhibiting nitrate assimilation (Bloom et al. 2012, 2014; Myers et al. 2014); (5) altering the rhizosphere environment and limiting the N available for plant uptake (Reich et al. 2006).

The present research reports the effect of [CO_2] on leaf photosynthetic physiology, growth, and C and N concentration in two wheat cultivars. The study aims to address the following questions. Will stimulation of leaf photosynthesis of two cultivars by e[CO_2] be altered with different N supply? Would e[CO_2] change C and N concentrations of wheat tissue at different N supply? How does N supply alter the response of wheat to e[CO_2]? By answering these questions, we can improve our understanding of the responses of a major food crop to e[CO_2] at different N supply.

Materials and methods

Plant culture and treatments

Two wheat cultivars (*Triticum aestivum)*, L. cv. RAC0875 and cv. Kukri was selected for the experiment. Squared bottom perforated pots, each of dimension of 5 cm × 5 cm were taken and were filled with vermiculite up to 12 cm from the bottom. Two growth chambers were used where one was set with a[CO_2] for 400 µmol mol^{-1} and other with e[CO_2] for 700 $µmol^{-1}$ keeping all other parameters same. Each chamber had four pallets (30 cm × 70 cm rectangular plastic pallet) with different N level nutrient solution as N1: 0.2 mM, N2: 0.5 mM, N3: 1.0 mM, and N4: 3.0 mM. Altogether, the experiment consisted of eight different CO_2 × N fertilization combinations, which were replicated eight times. Three seeds were sown in each pot and then eight replicates of both wheat cultivars were placed in each pallet at the same N levels. Then, all the pallets were filled with water up to 5 cm depth. After seven days, when the cultivars started germinating, water was replaced by a basal nutrient solution with pH 5.8–6 of the following composition: 0.8 mM KH_2PO_4, 0.5 mM $MgSO_4$, 0.6 mM $CaCl_2$, 40.0 µM H_3BO_3, 50.0 µM Fe-EDTA, 7.0 µM $MnSO_4$, 0.5 µM $ZnSO_4$, 0.2 µM $CuSO_4$, 0.1 µM Na_2MoO_4. The nitrogen supply was 0.1, 0.25, 0.5, 1.5 mM NH_4NO_3 as different nitrogen levels. The solution was renewed once a week. The pallets were interchanged weekly from one chamber to the other interchanging the [CO_2] among the chambers. The plants and [CO_2] were alternated between chambers every week to avoid the chamber effect.

The selected cultivars were grown in the growth chambers Bioline Australia, under controlled temperature (13.0 °C from 6 PM to 6 AM, 15.0 °C from 6 AM to 8 AM, 20.0 °C from 8 AM to 10 AM, 25.0 °C from 10 AM to 3 PM, 20.0 °C from 3 PM to 6 PM), light (14-hr photoperiods, 1250 µmol m^{-2} s^{-1} light intensity) and humidity (70%) for 6 weeks with four nitrogen levels (0.2, 0.5, 1.0, 3.0 mM).

Biomass, leaf areas, and C/N concentrations

Four pots of each treatment were harvested on the fourth and sixth week. The harvested plants were divided into leaf blades, stems, and roots. Leaf blade area was measured by an LI-3100 area meter (Lincoln Nebraska, USA). The blades, sheaths, and roots were oven-dried at 60°C for more than 48 hr and then weighed and milled (leaf and stem milled for N, and C analysis. Nitrogen analysis was carried out by using LECO CN628 elemental analyzer (LECO, St. Joseph, MI, USA), the C and N concentration from the dried ground material was determined).

Gas exchange measurements

Gas exchange measurements were conducted at the sixth week from last fully expanded leaf blade. One of the uppermost fully expanded leaves was randomly selected per pot (four leaves for each treatment). Gas exchange measurements were conducted using a portable gas exchange system (LI-COR 6400; LI-COR, Lincoln, Nebraska, USA). The [CO_2] in the leaf chamber was controlled by the LI-COR CO_2 injection system, and an irradiance of 1600 µmol (photons) m^{-2} s^{-1} was supplied using a built-in LED lamp (red/blue). The temperature in the $2 \times 3 \times 2.5\ cm^3$ leaf chamber was set at 25 °C. The vapor pressure deficit (VPD) on the leaf surface was between 1.9 and 2.1 kPa. Net photosynthetic rate (P_N), transpiration rate (Tr), stomatal conductance (g_s), and intrinsic water-use efficiency (WUE_i, $WUE_i = P_N/g_s$) were measured at the same irradiance, temperature, and vapor pressure. The [CO_2] in the leaf chamber was set to 400 µmol mol^{-1} for ambient [CO_2], and to 700 µmol mol^{-1} for e[CO_2] treatment. Measurements were done between 10 AM and 1 PM local time.

Statistical analyses

Four biological replicates for each of the treatments and controls were used for statistical analyses. All experimental data presented were analyzed with variance at $p \leq .05$ using SAS System 8.1 (SAS Institute Inc., Cary, NC, USA).

Results

Plant growth

The effects of [CO_2] and N level on biomass wereb measured at four and six weeks (Figure 1). Irrespective of [CO_2] treatment, raising the N supplies increased above-ground and root biomass of both the cultivars at the fourth and the sixth week (Figure 1, Table 1). At the fourth week, both the cultivars showed an increase in the above-ground biomass under e[CO_2] at all N levels but were not statistically significant ($p = .08$). Similarly, at the sixth week, an increase in the above-ground biomass was observed in both the cultivars at all N level except in N1 for RAC0875 and N4 for Kukri (Table 1).

The root biomass of RAC0875 under e[CO_2] increased at N1 and N2 whereas it decreased at N3 and N4 at the fourth week. In contrast at the sixth week, root biomass decreased at N1 and N2, whereas it increased at N3 and N4. Similarly, for Kukri, the root biomass was found to be

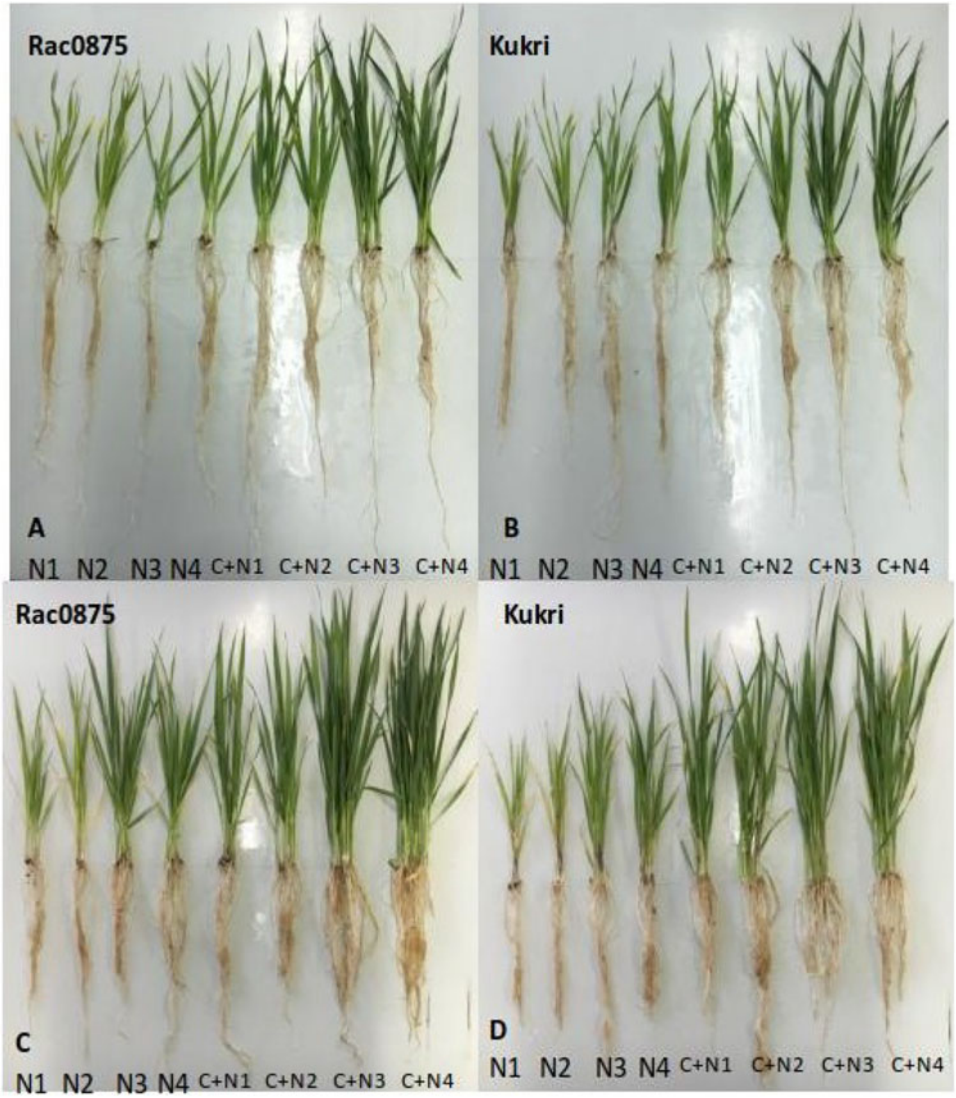

Figure 1. Effect of elevated [CO_2] on plant growth in wheat at different N supply. (A, B) Four weeks; (C, D) Six weeks.

increased at elevated [CO_2], except at N1 at the fourth week. Likewise, an increase in the root biomass was observed for each N treatment except at N1 and N3 at the sixth week (Table 1). Elevated [CO_2] did not affect the height of either cultivar different regardless of N level as measured at the fourth or the sixth week (Table 1), while high N supply remarkably enhanced the height of both cultivar compared to low N supply (Table 1). The leaf area of both cultivars growing at high N supply was also greater than at low N supply. Furthermore, an increase in leaf area of Kurki at N1, N2, and for RAC0875 at N4 was observed under e[CO_2] at the fourth and the sixth week (Table 1).

Photosynthesis

Both the cultivars at N2, N3, and N4 level show higher P_N value under e[CO_2] than a[CO_2] at the sixth week (Figure 2). But P_N decreased at N1 level under e[CO_2] compared to a[CO_2].

Table 1. Effect of different [CO_2] on plant growth in wheat at different N supply.

			Four weeks					Six weeks				
				Weight (g)		Leaf area(cm^2)			Weight(g)		Leaf area(cm^2)	
Variety	CO_2	N	Height (cm)	up-ground	root	fist	other	Height(cm)	up-ground	root	fist	other
		N1	19.15	0.17	0.14	2.85	3.44	19.15	0.35	0.25	3.99	7.98
	400	N2	21.53	0.27	0.17	3.8	5.62	23.45	0.62	0.38	6.87	14.96
		N3	22.95	0.33	0.23	5.77	7.21	28.18	0.87	0.46	10.24	21.95
R		N4	25.23	0.5	0.3	7.38	14.07	31.5	2.16	0.92	14.4	69.08
		N1	19.08	0.22	0.16	3.02	3.56	19.23	0.34	0.24	3.41	6.63
	700	N2	21.33	0.27	0.21	3.24	4.54	22.95	0.65	0.36	6.88	12.99
		N3	23.08	0.35	0.22	5.00	7.62	28.53	1.04	0.56	11.28	24.26
		N4	25.80	0.52	0.29	7.44	15.39	32.05	2.41	1.07	14.89	72.56
		N1	19.35	0.18	0.16	2.08	4.05	20.03	0.29	0.27	3.2	7.89
	400	N2	21.23	0.23	0.17	3.53	5	24.15	0.53	0.34	5.59	12.34
		N3	23.53	0.29	0.21	4.77	8.09	31.53	0.92	0.47	9.43	24.3
K		N4	27.88	0.45	0.29	6.86	15.02	35.83	1.94	0.79	12.13	58.05
		N1	19.63	0.2	0.15	2.55	3.78	21.53	0.36	0.32	4.07	8.57
	700	N2	22.6	0.29	0.22	3.87	6.08	23.93	0.57	0.34	6.29	16.71
		N3	23.93	0.34	0.23	4.54	9.04	28.95	1.13	0.61	9.28	33.71
		N4	27.3	0.47	0.32	6.86	18.74	32.88	1.95	0.77	11.5	56.41
		CO_2	0.44	.08	.02	0.69	.08	0.36	0.11	.05	0.36	0.28
		N	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
p-value		Variety	.00	0.21	0.49	.01	.02	.01	0.12	.09	.00	0.38
		C*N	0.91	0.98	0.21	0.39	0.14	0.66	0.74	0.27	0.87	0.62
		C*V	0.67	0.71	0.29	0.21	0.18	0.34	0.83	0.70	0.93	0.46
		N*V	0.19	0.86	0.83	0.22	0.47	0.73	0.1	.00	.00	.00
		C*N*V	0.49	0.81	0.38	0.78	0.63	0.30	0.77	0.34	0.15	0.60

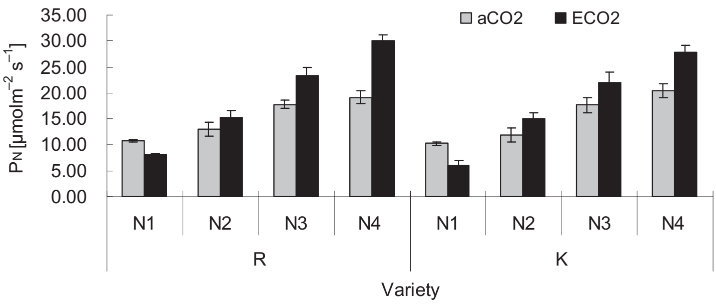

Figure 2. Effect of elevated [CO_2] on P_N in wheat at different N supply (p-value: Variety^N ($p = 0.18$), C **($p < .01$), C × N**($p < .01$), C × V^N ($p = 0.25$), N × V ^{N} ($p = 0.97$), C × N × V ^{N} ($p = 0.69$)).

Similarly, g_s and Tr of both the cultivars at all N level were found decreasing significantly under e[CO_2] (Figures 3 and 4). Likewise, at N2, N3, and N4 both the cultivars showed an increase in WUEi whereas no changes were observed at N1 level (Figure 5).

Nitrogen and carbon concentration

As compared to low N supply, high N supply significantly increased above-ground and root biomass N concentration of both the cultivars at same [CO_2] at the fourth and the sixth week (Table 2). The RAC0875 grown at all N levels showed significantly lower above-ground N concentration under e[CO_2] at both the fourth and the sixth week (Table 2). Likewise, the above-ground N concentration was decreased for Kukri at each N level except at N3 at the fourth week and N2 at the sixth week. However, at the N4 level, an increase in the root N concentration of RAC0875 was observed, while it was reduced to Kurki at the fourth week. In contrast, at the sixth week, the root N concentration of RAC0875 was decreased, whereas that of Kurki was increased.

Irrespective of [CO_2] treatment, raising the N supplies significantly changed above-ground and root biomass C concentration of both the cultivars at the fourth and the sixth week (Table 2). Furthermore, the above ground C concentration at all N levels were decreased under e[CO_2] for both the cultivars at the fourth week whereas was increased in the sixth week while the C concentration of root in both the cultivars were increased at the fourth week at N4 under e[CO_2] (Table 2).

Discussion

Plant growth response to elevated [CO_2] was largely determined by the genotype and [CO_2] interaction (Table 1). Many studies have shown an increase in dry matter content in wheat under e[CO_2] (Pal et al. 2005; Aranjuelo et al. 2013; Benlloch-Gonzalez et al. 2014).Our measurement showed a decrease in accumulated dry matter and green area under e[CO_2] for RAC0875 at low N supply at the sixth week of the experiment (Table 2). Similar results for the effect on dry matter accumulation in durum wheat were observed at low N supply of plants sampled at anthesis and early grain filling under e[CO_2] (Vicente et al. 2015a). Furthermore, some studies found no or negative effects of e[CO_2] on plant dry matter in wheat at early growth stages (Allard et al. 2005; Aranjuelo et al. 2011; Carlisle et al. 2012). In our study, an inhibition of photosynthesis at low N could be the cause of the decreased plant dry matter in RAC0875. In contrast to the low N supply, increase in dry matter accumulation and green area of RAC0875 was observed at high N supply under e[CO_2] than under a[CO_2]. But on Kukri, there was an increase in plant dry matter under e[CO_2] at low N supply at the sixth week. Increase in the green area may be contributed to this increase in dry weight of Kukri. The difference in each cultivar's response to e[CO_2] may be due to their difference in physiological plasticity.

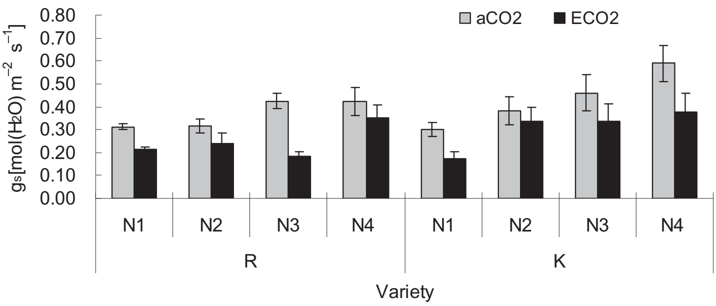

Figure 3. Effect of elevated $[CO_2]$ on g_s in wheat at different N supply (*p*-value: Variety* ($p = .02$), C **($p < .01$), $C \times N^N$($p = 0.34$), $C \times V^N$ ($p = 0.90$), $N \times V^N$ ($p = 0.25$), $C \times N \times V^N$ ($p = 0.32$)).

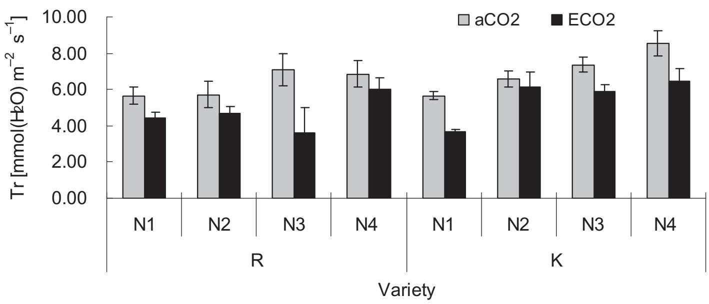

Figure 4. Effect of elevated $[CO_2]$ on Tr in wheat at different N supply (*p*-value: Variety* ($p = .02$), C **($p < .01$), $C \times N^N$($p = 0.10$), $C \times V^N$ ($p = 0.82$), $N \times V^N$ ($p = 0.22$), $C \times N \times V^N$ ($p = 0.27$)).

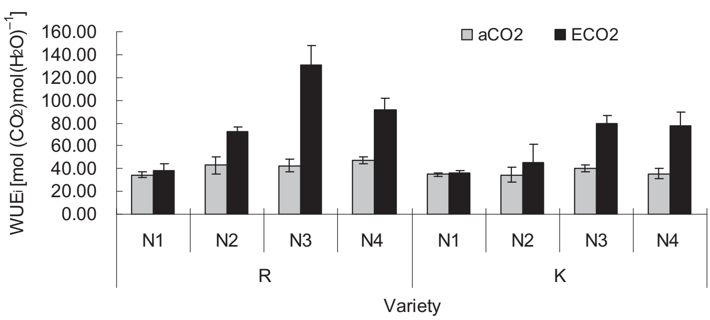

Figure 5. Effect of elevated $[CO_2]$ on WUEi in wheat at different N supply (*p*-value: Variety* *($p < .01$), C **($p < .01$), C × N* *($p < .01$), C × V*($p = .02$), $N \times V^N$ ($p = 0.15$), $C \times N \times V^N$ ($p = 0.13$)).

At low N supply, both the cultivars showed lower photosynthesis under $e[CO_2]$ than $a[CO_2]$. Different studies also reported a decrease in the photosynthetic rate at low N supply under $e[CO_2]$ in different plants including sorghum (Seneweera, Ghannoum, and Conroy 2001; Zhao, Mao, and Xu 2010) and durum wheat (Vicente et al. 2015b). It is possible that low N supply to growing leaf blades limits the cell expansion, division and the final leaf size (Seneweera 2011; Thilakarathne et al. 2015). The leaf area in RAC0875 was reduced at low N supply and $e[CO_2]$, while that of Kukri did not show any reduction. Therefore, decreased photosynthesis in Kukri may be ascribed to reduced photosynthetic related protein at low N supply. Overall, our findings demonstrate that $e[CO_2]$ and high N facilitate the improvement of photosynthesis and, thus, the biomass.

Table 2. Effect of different [CO_2] on plant C and N concentration in wheat at different N supply.

			Four weeks				Six weeks			
			above-ground		root		above-ground		root	
Variety	CO_2	N	Nitrogen (%)	Carbon (%)	Nitrogen (%)	Carbon (%)	Nitrogen (%)	Carbon (%)	Nitrogen (%)	Carbon (%)
		N1	1.17	40.92	1.15	41.69	1.32	40.45	1.2	41.69
	400	N2	1.4	41.07	1.38	41.39	1.4	40.81	1.36	41.84
		N3	1.81	41.6	1.49	41.3	1.77	41.66	1.5	40.94
R		N4	2.58	42.23	1.91	39.52	2.26	42.27	1.6	40.62
		N1	1.1	40.73	1.14	40.5	1.01	40.92	1.19	41.76
	700	N2	1.22	40.97	1.25	40.44	1.28	41.41	1.36	42.12
		N3	1.41	41.08	1.26	41.26	1.51	41.94	1.44	41.55
		N4	2.46	41.95	1.99	40.6	2.08	42.83	1.56	40.62
		N1	1.2	41.09	1.22	41.1	1.18	40.62	1.12	41.92
	400	N2	1.39	41.03	1.27	41.69	1.32	41.08	1.29	42.15
		N3	1.72	41.58	1.5	40.92	1.52	41.31	1.37	41.98
K		N4	2.78	42.43	1.92	39.3	2.1	42.4	1.36	40.64
		N1	1.12	40.7	1.08	40.95	1	41.06	1.32	42.37
	700	N2	1.3	40.82	1.25	40.23	1.42	41.56	1.35	41.81
		N3	1.75	41.25	1.73	40.2	1.51	42.26	1.37	41.52
		N4	2.75	41.56	1.75	40.29	1.66	42.55	1.43	41.31
		CO_2	.05	.00	0.22	0.14	.00	.00	0.41	0.25
		N	.00	.00	.00	.00	.00	.00	.00	.00
	p-value	Variety	.07	0.89	0.63	0.22	.01	0.32	.02	.03
		C*N	0.87	0.25	0.86	.00	.05	0.57	0.58	0.78
		C*V	0.21	0.26	0.51	0.88	0.33	0.83	.09	0.56
		N*V	0.53	0.75	.02	0.56	.05	0.41	0.12	0.57
		C*N*V	0.57	0.37	.02	0.45	0.11	.05	0.81	0.10

Furthermore, our study demonstrated that the WUEi of both the cultivars were significantly increased at high N level under e[CO_2] (Figure 5), which is consistent with other observations (Novriyanti et al. 2012). At high N supply under e[CO_2], the overall growth rate and WUE increased for wheat. In contrast, the g_s and Tr of both the cultivars at all N level were found to decrease under e[CO_2]. Similar to the finding of Katul et al. (2010), reduction of g_s and Tr in response to rising CO_2 has major effects on increasing water use efficiency during photosynthesis.

Previous studies showed a decrease in total plant N concentration of leaves in wheat under e[CO_2] (Bloom et al. 2010; Aranjuelo et al. 2011; Pleijel and Uddling 2012; Lekshmy et al. 2013; Butterly et al. 2015). Consenting with the above studies, our fourth and the sixth-week observationsalso reveals a significant decrease in above-ground N concentration in RAC0875 at all N levels under e[CO_2]. Also for Kukri, a decrease in the above-ground N concentration was observed except under N3 at the fourth week and N2 at the sixth week. According to Bloom et al. (2010), e[CO_2] inhibiting the assimilation of nitrate also exhibit the decrease in N concentration. Likewise, plants under e[CO_2] grow larger and dilute the protein within leaves, further N uptake by the plant tends to decrease the N concentration (Taub and Wang 2008; Kumari, Agrawal, and Tiwari 2013; Bloom et al. 2014). The impact of elevated CO_2 on reduction in the above-ground N concentration of RAC0875 and Kukri need further interpretation.

Butterly et al. (2015) showed no change in total C concentration under e[CO_2]. But our study shows a decrease in the above ground C concentration for both the cultivars under e[CO_2] irrespective of N addition at the fourth week and an increase at the sixth week. Reduction in the above ground C concentration at the fourth week might be attributed to increasing plant biomass, the so-called "dilution effect." Whereas greater C flow via photosynthesis is expected to enhance the above ground C concentration at the sixth week.

Conclusion

Our study showed changes in the different parameters of the two cultivars selected according to the N concentration used under e[CO_2]. At high N supply under e[CO_2], g_s, and Tr were decreased, while P_N andWUEi were increased. For RAC0875, the above-ground plant N concentrations were decreased under e[CO_2]. Hence, we conclude that the stimulation of plant growth under e[CO_2] will be eliminated under nitrogen limitation. Results indicate that more N fertilizer may be required to maintain the growth of wheat under future e[CO_2] environments.

Disclosure statement

No potential conflict of interest was reported by the authors.

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References

Ainsworth, E. A., and S. P. Long. 2004. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist* 165 (2):351–72. doi: 10.1111/j.1469-8137.2004.01224.x.

Allard, V., P. C. D. Newton, M. Lieffering, J. F. Soussana, R. A. Carran, and C. Matthew. 2005. Increased quantity and quality of coarse soil organic matter fraction at elevated CO_2 in a grazed grassland are a consequence of enhanced root growth rate and turnover. *Plant and Soil* 276 (1–2):49–60. doi: 10.1007/s11104-005-5675-9.

Aranjuelo, I., L. Cabrera-Bosquet, R. Morcuende, J. C. Avice, S. Nogués, J. L. Araus, R. Martínez-Carrasco, and P. Pérez. 2011. Does ear C sink strength contribute to overcoming photosynthetic acclimation of wheat plants exposed to elevated CO_2? *Journal of Experimental Botany* 62 (11):3957–69. doi: 10.1093/jxb/err095.

Aranjuelo, I., A. Sanz-Sáez, I. Jauregui, J. J. Irigoyen, J. L. Araus, M. Sánchez-Díaz, and G. Erice. 2013. Harvest index, a parameter conditioning responsiveness of wheat plants to elevated CO_2. *Journal of Experimental Botany* 64 (7):1879–92. doi: 10.1093/jxb/ert081.

Benlloch-Gonzalez, M., R. Bochicchio, J. Berger, H. Bramley, and J. A. Palta. 2014. High temperature reduces the positive effect of elevated CO_2 on wheat root system growth. *Field Crop Research* 165 (3):71–9. doi: 10.1016/j.fcr.2014.04.008.

Bloom, A. J., J. S. Asensio, L. Randall, S. Rachmilevitch, A. B. Cousins, and E. A. Carlisle. 2012. CO_2 enrichment inhibits shoot nitrate assimilation in C_3 but not C_4 plants and slows growth under nitrate in C_3 plants. *Ecology* 93 (2):355–67. doi: 10.1890/11-0485.1.

Bloom, A. J., M. Burger, J. S. R. Asensio, and A. Cousins. 2010. Carbon dioxide enrichment inhibits nitrate assimilation in wheat and *Arabidopsis*. *Science* 328 (5980):899–903. doi: 10.1126/science.1186440.

Bloom, A. J., M. Burger, B. A. Kimball, and P. J. Pinter. 2014. Nitrate assimilation is inhibited by elevated CO_2 in field-grown wheat. *Nature Climate Change* 4 (6):477–80. doi: 10.1038/nclimate2183.

Butterly, C. R., R. Armstrong, D. L. Chen, and C. X. Tang. 2015. Carbon and nitrogen partitioning of wheat and field pea grown with two nitrogen levels under elevated CO_2. *Plant and Soil* 391 (1–2):367–82.

Carlisle, E., S. Myers, V. Raboy, and A. Bloom. 2012. The effects of inorganic nitrogen form and CO_2 concentration on wheat yield and nutrient accumulation and distribution. *Frontiers in Plant Science* 3 (4):195.

Dier, M., R. Meinen, M. Erbs, L. Kollhorst, C. K. Baillie, D. Kaufholdt, M. Kücke, H. J. Weigel, and R. Hänsch. 2018. Effects of free air carbon dioxide enrichment (FACE) on nitrogen assimilation and growth of winter wheat under nitrate and ammonium fertilization. *Global Change Biology* 24:40–54.

Farage, P. K., I. F. McKee, and S. P. Long. 1998. Does a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO_2. *Plant Physiology* 118 (2):573–80.

Inauen, N., C. Korner, and E. Hiltbrunner. 2012. No growth stimulation by CO_2 enrichment in alpine glacier forefield plants. *Global Change Biology* 18 (3):985–99. doi: 10.1111/j.1365-2486.2011.02584.x.

IPCC 2013. Summary for policymakers. In *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*, ed. T. F. Stocker, D. Qin, G-K. Plattner, M. Tignor, S. K. Alle, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, 3–29. Cambridge, UK: Cambridge University Press.

Katul, G., S. Manzoni, S. Palmroth, and R. Oren. 2010. A stomatal optimization theory describe the effects of atmospheric CO_2 on leaf photosynthesis and transpiration. *Annals of Botany* 105 (3):431–42. doi: 10.1093/aob/mcp292.

Kumari, S., M. Agrawal, and S. Tiwari. 2013. Impact of elevated CO_2 and ozone on *Beta vulgaris* L.: Pigments, metabolites, antioxidants growth and yield. *Environmental Pollution* 174:279–88. doi: 10.1016/j.envpol.2012.11.021.

Langley, J. A., and J. P. Megonigal. 2010. Ecosystem response to elevated CO_2 levels limited by nitrogen-induced plant species shift. *Nature* 466 (7302):96–9. doi: 10.1038/nature09176.

Larsen, K. S., L. C. Andresen, C. Beier, S. Jonasson, K. R. Albert, P. E. R. Ambus, M. F. Arndal, M. S. Carter, S. Christensen, M. Holmstrup., et al. 2011. Reduced N cycling in response to elevated CO_2, warming, and drought in a Danish heathland: Synthesizing results of the CLIMAITE project after two years of treatments. *Global Change Biology* 17 (5):1884–99. doi: 10.1111/j.1365-2486.2010.02351.x.

Lekshmy, S., V. Jain, S. Khetarpal, and R. Pandey. 2013. Inhibition of nitrate uptake and assimilation in wheat seedlings grown under elevated CO_2. *Indian Journal of Plant Physiology* 18 (1):23–9. doi: 10.1007/s40502-013-0010-6.

Long, S. P., E. A. Ainsworth, A. Rogers, and D. R. Ort. 2004. Rising atmospheric carbon dioxide: Plants face the future. *Annual Review of Plant Biology* 55 (1):591–628. doi: 10.1146/annurev.arplant.55.031903.141610.

Ma, L., J. G. Zhu, Z. B. Xie, G. Liu, Q. Zeng, and Y. Han. 2007. Responses of rice and winter wheat to free-air CO_2 enrichment (China FACE) at rice/wheat rotation system. *Plant and Soil* 294 (1–2):137–46. doi: 10.1007/s11104-007-9241-5.

McCarthy, H. R., R. Oren, K. H. Johnsen, A. G. Budynek, S. G. Pritchard, C. W. Cook, S. L. LaDeau, R. B. Jackson, and A. C. Finzi. 2010. Re-assessment of plant carbon dynamics at the Duke free-air CO_2 enrichment site: Interactions of atmospheric [CO_2] with nitrogen and water availability over stand development. *New Phytologist* 185 (2):514–28. doi: 10.1111/j.1469-8137.2009.03078.x.

Mcgrath, J. M., and D. B. Lobell. 2013. Reduction of transpiration and altered nutrient allocation contribute to the nutrient decline of crops grown in elevated CO_2 concentrations. *Plant, Cell & Environment* 36 (3):697–705. doi: 10.1111/pce.12007.

Myers, S. S., A. Zanobetti, I. Kloog, P. Huybers, A. D. B. Leakey, A. J. Bloom, E. Carlisle, L. H. Dietterich, G. Fitzgerald, T. Hasegawa, and N. M. Holbrook. 2014. Increasing CO_2 threatens human nutrition. *Nature* 510 (7503):139–42. doi: 10.1038/nature13179.

Novriyanti, E., M. Watanabe, M. Kitao, H. Utsugi, A. Uemura, and T. Koike. 2012. High nitrogen and elevated CO_2 effects on the growth, defense and photosynthetic performance of two eucalypt species. *Environmental Pollution* 170 (8):124–30. doi: 10.1016/j.envpol.2012.06.011.

O'leary, G. J., B. Christy, J. Nuttall, N. Huth, D. Cammarano, C. Stöckle, B. Basso, I. Shcherbak, G. Fitzgerald, and Q. Luo. 2015. Response of wheat growth, grain yield and water use to elevated CO_2 under a free-air CO_2 enrichment (FACE) experiment and modeling in a semi-arid environment. *Global Change Biology* 21 (7):2670–86. doi: 10.1111/gcb.12830.

Pachauri, R. K., M. R. Allen, V. R. Barros, J. Broome, W. Cramer, and R. Christ. 2014. Climate change 2014: Synthesis report. Paper presented at the Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, 151. Geneva, Switzerland: IPCC.

Pal, M., L. S. Rao, V. Jain, A. C. Srivastava, R. Pandey, A. Raj, and K. P. Singh. 2005. Effects of elevated CO_2 and nitrogen on wheat growth and photosynthesis. *Biologia Plantarum* 49 (3):467–70. doi: 10.1007/s10535-005-0031-8.

Pérez, P., R. Morcuende, I. Martín del Molino, and R. Martínez-Carrasco. 2005. Diurnal changes of Rubisco in response to elevated CO_2, temperature and nitrogen in wheat grown under temperature gradient tunnels. *Environmental and Experimental Botany* 53 (1):13–27. doi: 10.1016/j.envexpbot.2004.02.008.

Pleijel, H., and Uddling, J. 2012. Yield vs quality trade-offs for wheat in response to carbon dioxide and ozone. *Global Change Biology* 18:596–605.

Reich, P. B., and Hobbie, S. E. 2013. Decade-long soil nitrogen constraint on the CO_2 fertilization of plant biomass. *Nature Climate Change* 3 (3):278–82. doi: 10.1038/nclimate1694.

Reich, P. B., S. E. Hobbie, T. Lee, D. S. Ellsworth, J. B. West, D. Tilman, J. M. H. Knops, S. Naeem, and J. Trost. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO_2. *Nature* 440 (7086):922–5. doi: 10.1038/nature04486.

Ruizvera, U. M., A. P. D. Souza, S. P. Long, and D. R. Ort. 2017. The role of sink strength and nitrogen availability in the down-regulation of photosynthetic capacity in field-grown *Nicotiana tabacum* L. at elevated CO_2 concentration. *Frontiers in Plant Science* 8:998.

Sanz-Sáez, A., G. Erice, I. Aranjuelo, S. Nogués, J. J. Irigoyen, and M. Sánchez-Díaz. 2010. Photosynthetic down-regulation under elevated CO_2 exposure can be prevented by nitrogen supply in nodulated alfalfa. *Journal of Plant Physiology* 167 (18):1558–65. doi: 10.1016/j.jplph.2010.06.015.

Seneweera, S. 2011. Reduce nitrogen allocation to expanding leaf blades leads to suppression of Ribulose-1,5-bisphosphate carboxylase/oxygenase synthesis and photosynthetic acclimation to elevated CO_2 in rice. *Photosynthetica* 49 (1):145–8. doi: 10.1007/s11099-011-0006-2.

Seneweera, S., A. Makino, T. Mae, and A. Basra. 2005. Response of rice to p(CO_2) enrichment: The relationship between photosynthesis and nitrogen metabolism. *Journal of Crop Improvement* 13 (1–2):31–53. doi: 10.1300/J411v13n01_03.

Seneweera, S. P., and J. P. Conroy. 2005. Enhanced leaf elongation rates of wheat at elevated CO_2: Is it related to carbon and nitrogen dynamics within the growing leaf blade? *Environmental and Experimental Botany* 54 (2):174–81. doi: 10.1016/j.envexpbot.2004.07.002.

Seneweera, S. P., O. Ghannoum, and J. P. Conroy. 2001. Root and shoot factors contribute to the effect of drought on photosynthesis and growth of the C4 grass *Panicum Coloratum* at elevated CO_2 partial. *Australian Journal of Plant Physiology* 28 (6):451–60.

Seneweera, S. P., O. Ghannoum, J. P. Conroy, K. Ishimaru, M. Okada, M. Lieffering, H. Y. Kim, and K. Kobayashi. 2002. Changes in source-sink relations during development influence photosynthetic acclimation of rice to free air CO_2 enrichment (face). *Functional Plant Biology* 29 (8):947. doi: 10.1071/PP01250.

Taub, D. R., and X. Wang. 2008. Why are nitrogen concentrations in plant tissues lower under elevated CO_2? A critical examination of the hypotheses. *Journal of Integrative Plant Biology* 50 (11):1365–74. doi: 10.1111/j.1744-7909.2008.00754.x.

Thilakarathne, C. L., S. Tausz-Posch, K. Cane, R. M. Norton, G. J. Fitzgerald, M. Tausz, and S. Seneweera. 2015. Intraspecific variation in leaf growth of wheat (*Triticum aestivum*) under Australian Grain Free Air CO_2 Enrichment (AGFACE): Is it regulated through carbon and/or nitrogen supply? *Functional Plant Biology* 42 (3):299–308. doi: 10.1071/FP14125.

Vicente, R., P. Pérez, R. Martínez-Carrasco, R. Feil, J. E. Lunn, M. Watanabe, S. Arrivault, M. Stitt, R. Hoefgen, and R. Morcuende. 2016. Metabolic and transcriptional analysis of durum wheat responses to elevated CO_2 at low and high nitrate supply. *Plant and Cell Physiology* 57 (10):2133. doi: 10.1093/pcp/pcw131.

Vicente, R., P. Perez, R. Martinez-Carrasco, E. Gutierrez, and R. Morcuende. 2015a. Nitrate supply and plant development influence nitrogen uptake and allocation under elevated CO_2 in durum wheat grown hydroponically. *Acta Physiologiae Plantarum* 37 (6):114.

Vicente, R., P. Pérez, R. Martínez-Carrasco, and R. Morcuende. 2017. Improved responses to elevated CO_2 in durum wheat at a low nitrate supply associated with the upregulation of photosynthetic genes and the activation of nitrate assimilation. *Plant Science* 260:119–28. doi: 10.1016/j.plantsci.2017.04.009.

Vicente, R., P. Perez, R. Martinez-Carrasco, B. Usadel, S. Kostadinova, and R. Morcuende. 2015b. Quantitative RT-PCR platform to measure transcript levels of C and N metabolism-related genes in durum wheat: Transcript profiles in elevated [CO_2] and high temperature at different nitrogen supplies. *Plant and Cell Physiology* 56 (8):1556–73. doi: 10.1093/pcp/pcv079.

Weigel, H. J., and R. Manderscheid. 2012. Crop growth responses to free air CO_2 enrichment and nitrogen fertilization: Rotating barley, ryegrass, sugar beet and wheat. *European Journal Agronomy* 43 (3):97–107. doi: 10.1016/j.eja.2012.05.011.

Zhang, X. C., X. F. Yu, and Y. F. Ma. 2013. Effect of nitrogen application and elevated CO_2 on photosynthetic gas exchange and electron transport in wheat leaves. *Photosynthetica* 51 (4):593–602. doi: 10.1007/s11099-013-0059-5.

Zhao, X., Z. Mao, and J. Xu. 2010. Gas exchange, chlorophyll and growth responses of *Betula Platyphylla* seedlings to elevated CO_2 and nitrogen. *International Journal of Biological* 2 (1):143–9.