Effects of increased ammonia on root/shoot ratio, grain yield and nitrogen use efficiency of two wheat varieties with various N supply

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ABSTRACT

The effects of elevated atmospheric NH_3 on growth and yield parameters of two winter wheat varieties, the high water and fertilizer-demanding variety Xiaoyan 6 (XY6) and the drought-resistant variety Changhan 58 (CH58), grown with two levels of N fertilization, were studied in Open-Top Chambers. The results showed that in combination with the high N treatment increasing the atmospheric NH_3 concentration to 1000 nl/l from the ambient level of 10 nl/l NH_3 significantly ($P < 0.05$) reduced the biomass and the root/shoot ratios of the plants, especially in XY6 plants, mainly because it negatively influenced root biomass production at anthesis and mature stages. In addition, the grain yield of XY6 was by 1.51% higher, while that of CH58 was 13.2% lower, following exposure to the elevated atmospheric NH_3 concentration rather than the ambient concentration in combination with the high N treatment. In contrast, in combination with the low N treatment, elevated atmospheric NH_3 had significantly and non-significantly positive effects on the grain yield of XY6 and CH58 plants, respectively. The Nitrogen Use Efficiency (NUE) and related parameters were all lower in plants of both varieties exposed to the high atmospheric NH_3 concentration together with either the high or low N treatment.

Keywords: winter wheat; elevated atmospheric NH_3; root/shoot ratio; grain yield; nitrogen use efficiency

Ammonia (NH_3) is an important atmospheric pollutant for semi-natural vegetation, causing eutrophication, nutrient imbalances and changes in species composition (Pearson and Stewart 1993, Sutton et al. 1993a). The most important source of NH_3 emissions to the atmosphere is volatilization from decomposing livestock waste, and the second most important source losses from agricultural plant canopies, particularly following the application of N fertilizer (e.g. Buijsman et al. 1987, Asman and van Jaarsveld 1992, Sutton et al. 1995, Bouwman et al. 1997, Pain et al. 1998). There are also indications in the cited studies that atmospheric NH_3 can be an important source of nitrogen for legumes and some forest vegetation, although at background levels NH_3 uptake by shoots may only play a minor role in the N-nutrition of higher plants according to the calculations by Raven (1988). Accordingly, Harper et al. (1987) found that when the soil nitrogen supply is restricted, wheat can absorb nitrogen from the atmosphere (at ambient concentrations) equivalent to 1% of the nitrogen dosage before flowering. However, Faller (1972) found that at elevated concentrations NH_3 may significantly contribute to the N-nutrition of higher plants, including commercially impor-

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Table 1. Experimental treatments

Treatment code	NH_3 concentration (nl/l)	N fertilization levels	Wheat variety
T1	10	HN	XY6
T2	10	HN	CH58
T3	10	LN	XY6
T4	10	LN	CH58
T5	1000	HN	XY6
T6	1000	HN	CH58
T7	1000	LN	XY6
T8	1000	LN	CH58

tant species, as shown in experiments with up to 1.6 mg/m^3 NH_3, in which growth of sunflower continued even if NH_3 was the only nitrogen source. Further, in experiments with *Lolium multiflorum* (ryegrass), Lockyer and Whitehead (1986) found that foliar NH_3 uptake at 520 μg/m^3 supplied 47.3% and 35.2% of total plant N at fertilization levels of 100 and 200 mg $^{15}NO_3^-$-N/kg dry soil, respectively. Similarly, Pérez-Soba and Vander Eerden (1993) exposed Scots pine (*Pinus sylvestris* L.) samplings fertilized with $(NH_4)_2SO_4$ in the range of 0~200 kg/ha year to 0 and 50 μg/m^3 NH_3 and found, after four months of growth, a 49.0% increase in the N content of the needles supplied by NH_3 alone at the highest dose, while fertilization with 200 kg $(NH_4)_2SO_4$/ha/year resulted in only an 8% increase.

In most cases, e.g. *Picea abies* (Zedler et al. 1986), plants exposed to NH_y also show increased concentrations of soluble proteins, and Pietilä (1991) found that the protein spectrum of *P. sylvestris* needles changed following exposure. Similar changes in pigment contents were also observed, e.g. as long as the tissue is not injured, chlorophyll concentrations in plants exposed to NH_y generally increase, as Van der Eerden et al. (1990) found in *Pinus sylvestris*.

However, our current knowledge of the effects of NH_3 on higher plants is predominantly derived from studies conducted in Europe focused on forest and grassland vegetation. Much less attention has been paid to the effects of atmospheric NH_3 in agro-ecosystems elsewhere. Therefore, in the study reported here a pot experiment was carried out in Open-Top Chambers (OTCs) to study the effects of atmospheric NH_3 concentrations on shoot and root characteristics, nutrient distributions, and grain yields of two Chinese winter wheat varieties fertilized with different levels of N to assess the effects of elevated atmospheric NH_3 concentrations on their growth, yield and nitrogen use efficiency parameters, including the possibility that atmospheric NH_3 may counter nitrogen deficiencies in their growth medium.

MATERIALS AND METHODS

Plant material and experimental design. In this experiment, two wheat varieties, Xiaoyan 6 (a high water and fertilizer-demanding variety) and Changhan 58 (a drought-resistant variety), were grown in 48 pots, with eight plants per pot. Three factors were varied: the atmospheric NH_3 concentration (at two levels: elevated and ambient, 1000 and 10 nl/l, respectively), wheat variety (the two varieties mentioned above) and N fertilization level (low and high (LN and HN), respectively; see below for details), in a complete factorial design experiment with eight treatments (Table 1), and six replications per treatment. The 48 pots were

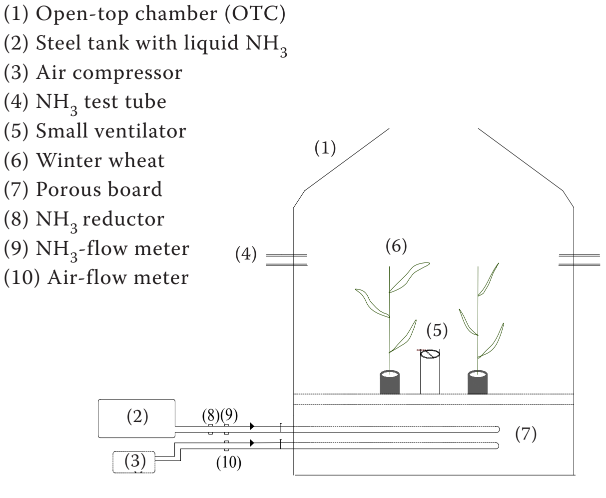

Figure 1. Experimantal equipment

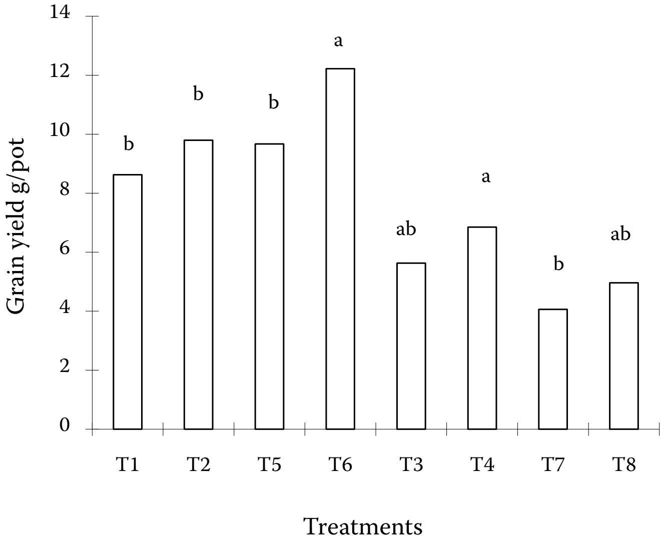

Figure 2. Grain yield of XY6 and CH58 plants subjeted to each of the treatments T1–T8 (see Table 1 for treatment code)

randomly placed in four Open-Top Chambers (OTCs), and in order to reduce the experimental error the pots were exchanged in the four OTCs every 10 days.

Initially, each pot was filled with 3.3 kg soil that had been ground and passed through a 6 mm sieve. All pots were watered to keep the soil water content at field water capacity. At seeding, 0.15 g P/kg soil was added to each pot in the form of KH_2PO_4, and 0.2 g N/kg soil (HN) in the form of KNO_3 was added to each of 24 pots, while no N was applied to the other 24 (LN). The pots were kept in an exposed site (consistent with field crop), until after the re-greening stage, when they were moved into the four OTCs (on March 3, 2008) and subjected to the ammonia treatments, as described below.

Experimental equipment. The Open-Top Chambers (OTCs) used in the experiments (Figure 1) are containers described by Paul and Bert (1993), initially designed for exposing plants to elevated CO_2 concentrations under close to natural conditions, with a square 1.2 × 1.2 m base and 1.5 m tall perpendicular glass walls topped by glass quadrilaterals inclined towards the centre in an iron frame (total volume circa 3 m^3). The chambers were each equipped with a fan and an air control system, which included a steel cylinder (inner diameter 600 mm, total length 1800 mm) containing 95% NH_3. The NH_3 was fed from the bottom into the OTCs through a YQA-441 NH_3 decrement gauge with a pressure range of 0–4 MPa (Shanghai Shuangying Boat Decompressor Manufacture Co., Ltd.) and Φ8 constant pressure oxygen pipes. The NH_3 flux was measured using an LZB-2 flux meter with anti-corrosion glass rotameter (measuring range 6–60 ml/min, rated working pressure ≤ 1 MPa). In addition, air was fed from the bottom of the OTCs using a ZB-0.10/8 air compressor (air displacement 0.1 m^3/min, rated air pressure 0.8 MPa) and Φ8 constant pressure oxygen pipes. The air flux was maintained at 1.7 l/min, as measured by an LZB-2 flux meter with an anti-corrosion glass rotameter (measuring range 0.25–2.5 m^3/h, rated working pressure ≤1 MPa).

The temperature, humidity and NH_3 concentration inside each chamber were regulated by passing air (heated and moistened as appropriate) and NH_3 through porous pipes at the bottom of the container, while the fan (providing air speeds of less than 0.5 m/s) was used to maintain close to uniform distribution of NH_3 and reduced temperature (if necessary) in the chamber. The temperature in the chambers was monitored to verify that the temperature was the same in the chamber

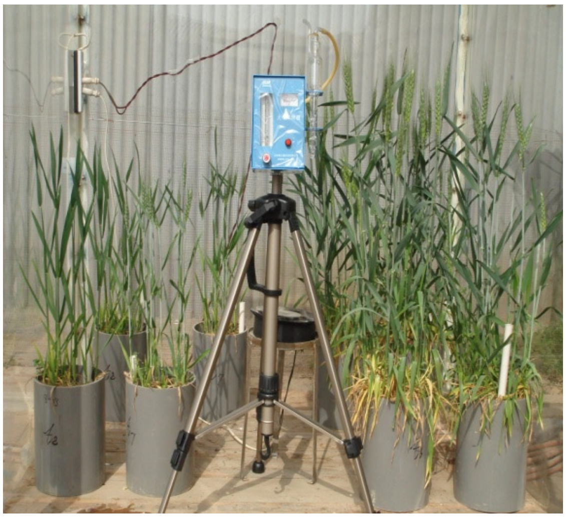

Figure 3. NH_3 concentration measured equipment

before and after NH_3 was supplied, and thus that the effects of varying the NH_3 concentration on the growth parameters or C and N metabolism of plants were not confounded by variations in temperature.

The NH_3 concentration in each chamber was measured four times per day (at 8:00, 11:00, 14:00 and 17:00) by a GTL-C indoor air detector equipped with a pH618 test pen (NH_3 testing precision, ± 0.01 mg/m) mounted on a tripod placed in the centre of the chamber before the gas was supplied (Figure 3). On each sampling occasion, 5 ml of NH_3 test reagent was extracted by an injector and injected into a glass bottle for sampling. The glass bottle was immediately plugged and connected to the instrument. During the tests, the flux was adjusted to 2 l/min and the exhaust time was controlled by the auto-timing device. When the sampling time was complete, the glass bottle was removed, unplugged, the reagent in the glass bottle was poured into the test cup and the test pen was inserted into the cup to measure the NH_3 concentration. Throughout the entire growth period, from 8:00–18:00 every day, the NH_3 concentration in the OTCs used for the background, ambient (control, CK) and elevated NH_3 treatments were maintained precisely at 10 nl/l and 1000 nl/l, respectively, by continuously supplying NH_3 and air at appropriate ratios.

Analytical measurements. At anthesis and mature stages, 3 pots representing each of the treatments were collected from each chamber and dried at 65°C for 48 h to constant weight to determine the dry weights of their roots and shoots. Their root/shoot dry weight ratios were then calculated and the samples were crushed to estimate their N contents.

At mature stage, basic economic parameters (spike length, spike number and grain numbers per spike) and (after threshing) the 1000-grain weight and grain weight per spike yield parameters of the remaining plants were determined, using scales with ± 0.01 mg precision.

The total nitrogen contents of the grain, root and shoot samples were determined by the Kjeldahl method using an automatic nitrogen analyzer (Gerhardt Vapodest 5), and their nitrogen accumulation content (NAA) were calculated by multiplying their N content and yield.

Nitrogen use efficiency evaluation. The Nitrogen Use Efficiency (NUE) was here defined (and calculated) as the ratio between the grain yield and the amount of N applied as fertilizer (mg grain/mg N_f). In addition, two primary factors of NUE based on major plant physiological processes were calculated: Nitrogen Uptake Efficiency (NUPE) and Nitrogen Utilization Efficiency (NUTE). Following Moll et al. (1982), the NUPE was defined as the total plant N content at maturity per unit N applied as fertilizer (mg N_{plant}/mg N_f), and the NUTE as the amount of grain produced per unit total plant N content at maturity (mg grain/mg N_{plant}). Finally, the Nitrogen Agriculture Efficiency (NAE) was calculated from the difference between the grain yields of plants subjected to the HN and LN treatments per unit N applied as fertilizer (mg grain/mg N_f), and the Nitrogen Harvest Index (NHI) was calculated as the grain N content per unit total plant N content at maturity (%).

Statistical analysis. The main and interactive effects of the factors atmospheric NH_3 concentration, N level and varieties on grain yield, yield components, and N-related parameters were analyzed by standard analysis of variance procedures, using SAS software, and the significance of between-treatment differences in means was assessed using significance rank (LSR) multiple comparison tests, determining differences to be significant if $P < 0.05$.

RESULTS AND DISCUSSION

Dry matter yield, R/S ratios and component factors of grain yield. The shoot, root and R/S biomass ratios of XY6 and CH58 plants subjected to each of the treatments are shown in Table 2. In combination with the HN treatment, exposure to the elevated atmospheric NH_3 concentration resulted in significantly lower mean R/S ratios for both XY6 and CH58 plants than the low NH_3 treatment (by 26.2% and 23.0% lower, respectively) at anthesis and mature stages. In addition, the shoot biomass of plants of both varieties exposed to high NH_3 was lower (albeit non-significantly) than their counterparts exposed to low NH_3. However, there were indications that the elevated ammonia concentration enhanced the growth of plants with limited supplies of N fertilizer. More specifically, the average R/S ratio of LN-treated XY6 and C58 plants exposed to the high NH_3 concentration were by 13.8% and 7.9% higher than those of plants exposed to the low NH_3 concentration, and their shoot biomass was also higher at both stages. These findings corroborate numerous previous studies in which enhanced growth of plants exposed to elevated atmospheric concentrations of NH_3 was observed, e.g. Krupa (2003) in experiments with

Table 2. Shoot and root dry weight and R/S ratio of XY6 and CH58 plants subjected to each of the treatments

Variety	NH_3 concentration (nl/l)	Anthesis stage			Mature stage		
		Shoot (g)	Root (g)	R/S ratio	Shoot (g)	Root (g)	R/S ratio
HN							
XY6	10	27.81	5.84	0.21^b	26.11	5.43	0.21^a
CH58	10	28.97	7.07	0.24^a	34.78	5.22	0.15^b
XY6	1000	26.66	4.56	0.17^c	27.32	3.84	0.14^b
CH58	1000	26.33	4.45	0.17^c	27.44	3.56	0.13^b
LN							
XY6	10	9.65	4.25	0.44^a	10.86	3.25	0.30^{ab}
CH58	10	8.34	2.96	0.36^b	12.97	4.23	0.32^a
XY6	1000	11.89	4.68	0.39^{ab}	14.38	3.73	0.26^{bc}
CH58	1000	10.76	4.31	0.40^{ab}	16.39	3.65	0.23^c

Different letters within columns indicate significant differences at the $P < 0.05$

sunflower, provided they are not toxic (Van Haut et al. 1979, Van der Eerden 1982). These results show that NH_3 assimilation can enhance plant growth and the canopy will respond to the elevated atmospheric NH_3 concentration first. Such enhancement may also be significant for plants in natural environments if the ammonia concentration rises, since nitrogen is a limiting factor for plant biomass production in most natural habitats.

The spike length, spike numbers per pot and grain numbers per spike were lower in HN-treated plants of both varieties exposed to the elevated atmospheric NH_3 concentration than in their counterparts exposed to the ambient concentration; these responses were however more pronounced in CH58 than in XY6 plants (Table 3). In addition, the 1000-grain weight values of CH58 and XY6 plants exposed to the elevated NH_3 concentration were by 15.2% lower (significant) and by 0.76% lower (non-significant), respectively.

In contrast, among plants of both varieties subjected to the LN treatment, the elevated atmospheric NH_3 concentration had significantly positive effects on all of the tested yield component parameters (except spike numbers per pot) of both XY6 and CH58 plants (Table 3). There were only slight, non-significant differences between LN-treated plants of the two varieties in spike length and

Table 3. Component factors of yield of XY6 and CH58 plants subjected to each of the treatments

Variety	NH_3 concentration (nl/l)	Spike length (cm)	Spike number/pot	Grain number/spike	1000-grain weight (g)
HN					
XY6	10	7.53 ± 0.25	11.67 ± 1.52	31.83 ± 3.72	26.28 ± 0.56^b
CH58	10	7.93 ± 0.55	12.00 ± 1.00	31.03 ± 3.67	33.00 ± 1.47^a
XY6	1000	7.43 ± 0.40	11.00 ± 1.00	26.46 ± 3.75	26.08 ± 1.98^b
CH58	1000	7.67 ± 0.29	10.33 ± 2.31	35.05 ± 9.33	28.00 ± 2.91^b
LN					
XY6	10	5.03 ± 0.55	8.33 ± 0.58	17.18 ± 0.46	28.40 ± 1.50^b
CH58	10	5.73 ± 0.31	8.33 ± 0.58	17.16 ± 5.05	35.39 ± 2.07^a
XY6	1000	6.77 ± 0.25	8.33 ± 0.58	22.33 ± 1.26	30.25 ± 2.42^b
CH58	1000	7.07 ± 0.75	8.67 ± 0.58	22.47 ± 9.94	36.28 ± 1.95^a

Different letters within columns indicate significant differences at the $P < 0.05$

Table 4. Effects of atmospheric NH_3 concentration (mg/pot) on N accumulation of XY6 and CH58 plants with high (HN) and low (LN) levels of N fertilization

N levels	Variety	NH_3 concentration (nl/l)	Anthesis stage NAA			Mature stage NAA			GNA (mg/pot)
			Shoot	Root	TN	Shoot	Root	TN	
HN	XY6	10	380.72	54.71	435.43^{a}	535.83	62.93	598.76^{a}	347.19^{b}
	CH58	10	378.34	84.67	463.01^{ab}	578.57	58.07	636.63^{a}	395.26^{a}
	XY6	1000	336.23	51.74	387.96^{b}	502.27	44.89	547.16^{b}	330.97^{b}
	CH58	1000	376.99	56.91	433.90^{a}	582.34	45.28	627.62^{a}	354.05^{b}
LN	XY6	10	70.14	24.91	92.48^{bc}	108.86	26.40	135.26^{a}	85.04^{a}
	CH58	10	64.35	22.25	84.56^{c}	131.52	21.18	152.71^{a}	76.89^{a}
	XY6	1000	84.71	34.25	115.68^{a}	161.30	29.95	191.25^{a}	118.73^{a}
	CH58	1000	85.24	32.59	104.08^{ab}	167.13	28.64	195.77^{a}	130.83^{a}

Different letters within columns indicate significant differences at the $P < 0.05$

grain numbers per spike. However, elevated NH_3 led to a significantly different increase, of 1.85 g and 0.89 g, in the 1000-grain weight of LN-treated XY6 and CH58 plants, respectively.

The HN treatment resulted in significantly higher average grain yield than the LN treatment (Figure 2). Yet, this effect was significant for CH58, but not XY6 plants. In addition, the elevated NH_3 concentration had significant ($P < 0.05$) effects on grain yields of XY6 and CH58, and the yield of CH58 was significantly higher following this combination of treatments compared to XY6. These results suggest that elevated atmospheric NH_3 concentration may suppress potential increase in grain yield of the drought-resistant variety in soils with no N deficit. Similar results were observed in the experiment with *Acacia auriculaeformis* supplied with different N sources reported by Zhao (2003).

NUE and N-related parameters. The absorption and utilization of N fertilizer supplied to the plants was evaluated by calculating NUE and N-related parameters. HN-treated XY6 plants exposed to the high NH_3 concentration had significantly (10.6%) higher total N (TN) contents than counterparts exposed to the low NH_3 concentration. However, the NH_3 concentration effect was not significant for CH58 plants in this respect (Table 4). Among LN-treated plants, the high NH_3 concentration led to 34.8 and 26.4% increase in the TN of XY6

Table 5. Effects of atmospheric NH_3 concentration on N utilization in plants of both varieties with high (HN) and low (LN) levels of N fertilization

Variety	NH_3 concentration (nl/l)	NUTE (mg grain/mg N_{pl})	NUPE (mg N_{pl}/mg N_f)	NUE (mg grain/mg N_f)	NHI (%)	NAE (mg grain/mg N_f)
HN						
XY6	10	19.26 ± 0.76^{ab}	0.91 ± 0.01^{a}	14.65 ± 0.97^{b}	63.58 ± 2.67^{a}	8.49 ± 0.10^{a}
CH58	10	21.13 ± 1.82^{a}	0.96 ± 0.03^{a}	18.52 ± 0.48^{a}	62.13 ± 2.67^{a}	11.00 ± 0.32^{a}
XY6	1000	16.10 ± 0.15^{b}	0.83 ± 0.06^{b}	13.07 ± 0.16^{b}	55.28 ± 0.70^{b}	4.54 ± 0.25^{b}
CH58	1000	16.80 ± 2.80^{b}	0.95 ± 0.02^{a}	14.84 ± 0.66^{b}	56.37 ± 4.42^{b}	4.46 ± 0.03^{b}
LN						
XY6	10	37.30 ± 1.93^{a}	–	–	62.92 ± 2.36^{a}	–
CH58	10	38.00 ± 0.68^{a}	–	–	69.41 ± 1.11^{a}	–
XY6	1000	34.82 ± 2.03^{a}	–	–	62.03 ± 1.47^{a}	–
CH58	1000	41.63 ± 2.96^{a}	–	–	66.95 ± 2.19^{a}	–

Different letters within columns indicate significant differences at the $P < 0.05$

Table 6. Significance, *P* value, obtained from ANOVA, of the effects of NH_3 level, variety, N level and their interactions on yield, R/S ratio and N-related parameters

	NH_3	N	V	$NH_3 \times N$	$NH_3 \times V$	N × V	$NH_3 \times N \times V$
1000-grain weight (g)	0.4771	0.0002**	< 0.0001**	0.0344*	0.1109	0.2178	0.2773
Grain yield (g/pot)	0.9774	< 0.0001**	0.0062**	0.0019**	0.583	0.3851	0.3748
R/S ratio	0.0483*	< 0.0001**	0.0818	0.0005**	0.0029**	0.1625	0.4162
NUTE (mg grain/mg N_{pl})	0.2438	< 0.0001**	0.0737	0.1195	0.3609	0.3579	0.1845
NUPE (mg N_{pl}/mg N_f)	0.0280*	< 0.0001**	0.0292*	0.3451	0.2238	0.1175	0.4231
NHI (%)	0.0677	0.0165*	0.23	0.2439	0.9141	0.2018	0.6474

NH_3 – atmospheric NH_3 concentration; N – nitrogen levels; V – wheat variety

and CH58 plants, relative to counterparts exposed to the ambient concentration, respectively. The wheat variety had a significant influence on TN at the anthesis stage, but not at the maturity stage. There were no significant differences in grain nitrogen accumulation (GNA) between XY6 and CH58 plants supplied with the same level of N fertilization, but the GNA of wheat was significantly affected by N levels; the elevated NH_3 concentration led to increases in the GNA of LN-treated plants and reductions in the GNA of HN-treated plants of both varieties. The results show that the elevated atmospheric NH_3 concentration played a direct role in the N accumulation of the plants, especially in their grain.

Exposure to the elevated atmospheric NH_3 concentration led to reduction in both NUE and NAE (Table 5); reductions of 10.78% and 46.52% were observed, respectively, for XY6 plants relative to values of plants exposed to the ambient NH_3 concentration, and reductions of 19.87% and 59.45%, respectively, for CH58 plants. The differences in NUE and NAE between XY6 and CH58 plants exposed to the same NH_3 concentration were not significant. In addition, the NUPE and NUTE of HN-treated XY6 and CH58 plants were lower when the atmospheric NH_3 concentration was increased. However, the differences between varieties in these variables were very slight. Among LN-treated plants there were no significant differences related to the atmospheric NH_3 concentration or variety, but the NUTE of both XY6 and CH58 plants was significantly higher than in HN-treated counterparts of the same variety exposed to the same NH_3 concentration.

The other N efficiency parameter (NHI) reflects the allocation of nitrogen between vegetative and reproductive organs. Among HN-treated XY6 and CH58 plants, the NHI was circa by 13.1% and 9.27% lower, respectively, in those exposed to the elevated atmospheric NH_3 concentration than in those exposed to the ambient level. The results show that the effects of the elevated atmospheric NH_3 concentration on NUTE and associated parameters were related to the N fertilizer levels, in accordance with the findings of many previous experiments.

Analysis of variance (Table 6) indicated that most of the observed variations in grain yield, yield components and N-related parameters could be explained by the effect of N fertilizer. Atmospheric NH_3 concentration only had significant effects on the R/S ratio and NUPE ($P < 0.05$). Wheat variety had significant effects on the 1000-grain weight, grain yield ($P < 0.01$) and NUPE ($P < 0.05$). The interaction effects of NH_3 concentration and N level on 1000-grain weight, grain yield and R/S ratio were significant, but the interaction of all three experimental factors had no significant effects on any of the considered variables.

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