CO_2 Enrichment Effects on Forage and Grain Nitrogen Content of Pasture and Cereal Plants

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SUMMARY

Increasing atmospheric CO_2 concentrations [CO_2] have the potential to enhance growth and yield of agricultural plants. Concomitantly plants grown under high [CO_2] show significant changes of the chemical composition of their foliage and of other plant parts. Particularly, high [CO_2] result in a decrease of plant nitrogen (N) concentration, which may have serious consequences for crop quality. This presentation summarizes the results of a variety of CO_2 enrichment studies with pasture plants (*Lolium spp*., *Trifolium repens*) and cereal species (*Triticum aestivum*, *Hordeum vulgare*) which were conducted at our laboratory under different growth and CO_2 exposure conditions ranging from controlled environment studies to investigations under free air carbon dioxide enrichment (FACE). With the exception of clover in all experiments a CO_2-induced decline of forage and grain N concentration was observed. The magnitude of this reduction differed between species, cultivars, management conditions (N fertilization) and CO_2 exposure conditions. No unambiguous evidence was obtained whether N fertilization can contribute to meet the quality requirements for cereals and grass monocultures with respect to tissue N concentrations in a future high-CO_2 world. As shown in the FACE experiments current application rates of N fertilizers are inadequate to achieve quality standards.

KEYWORDS. Elevated atmospheric CO_2, nitrogen content, wheat, barley, ryegrass, clover, grain and forage quality

INTRODUCTION

There is no doubt that the atmospheric carbon dioxide (CO_2) concentration will continue to rise rapidly during the next decades and is expected to reach ca. 550 ppm by the middle of the present century (Houghton et al., 2001). Evidence based on numerous experimental studies clearly indicates that along with the enhancement of net photosynthesis, elevated CO_2 concentrations have the potential to increase growth and biomass of plants. This is particularly true for agricultural plants under conditions of favorable supply of other growth resources (Rosenzweig and Hillel, 1998; Reddy and Hodges, 2000).

Concomitantly to an increase in biomass production, a frequently observed phenomenon is that plants grown in CO_2-enriched air exhibit significant changes of the chemical composition of their foliage and of other plant parts (Idso and Idso, 2001), which may have serious ecological and economic consequences. One of the most often observed consequence of a CO_2 enrichment is a decrease of the foliar nitrogen (N) concentration and also of the N content of seeds and grains, respectively (Conroy, 1992; Owensby et al., 1996; Cotrufo et al., 1998). Among the explanations of possible causes of such a decline of N concentrations are a "biomass dilution effect" due to an increase in total nonstructural carbohydrate status of the plants, reductions in Calvin cycle enzymes, particularly of ribulose-bisphosphate carboxylase/oxygenase and/or reduced uptake of nitrate due to CO_2-induced lower transpiration rates (Conroy, 1992; Idso and Idso, 2001). Moreover, plant N concentration depends on the developmental stage and the total biomass (Greenwood et al., 1990). Thus, CO_2-induced reductions in plant N concentration can also result from a stimulation in plant development and biomass (Colemann et al., 1993).

With regard to the nutritive value of fodder crops CO_2-induced alterations in leaf N concentration may be critical. When plant foliage is directly consumed by animals the forage nutritive value is highly dependent on the leaf protein and N content, respectively. This is of particular relevance for forage quality of plant species of productive temporary and permanent grasslands as wells as of rangeland ecosystems which provide the majority of food resources, e.g., for ruminants (Owensby et al., 1996; Nösberger et al., 2000). Beside fiber content, non-structural carbohydrates, minerals and secondary compound concentration of crude protein is one of the key quality parameters for grassland forage. A variety of experiments have shown changes in mineral concentrations and particularly negative effects on forage quality as plant N usually declines at elevated CO_2 over a wide range of N availability (e.g., Overdieek, 1993; Cotrufo et al., 1998; Polley et al., 2000; Lilley et al., 2001). While individual species may be affected positively or negatively by elevated [CO_2], the total quantity of nutrients on offer to a grazing animal is determined by the relative abundance of a particular plant species in a vegetation type. Shifts in species composition of grassland under CO_2 enrichment have repeatedly been observed (e.g., Clark et al., 1995; Lüscher et al., 1996) and this may also have consequences for animal nutrition. Consequently, one might speculate that the productivity of domestic and native animals in a future high CO_2 world may be affected by changes in leaf composition of individual species as well as changes in species distribution.

With respect to cereals and particularly wheat, quality and related bread-making quality might be changed as a consequence of a CO_2 induced reduction of grain N and grain protein. However, reports on the effects of elevated CO_2 concentrations on wheat grain quality are contradictory (Idso and Idso, 2001). While Havelka et al. (1984), Rogers et al. (1998), and Dijkstra et al. (1999) found little or no changes of wheat grain nutritional or bread-making quality, significant decreases in the protein concentration along with reduced nutritional and bread-making quality of wheat grown under elevated CO_2 concentrations were found, e.g., by Conroy et al. (1994), Blumenthal et al. (1996), Thompson and Woodward (1994), Fangmeier et al. (1999), and Pleijel et al. (1999). While all these studies were conducted in some type of chamber environments, recent results of free air CO_2 enrichment (FACE) experiments from Arizona/USA revealed only a slight decrease of wheat grain protein concentration at ample supply of soil N (Kimball et al., 2001). However, in these experiments, which may be regarded as most relevant to real agronomic conditions, high CO_2 concentrations exacerbated deleterious effects of low soil N supply on grain protein. Thus, whether or not future atmospheric CO_2 concentration will affect grain quality remains a matter of debate.

CO_2-induced changes in grain N and consequently grain protein content have to be related to the general observation that there is a close relationship between decreasing grain protein concentration and Increasing grain yield (Evans, 1993) irrespective of what are the causes of the biomass increase. Moreover, this relationship is greatly affected by soil N availability. Hence one might expect a decline of grain N concentrations along with any increase in grain biomass due to a CO_2 enrichment of ambient air (Pleijel et al., 1999). Overall, responses of the element concentration in forage and grain tissues to a CO_2 enrichment vary with species, cultivars, growth stage and limitations by other resources, e.g., nutrients, water, light as well as with inter- and intraspecific competition and with the overall growth conditions, i.e., the CO_2 exposure system used in a particular experiment (Cotrufo et al., 1998).

It is, therefore, important to investigate the effects of elevated CO_2 concentrations on food and fodder crops in order to develop scenarios of how future agricultural management considerations have to be adjusted in order to meet quality requirements. The objective of the present paper is to provide a compilation of results of various experiments carried out in our laboratory during recent years on the effects of elevated atmospheric CO_2 concentrations on foliage N content of pasture species (*Lolium ssp.*, *Trifolium repens*) and on grain N content of cereal species (wheat and barley). The experiments described cover a range of conditions which are known to influence CO_2 effects on tissue N concentrations, including N supply via the growth medium, cultivar selection and growing season. In addition, it is shown if CO_2 effects are consistent across various CO_2 exposure systems and growth conditions (e.g., pot studies in controlled environments to field studies in open-top chambers and under free air CO_2 enrichment).

MATERIALS AND METHODS

CO_2 enrichment experiments described in the present paper (Table 1) were carried out either in controlled environment chambers (continuous stirred tank reactors, CSTR; Heck et al., 1978), open-top field chambers (OTC; 3.2 m diameter; 3.0 m height) equipped with a CO_2 dispensing and monitoring system as described by Weigel et al. (1992) of using a large free air carbon dioxide enrichment (FACE; Hendrey, 1993) facility (20 diameter rings) installed on a 20 ha field plot in a local crop rotation of winter barley, sugar beet and winter wheat (Weigel and Dämmgen, 2000).

While in the CSTR studies plants were grown in 2.8 l pots, in the OTC studies plants were grown either in pots (cereals 4.2 l volume; grass and clover 12 l volume) or in natural soil at a wheat field site. Pot studies were done using either a standard prefertilized mix of peat and soil (ED73 containing 0.3 g l^{-1} P_2O_5, 0.4 g l^{-1} K_2O, and 0.4 g l^{-1} plant available N), with additional N supply (NPK fertilizer) if necessary or a field soil (cambisol, pH 6.5; organic matter content 1.5%) with appropriate fertilization. Fertilization in the field experiments was carried out according to local agricultural practice including organic and mineral fertilizers. CO_2 treatment concentrations indicated in Table 1 are round values based on 24-h (chamber experiments) of daylight-hour (FACE experiments) seasonal mean CO_2 concentration values. Details describing materials and methods of the different experiments can be found in the papers listed in Table 1.

TABLE 1. Summary of the different experiments contributing to the present study.

Species	**Cultivar**	**Growth conditions**	**Year of study**	**Soil type**	**CO_2 (ppm)**	**Remarks**	**Ref.**
Cereals							
Triticum aestivum	Turbo	OTC/pot study	1992	ED73	365/700	> 500 kg ha^{-1} N	1
	Turbo	OTC/pot study	1994	ED 73	365/700		2
	Nandu	OTC/pot study	1994	ED 73	365/700		3
	Minaret	OTC/pot study	1994	ED 73	365/700		3
	Janetzkis Früher 1914	OTC/pot study	1994	ED 73	365/700		2
	Heines Kolben 1890	OTC/pot study	1994	ED73	365/700		2
	Nandu	OTC/pot study	1994	Cambisol	365/700	200 kg ha^{-1} N	4
	Minaret	OTC/pot study	1994	Cambisol	365/700	200 kg ha^{-1} N	4
	Minaret	OTC/field sown	1999	Cambisol	365/660	200 kg ha^{-1} N	5
Hordeum vulgare	Alexis	OTC/pot study	1992	ED73	365/700	> 500 kg ha^{-1} N	1
	Alexis	OTC/pot study	1995	ED73	365/700		6
	Arena	OTC/pot study	1992	ED73	365/700		1
	Krona 1990	OTC/pot study	1995	ED73	365/700		6
	Baronesse 1989	OTC/pot study	1995	ED73	365/700		6
	Franken 1930	OTC/pot study	1995	ED73	365/700		6
	Intensiv 1921	OTC/pot study	1995	ED73	365/700		6
	Heines Hanna 1899	OTC/pot study	1995	ED73	365/700		6
	Theresa	FACE/field sown	1999/2000	Cambisol	370/550	260/130 kg ha^{-1} N	7
	Eckendorfer Mammut (1934)						
Pasture species							
Trifolium repens	Karina	CSTR/pot study	1993	Cambisol	365/700		9
	Karina	OTC/pot study	1993/1994	Cambisol	380/700	Seeding density	8
Lolium perenne	Parcour	CSTR/pot study	1993	Cambisol	365/700	Seeding density	9
	Parcour	OTC/pot study	1993/1994	Cambisol	380/700	110-700 kg ha^{-1} N	10
Lolium p. / Trifolium r. (mini swards)	Parcour / Karina 75:25	OTC/pot study	1992 + 1993	Cambisol	365/700	Species mixture	11
Lolium multiflorum	Lippstädter Futtertrio	FACE/field sown	2000	Cambisol	370/550	195/100 kg ha^{-1} N	12

References: 1. Manderscheid et al. (1995); 2. Manderscheid and Weigel (1997); 3., 4. Unpublished; 5. Manderscheid et al. (2000); 6. Unpublished; 7. Manderscheid et al. (2001); 8. Manderscheid et al. (1997b); 9. Schenk et al. (1995); 10. Manderscheid et al. (1997a); 11. Schenk et al. (1997); 12. Aulrich et al. (2001)

RESULTS AND DISCUSSION

Response of Foliage N Content of Pasture Species

Cultivation of clover in controlled environments (CSTR) at different plant densities did not result in a significant decrease in shoot N concentration due to the CO_2 enrichment (Table 2). In open-top chambers experiments over two growing seasons a clear decrease in shoot N concentration was observed only at the beginning but not at the end of the growing season. This may be attributed to the fact that N supply of the plants via N_2 fixation was not yet fully developed at the begin of the growing season. Averaged over all experiments and additional modifying factors like intraspecific competition, growing season and harvest date, tissue N concentration of clover monocultures decreased by ca. -5%.

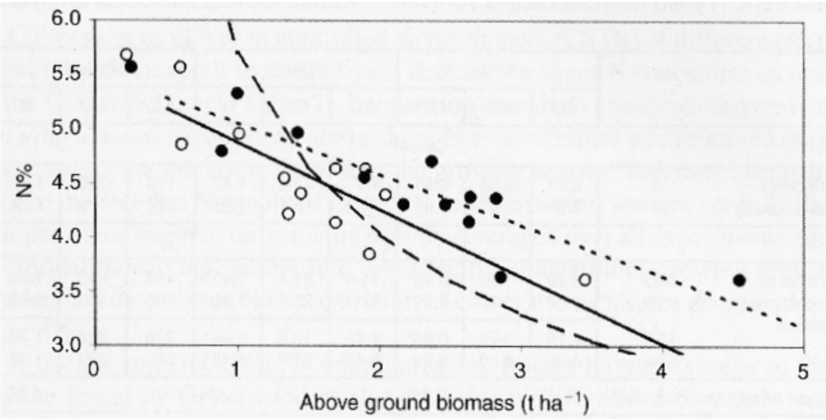
TABLE 2. Summary of effects of elevated CO_2 concentrations on shoot N concentration (%), yield (g pot^{-1}; FACE experiment g m^{-2}) and N yield (mg pot^{-1}; FACE experiment 9 m^{-2}) of clover (*Trifolium repens* L. "Karina") and grass (*Lolium perenne* L. "Parcour"; FACE experiment = *L. multiflorum*, 2 harvests). Plants were exposed to ambient (AC) and elevated (EC) CO_2 concentrations under different growth conditions as described in Table 1. R = ratio EC/AC. N treatments = kg ha^{-1} N; Plant density treatment = plants pot^{-1}. OTC = open top chamber. P = pot. * Is indicating a significant effect of the elevated CO_2 treatment. N yield was calculated from mean values without statistical analysis.

			% N			**Yield**			**N yield**		
			AC	**EC**	**R**	**AC**	**EC**	**R**	**AC**	**EC**	**R**
Clover											
Effects of plant density		4	3.94	3.60	**0.91**	4.47	6.58	**1.47***	176	236	**1.36**
		36	3.60	3.63	**1.00**	10.4	13.1	**1.27***	374	475	**1.28**
Effects of season and harvest		1/93	3.28	3.06	**0.93***	14.8	21.1	**1.43***	485	646	**1.33**
		9/93	4.64	4.37	**0.95***	17.1	25.4	**1.49***	793	1110	**1.40**
		1/94	4.19	3.75	**0.89***	7.29	10.6	**1.45***	305	398	**1.30**
		6/94	4.86	4.80	**0.98**	5.46	7.99	**1.46***	265	384	**1.45**
Mean of all clover studies					***0.95***			***1.42***			***1.35***
Grass											
Effects of plant density		4	3.26	2.77	**0.84***	4.20	4.89	**1.16**	136	135	**0.99**
		16	2.01	1.58	**0.78***	6.77	8.28	**1.22***	136	130	**0.96**
		36	1.63	1.42	**0.87***	8.14	9.06	**1.11***	132	128	**0.97**
Effects of N supply	110 OTC; pot		2.29	2.24	**0.98**	2.62	2.46	**0.94**	60	55	**0.93**
	310		4.15	3.46	**0.83***	3.01	3.86	**1.28***	124	133	**1.07**
	700		4.56	4.41	**0.97**	2.58	3.33	**1.29***	118	147	**1.25**
	195^{a} FACE		3.41	2.75	**0.80***	373	460	**1.23**	12.7	12.6	**0.94**
	100^{a}		2.57	2.27	**0.88***	350	379	**1.08**	8.99	8.60	**0.95**
	195^{b}		2.65	2.20	**0.83***	484	543	**1.12**	12.9	11.9	**0.92**
	100^{b}		1.97	1.63	**0.83***	484	531	**1.10**	9.53	8.61	**0.90**
Mean of all grass studies					***0.87***			***1.16***			***1.03***
Grass/clover mixture											
1992		grass	1.76	1.59	**0.90***	57.8	57.3	**0.99**	1018	912	**0.89**
		clover	3.74	3.70	**0.98**	59.5	83.4	**1.40***	2227	3107	**1.39**
	75:25	mixture	2.75	2.80	**1.01**	118	143	**1.21***	3245	4019	**1.23**
1993		grass	1.82	1.59	**0.87***	46.5	49.2	**1.05**	848	783	**0.92**
		clover	3.70	3.60	**0.97**	45.0	64.2	**1.42***	1716	2314	**1.34**
	75:25	mixture	2.75	2.71	**0.98**	93.2	114	**1.22***	2564	3098	**1.20**
[a] harvested 48 days after emergence, [b] harvested 71 days after emergence											

A decline in percent (%) N with increasing foliage biomass similar to the decline found by Greenwood et al. (1990) for well-fertilized C_3-plants was also observed in the present study with clover (Figure 1). However, this decrease in percent (%) N was smaller under CO_2 enrichment than under ambient CO_2 and resulted in a greater tissue N concentration of the high CO_2 plants at a similar plant dry weight. Based on a linear regression analysis between percent (%) N and plant dry weight, the N concentration of the high CO_2 plants increased by about 4% and 26% at a plant dry weight of 1 and 4 t/ha, respectively. Such an effect might be explained by a CO_2-induced increase in leaf area ratio which was observed in our (data not shown) as well as in other studies (Ryle et al., 1992). The effect might also contribute to increase the competitive ability of clover in mixed grass/clover swards.

A large growth enhancing effect of ca. + 27% ± 49% of the high CO_2 treatments was found for clover. This is in line with other studies where a variation in the response of clover to elevated CO_2 concentrations has been found to range between 9% and 75% (e.g., Nijs et al., 1988; Nösberger et al., 2000). These results again support the assumption that legumes will profit more from the rise of the atmospheric CO_2 concentration than non-legume plant species (see below) because of the large sink-strength of the N_2 fixing species (Lüscher et al., 2001). White clover is the most important pasture legume in temperate zones and contributes significantly to the economy of pastures by fixation of atmospheric N.

FIGURE 1. Relationship between above ground biomass and N concentration of white clover grown at ambient (open circles) and elevated CO_2 concentrations (675 ppm; filled circles). Data were taken from several harvests during two consecutive growing seasons. Linear regression analysis yielded for ambient CO_2 (solid line): $y = 5.5-0.691 *x$, $r^2 = 0.73$; for high CO_2 (dotted line): $y = 5.53-0.522*x$, $r^2 = 0.81$. The dashed line shows the general relationship for C_3 plants under ambient CO_2 ($y = 5.7*x-0.5$) as described by Greenwood et al. (1990). Adapted from Manderscheid et al. (1997b).



As a consequence of the small effect of CO_2 on leaf N concentration and the strong growth enhancement, total N yield of the clover swards increased by more than 30% which has also been shown in other studies (Murphy, 1986; Ryle and Powell, 1992; Lilley et al., 2001). Consequently, under future atmospheric CO_2 concentrations clover monocultures could contribute to additional sequestration of N into grassland ecosystems.

Percent tissue N concentration of the grass *Lolium perenne* tested in our studies was more negatively affected in monocultures by a CO_2 enrichment than clover (Table 2). Irrespective of the growth conditions in the individual experiments leaf N concentration decreased by ca. -13%. This again supports the common feature of declining tissue N concentrations (Conroy and Hocking, 1993; Cotrufo et al., 1998) with increasing CO_2 concentrations. While variations in N availability by altering either plant density in controlled environment studies (CSTR) or nutrient addition in OTC experiments clearly affected percent (%) shoot N, the relative CO_2 response in these experiments was not related to the N availability.

In comparison to clover the growth enhancement by elevated CO_2 concentrations of grass monocultures was considerably smaller (average ca. + 16%). The stimulation of above-ground biomass production was most evident at ample soil N supply, which supports the overall assumption that the magnitude of a CO_2 induced growth stimulation of ryegrass is determined by the N supply of the plants (Schenk et al., 1996; Hebeisen et al., 1997; Daepp et al., 2001). As shown in other studies (Soussana et al., 1996; Zanetti et al., 1997), average N yields remained unaffected or were hardly affected as a result of the CO_2 enrichment (average ca. +3%). A strong positive response (+25%) on N yield only occurred under ample N supply as used in the OTC study.

The CO_2 response observed in the FACE study in the field with a mixture of three cultivars of *Lolium multiflorum*, was quite similar to the above mentioned findings with *Lolium perenne*. High CO_2 concentrations decreased foliage N by more than 10% and this effect was independent of the N supply. Due to insignificant effects of elevated CO_2 concentrations on biomass yield there was hardly any effect on N yield of the grass mixture.

It may thus be speculated that pure ryegrass stands may only benefit from the increase of the atmospheric CO_2 if there is sufficient N supply from the soil. On the other hand, especially under low N input scenarios via mineral fertilization which is one option of future sustainable agricultural management, yield losses of ryegrass may be partly compensated by increasing CO_2 levels, however, with severe problems for the nutritive quality of this grass species.

As mixed perennial ryegrass (*L. perenne*) / white clover (*T. repens*) swards form one of the most important associations in cool temperate grasslands with a high productivity (Nösberger et al., 2000), a model study over two growing seasons with a grass dominated (75%) mixture of grass and clover was carried out. As shown in Table 2, N concentrations and biomass yields of the monocultures responded in a similar manner as in the above mentioned studies with these species. However, in the mixtures N concentration of the forage total yield was not decreased under CO_2 enrichment and there was a significant increase of biomass and N yield.

Response of Cereal Grain N Content

Wheat grain protein concentration (% N x 5.7) in control plants of the present studies met the values (12%-14%) required for high bread-baking quality (Engel and Zubrinski, 1982). It has been argued that elevated CO_2 concentrations will decrease the grain N and hence protein concentrations irrespective of the N availability (Conroy, 1992), i.e., the reduction in grain quality may not easily be overcome by additional N fertilization (Fangmeier et al., 1999). In our pot studies the negative CO_2 effect on wheat grain N was greater at low N supply levels (Table 3). Increasing the amount of N fertilization to levels, which are no longer common in current agricultural practice (> 500 kg ha^{-1} N), ameliorated the CO_2-induced reduction of grain N of the wheat cultivars tested (Table 3). On the other hand, no such an effect could be observed in the FACE experiment (Table 4) with a current and an old winter barley cultivar. In this experiment N supply of the control treatment was related to local agronomic practices (265 kg ha^{-1} N) and resulted in average final grain yields. However, a significant reduction of grain N (ca. -15%) under the high CO_2 treatments was observed at both N supply levels. This result is in contrast to the findings of the Arizona wheat FACE experiments where high N fertilization rates (ca. 350 kg ha^{-1}) nearly completely ameliorated negative CO_2 effects on wheat grain N concentrations (-11% reduction) under low N supply rates (Kimball et al., 2001).

For cereals and particularly wheat there are indications that sink strength of current wheat cultivars has declined during the recent decades, e.g., as plant breeding has improved grain yield primarily by increasing harvest index and leaf area duration after ear emergence. Concomitantly, a decline of the grain N (i.e., protein) concentration has occurred. To test whether there are relationships between the relative effects of elevated CO_2 concentrations and the year of introduction of wheat and barley cultivars and how this is related to yield and grain quality, a comparison was made of the CO_2 response of old and modem wheat and barley cultivars, i.e., cultivars introduced between 1890-1990 (Tables 3 and 4).

TABLE 3. Summary of effects of elevated CO_2 concentrations on grain N concentration (%), yield (g pot^{-1}; g m^{-2} for field grown wheat) and N yield (mg pot^{-1}; g m^{-2} for field grown wheat) of different wheat (*Triticum aestivum* L.) cultivars. Plants were exposed to ambient (AC) and elevated (EC) CO_2 concentrations under different growth conditions as described in Table 1. R = ratio EC/AC. HN, LN = high, low N supply. * Is indicating a statistical significant effect (P < 0.05) of the elevated CO_2 treatment. N yield was calculated from mean values without statistical analysis.

		% N			**Yield**			**N yield**		
		AC	**EC**	**R**	**AC**	**EC**	**R**	**AC**	**EC**	**R**
Effects of N supply										
Nandu	LN	3.01	2.29	**0.74***	10.4	15.6	**1.51***	313	357	**1.14**
	HN	3.23	3.02	**0.93***	14.4	19.9	**1.38***	465	601	**1.29**
Minaret	LN	2.42	1.92	**0.79***	5.24	7.66	**1.46***	127	147	**1.16**
	HN	2.71	2.70	**0.99**	6.91	8.80	**1.27***	187	238	**1.27**
Comparison of old and modern cultivars										
Nandu	(1988)	3.23	3.02	**0.93***	14.4	19.9	**1.38***	465	601	**1.29**
Turbo	(1979)	3.20	2.97	**0.92**	15.7	18.8	**1.20***	504	558	**1.11**
Janetzkis Früher	(1914)	3.42	3.30	**0.96**	15.2	22.3	**1.47***	520	736	**1.42**
Heines Kolben	(1890)	3.42	3.33	**0.97***	14.8	20.6	**1.39***	506	686	**1.36**
Mean old cultivars		3.42	3.31	**0.97**	15.0	21.5	**1.43**	513	711	**1.39**
Mean modern cultivars		3.22	3.00	**0.93**	15.1	19.3	**1.28**	485	580	**1.20**
Comparison of growth condition and growing season										
Minaret	pot	2.42	1.92	**0.79***	5.24	7.66	**1.46***	127	147	**1.16**
	field	2.13	1.60	**0.75***	826	968	**1.17**	17.6	15.5	**0.88**
Turbo	1992	2.42	1.75	**0.72***	24.3	30.8	**1.27**	740	666	**0.90**
	1994	3.20	2.97	**0.92**	15.7	18.8	**1.20***	504	558	**1.11**
Mean of all wheat studies				**0.87**			**1.35**			**1.17**

TABLE 4. Summary of effects of elevated CO_2 concentrations on grain N concentration (%), yield (g pot^{-1}; g m^{-2} = field grown) and N yield (mg pot^{-1}; g m^{-2} = field grown) of different barley (*Hordeum vulgare* L.) cultivars. Plants were exposed to ambient (AC) and elevated (EC) CO_2 concentrations under different growth conditions as described in Table 1. R = ratio EC/AC. HN, LN = high, low N supply. * Is indicating a statistical significant effect (P < 0.05) of the elevated CO_2 treatment, n.d. = not determined. N yield was calculated from mean values without statistical analysis.

		% N			**Yield**			**N yield**		
		AC	**EC**	**R**	**AC**	**EC**	**R**	**AC**	**EC**	**R**
Comparison of o/d and modern cultivars										
Krona	(1990)	2.47	2.31	**0.93**	n.d.					
Baronesse	(1989)	2.28	1.94	**0.85***						
Alexis	(1986)	2.21	1.95	**0.88***						
Franken	(1930)	2.64	2.25	**0.85***						
Intensiv	(1914)	2.49	2.21	**0.88***						
Heines Hanna	(1890)	2.95	2.39	**0.81***						
Cultivar comparison										
Arena 1992		2.73	2.25	**0.82**	11.2	21.2	**1.89**	0.45	0.85	**1.78**
Alexis 1992		2.17	1.65	**0.76***	18.0	27.4	**1.52**	0.58	0.68	**1.16**
Effects of N supply (FACE)										
Theresa	HN	1.93	1.64	**0.85***	952	1023	**1.08***	18.8	16.8	**0.91**
	LN	1.65	1.42	**0.86***	784	850	**1.09**	12.9	12.1	**0.94**
Eckendorfer Mammuth II	HN	1.96	1.76	**0.90***	530	564	**1.06**	10.4	9.92	**0.95**
(1934)	LN	1.94	1.60	**0.82***	359	461	**1.28**	6.96	7.37	**1.06**
Mean of all barley studies				**0.85**						

The mean reduction of grain N content (ca. 3%-8%) due to the CO_2 enrichment was small for the wheat cultivars tested (Table 3), with a slightly higher reduction in the modern compared to the old cultivars, which resulted in a significant CO_2 X cultivar interaction (data not shown). Under comparable growth conditions as for wheat (i.e., pot study with similar N supply) grain N concentration in old and modern barley cultivars (Table 4) was more affected by elevated CO_2 concentrations (ca. 7%-19%). However, it has to be taken into account that the experiments with the wheat and the barley cultivars were performed in different years. Although there was a tendency that old cultivars were mare affected, there was no significant CO_2 X cultivar interaction. In the FACE experiment with barley there were also no differences between the old and modern cultivar with respect to the reaction of grain N content to high CO_2 concentrations. As with the old wheat cultivars, the old barley cultivars had higher grain N concentrations compared to the modern ones, but there was no difference in the reaction to elevated CO_2 concentrations.

Irrespective of whether the plants were grown in pots or under common agricultural management conditions in the field, a similar magnitude of a CO_2 induced reduction of grain N concentration (≥ 20%) was observed for the wheat cultivar 'Minaret'. 'Minaret' was used as a common test plant in the European, multiple-site experiment ESPACE-Wheat (Bender et al., 1999; Fangmeier et al., 1999) and has not been in use in Germany as a common cultivar. As demonstrated for the wheat cultivar 'Turbo' significant differences in the magnitude of the reaction of grain N to elevated CO_2 between two growing seasons could be observed although the plants were grown under near identical conditions.

Wheat grain yield was significantly (up to +51 %) stimulated by elevated CO_2 under the different N supply levels. Consequently N yield, i.e., the unit area production of protein of wheat was also enhanced. A similar large CO_2 response was observed for barley cultivars grown in OTC studies with pots. On the other hand, in the FACE experiment with the barley cultivars only a small increase of grain yield (<+ 10%) was observed. Consequently, N yields of barley remained unchanged by the CO_2 treatment under free air enrichment conditions or were even reduced (- 9%) for the modern cultivars under high N supply. There seemed to be a tendency that N yield of the old barley cultivar was less negatively affected by the FACE treatment than that of the modern one. At elevated CO_2 concentration the mean increase in wheat grain yield was higher (ca. 43%) for the old (1890-1914) than for the modern cultivars (ca. 28%).

Averaged over all experiments it can be concluded that in almost all cases season-long CO_2 fertilization resulted in a considerable decrease of grain N concentration of wheat and barley (Tables 3 and 4), albeit the magnitude of this reduction differed due to differences, e.g., in nutrient supply and between cultivars investigated. The mean reduction of grain N concentration as a result of the CO_2 enrichment amounted -13% far the wheat cultivars and -15% for the barley cultivars investigated in the present studies. For wheat, these changes in grain N content are in a similar order of magnitude as those found in the studies of Conroy et al. (1994) (-1 % to -14% depending on CO_2 and N level), Blumenthal et al. (1996) (-14%), Monje and Bugbee (1998) (-9%) and Hakala (1998) (-7%) and Fangmeier et al. (1999) (-15%). However, as outlined in the introduction, there is a considerable number of high CO_2 experiments that failed to detect a reduction of wheat grain N. There are no comparable results for barley.

In the pot studies, the reduction in grain N almost always was accompanied by a considerable increase of grain yield (+34% for wheat, > +50% for barley), while the yield enhancing effect was much smaller when plants were grown in the field soil (OTC, FACE). However, when the ratio % N of elevated/ambient CO_2 of all wheat results was plotted against the corresponding ratio for wheat yields, no consistent relationship was found (data not shown). Hence the results do not clearly support the overall assumption that increased yields brought about by elevated CO_2 concentrations might reduce grain quality (Rogers et al., 1998; Pleijel et al., 1999).

CONCLUSION

The present compilation of results of a number of CO_2 enrichment studies conducted over several years with different cultivars of pasture and cereals species under different growth conditions indicates that future atmospheric CO_2 concentrations may affect the quality of fooder and food crops. Except for clover, in all experiments a CO_2-induced decline of forage and grain N concentration, which is one of the key quality parameters for these plants, could be observed, albeit the magnitude of this reduction differed between species, cultivars, management conditions and CO_2 exposure conditions. No unambiguous evidence was obtained whether N fertilization can contribute to meet the quality requirements for cereals and grass monocultures with respect to tissue N concentrations in a future high-CO_2 world. However, as shown in the FACE experiments under real agricultural management conditions, current application rates of N fertilizers are inadequate to achieve this quality standard. Due to a lack of relevant field studies, it remains open whether this is a general phenomenon for other cereal species and whether the production of N and hence protein per unit area will increase under future CO_2 concentrations.

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