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Scientific Research

Corn Growth Response to Elevated CO_2 Varies with the Amount of Nitrogen Applied

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ABSTRACT

Corn, with C_4 photosynthetic metabolism, often has no photosynthetic or yield response to elevated carbon dioxide concentrations. In C_3 species, the yield stimulation at elevated carbon dioxide concentrations often decreases with nitrogen limitation. I tested whether such a nitrogen interaction occurred in corn, by growing sweet corn in field plots in open top chambers at ambient and elevated (ambient + 180 mmol·mol^{-1}) carbon dioxide concentrations for four seasons, with six nitrogen application rates, ranging from half to twice the locally recommended rate. At the recommended rate of nitrogen application, no carbon dioxide effect on production occurred. However, both ear and leaf plus stem biomass were lower for the elevated carbon dioxide treatment than for the ambient treatment at less than the recommended rate of nitrogen application, and higher at the highest rates of nitrogen application. There were no significant responses of mid-day leaf gas exchange rates to nitrogen application rate for either carbon dioxide treatment, and elevated carbon dioxide did not significantly increase leaf carbon dioxide assimilation rates at any nitrogen level. Leaf area index during vegetative growth increased more with nitrogen application rate at elevated than at ambient carbon dioxide. It is concluded that elevated carbon dioxide increased the responsiveness of corn growth to nitrogen application by increasing the response of leaf area to nitrogen application rate, and that elevated carbon dioxide increased the amount of nitrogen required to achieve maximum yields.

KEYWORDS

Corn; Yield; Nitrogen; Elevated CO_2; Photosynthesis; Stomatal Conductance; Leaf Area Index

1. Introduction

There would be substantial environmental benefits to reducing the amount of nitrate and nitrous oxide lost to runoff, ground water and the air from agricultural ecosystems. Losses of these nitrogenous compounds increase with nitrogen fertilizer application rates, which may increase with rising atmospheric carbon dioxide concentrations. The concentration of nitrogen in plant tissue often decreases when plants are grown at elevated carbon dioxide concentrations [1]. This can result in lower tissue nitrogen concentrations required for maximum growth, but could also result in an increase in the amount of applied nitrogen required for maximum yield [2,3], although this has not been tested under field conditions. A higher nitrogen requirement for maximum yield would tend to increase the amount of nitrogen that farmers apply as atmospheric carbon dioxide concentration increases, resulting in more environmental contamination. This work tested for an effect of elevated carbon dioxide concentration on the response curves relating the yield of sweet corn to nitrogen application rate under field conditions.

In species with C_3 photosynthetic carbon metabolism, responses of photosynthesis and growth to elevated carbon dioxide concentrations are sometimes reduced under conditions of nitrogen deficiency [4-7]. This is often attributed to a larger down-regulation of photosynthesis at elevated carbon dioxide at low nitrogen [8]. In C_4 species, there is often no increase in photosynthesis at elevated carbon dioxide, and no down regulation of photosynthesis. However, because reduced transpiration rate at elevated carbon dioxide is thought to be a primary cause of slower nitrogen uptake by plants [1,9,10], and because stomatal conductance is often reduced by elevated carbon dioxide in C_4 species as well as C_3 species [11-13], elevated carbon dioxide might also induce nitrogen deficiency in C_4 species. In corn, nitrogen deficiency may reduce leaf size without affecting photosynthesis or nitrogen content per unit of leaf area [14]. Effects of elevated carbon dioxide on the responses of leaf area and leaf gas exchange rates to nitrogen application rate were also tested in this study. The overall aim of this research was to determine whether the fertilizer nitrogen requirement for maximum yield was increased at elevated carbon dioxide in corn.

2. Materials and Methods

2.1. Site and Carbon Dioxide Treatments

The study was conducted over four years, at the South Farm of the Beltsville Agricultural Research Center, in Beltsville, Maryland, USA. Sweet corn (*Zea mays* L. cv. Silver Queen) was grown in the summers of 2004, 2006, 2008, and 2010, after soybean crops, as part of a two-year, corn, winter wheat, soybean rotation. Corn was grown in twelve open top chambers each summer and also in plots without chambers in 2006, 2008, and 2010. Each chamber was rectangular and covered 2.8 m^2 of ground, and the walls were clear acrylic panels 2.4 m high. Air was blown into all chambers through a perforated PVC pipe on the ground, centered on a short side of the rectangle and extending the full length of the chambers. The volumetric turnover time of chamber air was 0.6 minutes. Six randomly selected chambers had pure carbon dioxide continuously added to the intake of the blowers at a flow rate sufficient to increase the concentration by 180 ± 20 $mmol \cdot mol^{-1}$ above that of the outside air. Six of the chambers had no added carbon dioxide. Samples of air from one "ambient CO_2" chamber and all of the "elevated CO_2" chambers were pumped into an adjacent shed and were sequentially sampled every 45 minutes by an absolute infrared carbon dioxide analyzer (WMA-4, PP Systems, Haverhill MA), with the data stored on a logger. Flow rates of carbon dioxide were adjusted daily, as needed. A standard weather station about 200 m from the plots collected data on air temperature, humidity, wind and precipitation.

2.2. Fertilizer Treatments

The soil at the site was a Codorus silt loam, a fine-loamy, mixed, mesic Fluvaquentic Dystrochrept, with a water table at about 1.5 m depth. The soil in the chambers was tilled and corn was planted on May 21, 2004, June 7, 2006, May 29, 2008, and June 1, 2010. Plots outside of chambers were planted on the same dates in 2006, 2008, and 2010. Seeds were planted in three rows 40 cm apart. After emergence, plants were thinned to an overall density of 7.5 plants per m^2 of ground. Nitrogen was applied as ammonium nitrate, with half applied at tilling, and half applied when plants were about 30 cm in height. The amount of nitrogen recommended by the Nutrient Management for Maryland System (version 1.28) for this crop and soil system was 150 $kg \cdot ha^{-1}$. Six N treatments were each applied to one elevated CO_2 and one ambient CO_2 chamber. The six treatments were 0.5, 0.75, 1.0, 1.25, 1.5, and 2.0 times the recommended amount. All chambers also received 40 $kg \cdot ha^{-1}$ of phosphorous and 95 $kg \cdot ha^{-1}$ of potassium. The chambers received normal precipitation, and were not irrigated. All weeds were removed by hand. Because the treatments were also intended to test for long-term changes in soil carbon content, the same CO_2 and nitrogen treatments were applied to the same chambers each year, following an initial mixing of the top 30 cm of soil among all chambers and spatial randomization of the treatments. No nitrogen was applied to the soybean crops, but the winter wheat crops also received the same fractions of the recommended nitrogen fertilizer as did the corn crops. The recommended nitrogen fertilizer for the winter wheat was 100 $kg \cdot ha^{-1}$. The plots of corn without chambers received the recommended nitrogen fertilizer application and the same P and K application rates as the chambers, and were used for final destructive harvests.

2.3. Non-Destructive Measurements

Non-destructive measurements of leaf area index were made once per year during vegetative growth, during the last week of June or the first week of July in each year. Measurements were made on overcast days, using a Li-Cor LAI 2000 (Li-Cor, Inc., Lincoln, Nebraska) with two replicate measurements per chamber.

Leaf gas exchange measurements were made three times each summer about a week apart, starting when the fifth leaf was fully expanded, and ending when the crops were harvested in August. All leaf gas exchange and growth measurements were made on interior plants in the center row of each chamber. Stomatal conductance (g_s) and CO_2 assimilation rate (A) were determined near midday on clear days on upper, fully expanded and fully illuminated leaves. A CIRAS-1 portable photosynthesis system (PP Systems, Haverhill, MA) was used to expose the leaves to the ambient air temperature, water vapor content and sunlight at controlled concentrations of CO_2 for the measurement of g_s, A, and substomatal CO_2 concentration (C_i). Plants grown in elevated CO_2 chambers were measured only at the nominal daytime CO_2 concentration of 560 $mmol \cdot mol^{-1}$, and plants from the ambient

CO_2 chambers were measured at both 380 and 560 $mmol \cdot mol^{-1}$. Two leaves were measured from each of the 12 chambers on each measurement date. Chambers were measured in random order. Statistical analysis was conducted on the mean value for each chamber on each date.

2.4. Harvests

No treatment differences in the rate of development of the tassels, silk, or ears were detected, and all plants in all chambers were harvested on the same date. Plants were harvested during the first or second week of August each year. At harvest, ear fresh weight was determined, and then ear, seed and husk dry weight, and total leaf and stem dry weight were determined after drying in a forced air oven at 70˚C. A mean value for each chamber was determined for each parameter, based on 5 interior plants in the center row of each chamber.

2.5. Statistics

Tests for effects of the CO_2 treatment on responses of growth to nitrogen fertilizer were conducted using analysis of covariance to compare the linear regressions of responses on fertilizer level. It was presumed that some transformation of the data might be required to generate linear responses for the analysis of covariance tests. However, that proved to be unnecessary (see results), and tests were conducted on untransformed data. For the leaf gas exchange data, linear and simple curvilinear responses to nitrogen level were first tested separately for each CO_2 treatment on each measurement date. Because no significant responses to nitrogen level were detected for either CO_2 treatment, leaf gas exchange data were pooled across nitrogen treatments, and CO_2 effects were tested with 6 chambers per treatment. Within each growing season, tests of CO_2 effects on leaf gas exchange parameters were conducted using repeated measures analysis of variance, combining measurements across dates.

3. Results

The weather during flowering and ear formation in July was abnormally wet in 2004, and in 2010 July had more days with maximum temperatures above 35˚C than the other years of this study (**Table 1**). The high precipitation in 2004, and the high temperatures of July 2010 had no apparent effects on vegetative growth, as indicated by the stem plus leaf dry mass being similar for all years (**Figure 1**). However, ear fresh mass was lower at each nitrogen fertilizer level in 2010 than in the other years for both CO_2 treatments (**Figure 1**). The test for differences between the CO_2 treatments of the responses of stem plus leaf dry weight to nitrogen therefore combined data for all years, while for ear weight, the data for 2010 was tested separately from the other three years.

Table 1. July temperature (T) and precipitation data for the summers of these experiments.

Year	Mean maximum T (˚C)	Total precipitation (cm)	Number of days $T_{max} > 35$˚C (days)
2004	29.6	23.5	0
2006	31.6	5.0	2
2008	30.8	7.7	0
2010	32.7	9.0	8

Ear fresh weight increased linearly with nitrogen application rate at elevated CO_2, but did not increase significantly with nitrogen at ambient CO_2 (**Figure 1**). This was true both for the 2004, 2006 and 2008 data combined, and for the 2010 data. The CO_2 effect on the slope of the response of ear fresh weight was significant in the combined data of 2004, 2006, and 2008 ($P < 0.001$) and also in 2010 ($P = 0.009$) (**Table 2**). From the regressions, in 2004, 2006 and 2008, equal ear weight for both CO_2 treatments would have occurred at about 180 $kg \cdot N \cdot ha^{-1}$, with lower yield at elevated than ambient CO_2 at lower N, and higher yields at elevated CO_2 at higher N levels. In 2010, the elevated CO_2 treatment had lower ear fresh weight over the whole range of N application rates, although the difference was small at the highest fertilizer rates. The ear fresh weight to dry weight ratio averaged 4.0, and did not differ with CO_2 or nitrogen treatment.

At elevated CO_2, there was a linear increase in the stem plus leaf dry weight with nitrogen fertilizer application rate, but there was no significant response for the ambient CO_2 treatment (**Figure 1**). Analysis of covariance indicated a difference in slope of the response between the CO_2 treatments at $P = 0.014$ (**Table 2**). From the regressions, equal stem plus leaf weight would have occurred at about 108 $kg \cdot N \cdot ha^{-1}$, with higher weight at elevated than at ambient CO_2 at higher nitrogen application rates.

Leaf area index during vegetative growth increased significantly with nitrogen application rate for plants grown at elevated CO_2 in all four years, but never increased significantly with nitrogen for plants grown at ambient CO_2 (**Figure 2**).

For the recommended nitrogen fertilizer treatments in 2006, 2008, and 2010, the total dry mass averaged 1355 $g \cdot m^{-2}$ for the field plots without chambers, and 1483 $g \cdot m^{-2}$ for the ambient CO_2 plots inside chambers. This difference was not significant at $P = 0.05$.

Leaf temperatures during the midday measurements of leaf gas exchange rates ranged from 28˚C to 35˚C, and leaf to air water vapor differences ranged from 0.7 to 2.5 kPa. Leaf A and g_s were not significantly correlated with

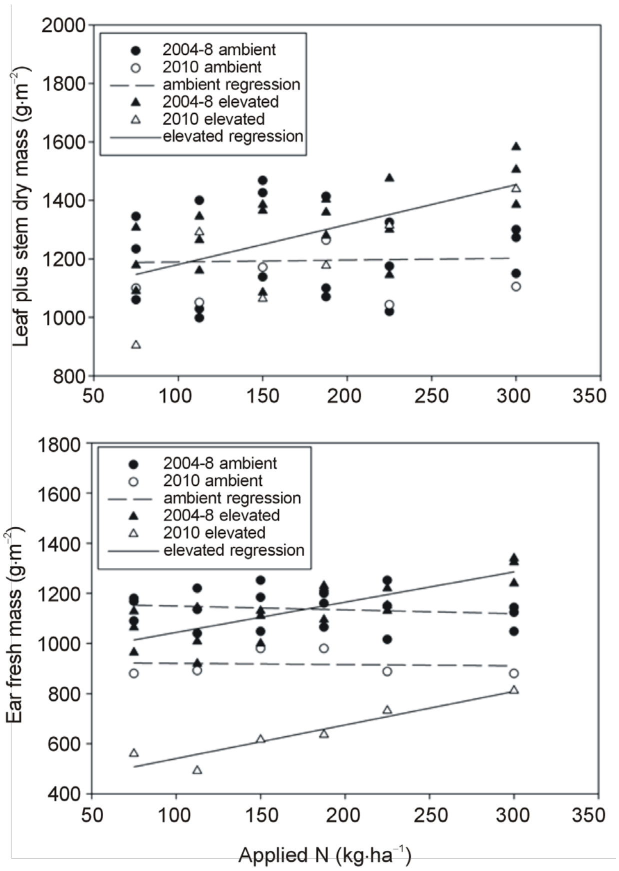

Figure 1. Leaf plus stem dry mass, and ear fresh mass of sweet corn grown at ambient and elevated CO_2 with a range of nitrogen fertilizer application rates. For leaf plus stem dry mass, linear regressions for all years combined are shown. For ear mass, separate regressions are shown for 2010 and for the other three years combined. Statistical analysis of linear regressions and ANCOVA tests of CO_2 effects are presented in Table 2.

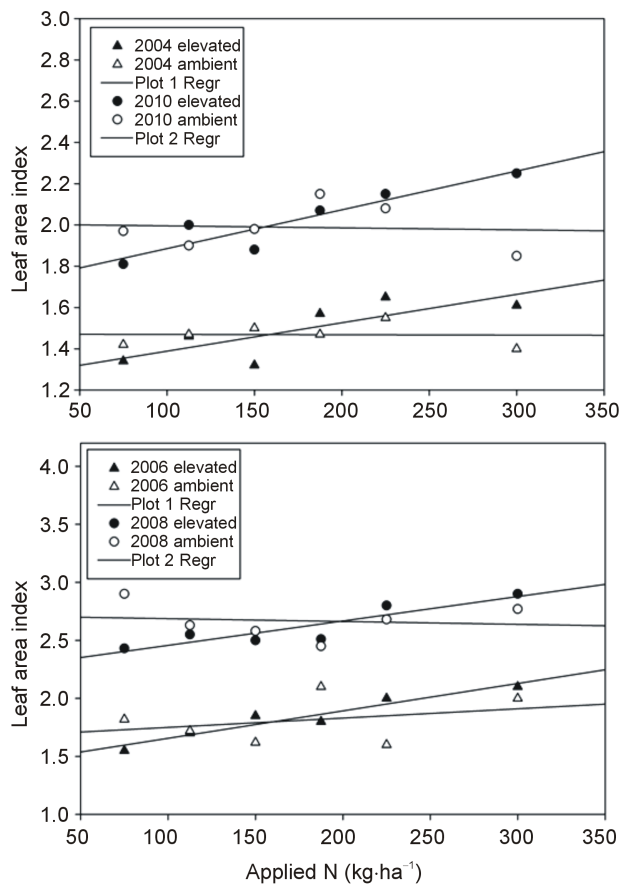

Figure 2. Leaf area index of sweet corn grown at ambient and elevated CO_2 with a range of nitrogen fertilizer application rates. Data are from vegetative plants each year of the study. Plots of years were arranged only for clarity. Linear regressions of leaf area index on nitrogen application rate were significant at elevated CO_2 each year at P = 0.05, but were never significant at ambient CO_2.

nitrogen fertilizer application rate for either CO_2 treatment. The highest r^2 values for data combined within individual years were 0.06 for A, and 0.21 for g_s. Leaf A of the plants grown at ambient CO_2 was always slightly increased by increasing the measurement CO_2, but the effect was not statistically significant in any year (Table 3). Leaf A of plants grown and measured at elevated CO_2 was not significantly different from that of leaves grown at ambient CO_2 but measured at elevated CO_2. Leaf g_s averaged 38% less in leaves grown and measured at elevated CO_2 compared with leaves grown and measured at ambient CO_2, with most of that reduction due to the measurement concentration (Table 3).

4. Discussion

The fact that the growth and yield of this sweet corn cultivar at the ambient CO_2 concentration were apparently saturated for N fertilizer at the lowest rate of application used was unexpected, but simplified the comparison with the elevated CO_2 treatment. Saturation of growth with 75 kg·m^{-2} of applied N could have been the result of substantial N remaining in the soil after the wheat and soybean crops. Keeping the plots free of weeds may also have contributed to their low N requirement. In field corn in Illinois, adding no nitrogen at all only reduced total biomass by about 20% compared with fertilizing with 168 kg·ha^{-1}, after a soybean crop [15]. In light of this result, it may not be surprising that adding 50% of the recommended nitrogen did not reduce the yield at ambient CO_2 in this study.

The lack of a CO_2 effect on yield at the recommended rate of N fertilizer application that we observed in three of the four years is similar to other studies with field corn using recommended rates of N application, where elevated CO_2 had no significant effect on yield in the absence of water stress [11,12,15,16]. However, our results indicate that this lack of response of corn growth and

Table 2. Regressions and ANCOVA results for growth responses to N fertilizer application. Plants were grown at ambient (amb) or elevated (elev) CO_2 at a range of N application rates. Linear regressions of mass against N are presented for the ambient and elevated CO_2 treatments, and a test of the CO_2 × N is presented when the regression was significant. For stem plus leaf mass, data was combined across all years. For ear fresh mass, data from 2010 is presented separately from the combined data for the other years (2004, 2006 and 2008).

Variable	Year	CO_2	Intercept ($g \cdot m^{-2}$)	Slope ($g \cdot g^{-1}$)	r^2	Probability of >F	
						Regression	CO_2 × N
Stem plus leaf dry mass	2004-10	amb	1185	0.64	0.004	0.93	
	2004-10	elev	1042	13.7	0.42	<0.001	0.014
Ear fresh mass	2004-8	amb	1164	−1.5	0.025	0.46	
	2004-8	elev	923	12.1	0.62	<0.001	<0.001
	2010	amb	925	−0.5	0.006	0.86	
	2010	elev	407	13.4	0.88	<0.001	0.009

Table 3. Mean values of midday leaf CO_2 assimilation rate (A) and stomatal conductance (g_s) for each year of the study, probability of greater F ratios for CO_2 treatment effects on A and g_s. AA refers to plants grown and measured at ambient CO_2, EE refers to plants grown and measured at elevated CO_2, and AE refers to plants grown at ambient CO_2 but measured at elevated CO_2.

Year	A ($mmol \cdot m^{-2} \cdot s^{-1}$)			g_s ($mmol \cdot m^{-2} \cdot s^{-1}$)			Probability of >F	
	AA	AE	EE	AA	AE	EE	A	g_s
2004	54.8	58.0	58.4	594	505	474	0.26	0.012
2006	51.3	51.7	53.1	722	523	460	0.31	0.001
2008	61.4	63.7	64.0	1650	822	658	0.11	0.001
2010	49.3	51.0	52.6	749	529	490	0.23	0.029

yield to elevated CO_2 may not occur at either higher or lower rates of N application, because of a stronger response of yield to N application rate at elevated than at ambient CO_2.

At the lowest rates of N application used in this study, elevated CO_2 reduced the leaf area index during vegetative growth as well as the final mass and yield of corn. The average 38% reduction in leaf stomatal conductance at elevated CO_2 would have reduced transpiration. Lower transpiration at elevated CO_2 could have reduced whole plant N uptake by reducing the delivery of N to the root system in the transpiration stream [1,9-11]. In corn, as in many grass species, N deficiency often reduces leaf size and leaf area index without any reduction in photosynthetic rates or nitrogen contents per unit of area [14, 15,17]. Because elevated CO_2 decreases or does not change the percentage of nitrogen in plant tissues [1,12], the lower total biomass observed at the lowest N application rates at elevated CO_2 would also reflect lower total N uptake in those treatments.

The cause of the yield stimulation by elevated CO_2 at the highest rates of N application observed in the three cooler summers could be improved water status because of lower stomatal conductance and transpiration rate. This could have caused the higher LAI at elevated CO_2 at the high N application rates. A similar increase in growth at elevated CO_2 without any increase in photosynthesis per unit of leaf area has been previously reported for corn [18], and elevated CO_2 has been found to ameliorate effects of water stress on corn in the field [16,19]. Water stress often reduces leaf area growth before photosynthesis in corn [20].

In 2010, when ear yield was reduced by the elevated CO_2 treatments at all N application rates, the ear yield was reduced in both CO_2 treatments compared with the other seasons, yet stem plus leaf mass was not reduced. This specific reduction in ear yield was probably caused by high temperature stress during flowering and ear development (Table 1), which often reduces yield in corn [21,22]. Tissue temperatures were undoubtedly higher at elevated than at ambient CO_2 during the high temperature stress as a result of lower transpiration caused by the observed lower stomatal conductance [11]. A greater reduction in yield at high air temperatures at elevated than at ambient CO_2 because of warmer tissue temperatures at elevated CO_2 was found in sorghum [13].

In the three cooler years, the yield increase caused by elevated CO_2 averaged about 14% at twice the recommended rate of N application (Figure 2). Whether this amount of yield stimulation would cause producers to increase nitrogen application rates above those currently recommended would depend on the cost of nitrogen fertilizer compared with other costs of production. In 2011 total costs of fertilizer, lime, and soil conditioners averaged less than 13% of crop production costs [23], so it might be profitable to increase the N application rate. However, the relative production costs may change in the time it takes atmospheric CO_2 to reach the elevated concentration used in these experiments.

Regardless of the economics, the results presented here indicate that in sweet corn, as in many C_3 crops, the yield response to elevated CO_2 can be sensitive to the nitrogen fertilizer treatment. The results also indicate that elevated CO_2 can increase the nitrogen requirement for maximum yield under field conditions. If this also occurs in other crop species, rising atmospheric CO_2 may lead to higher rates of nitrogen fertilizer application.

REFERENCES

[1] D. R. Taub and X. Wang, "Why Are Nitrogen Concentrations in Plant Tissues Lower under Elevated CO_2? A Critical Examination of the Hypotheses," *Journal of Integrative Plant Biology*, Vol. 50, No. 11, 2008, pp. 1365-1374. http://dx.doi.org/10.1111/j.1744-7909.2008.00754.x

[2] S. K. Aben, S. P. Seneweera, O. Ghannoum and J. P. Conroy, "Nitrogen Requirements for Maximum Growth and Photosynthesis of Rice, *Oryza sativa* L. cv. Jarrah Grown at 36 and 70 Pa CO_2," *Australian Journal of Plant Physiology*, Vol. 26, No. 8, 1999, pp. 759-766. http://dx.doi.org/10.1071/PP99067

[3] G. S. Rogers, L. Payne, P. Milham and J. Conroy, "Nitrogen and Phosphorus Requirements of Cotton and Wheat under Changing Atmospheric CO_2 Concentrations," *Plant and Soil*, Vol. 155-156, No. 1, 1993, pp. 231-234. http://dx.doi.org/10.1007/BF00025026

[4] O. Ghannoum and J. P Conroy, "Nitrogen Deficiency Precludes a Growth Response to CO_2 Enrichment in C_3 and C_4 *Panicum* Grasses," *Australian Journal of Plant Physiology*, Vol. 25, No. 5, 1998, pp. 627-636. http://dx.doi.org/10.1071/PP98026

[5] H. Harmens, C. M. Stirling, C. Marshall and J. F. Farrar, "Does Down-Regulation of Photosynthetic Capacity by Elevated CO_2 Depend on N Supply in *Dactylis glomerata*?" *Physiologia Plantarum*, Vol. 108, No. 1, 2000, pp. 43-50.

[6] H. Y. Kim, M. Lieffering, K. Kobayashi, M. Okada, M. W. Mitchell and M. Gumpertz, "Effects of Free-Air CO_2 Enrichment and Nitrogen Supply on the Yield of Temperate Paddy Rice Crops," *Field Crops Research*, Vol. 83, No. 3, 2003, pp. 261-270. http://dx.doi.org/10.1016/S0378-4290(03)00076-5

[7] L. H. Ziska, W. Weerakoon, O. S. Namuco and R. Pamplona, "The Influence of Nitrogen on the Elevated CO_2 Response in Field-Grown Rice," *Australian Journal of Plant Physiology*, Vol. 23, No. 1, 1996, pp. 45-52. http://dx.doi.org/10.1071/PP9960045

[8] M. Stitt and A. Krapp, "The Interaction between Elevated Carbon Dioxide and Nitrogen Nutrition: The Physiological and Molecular Background," *Plant, Cell and Environment*, Vol. 22, No. 6, 1999, pp. 741-621. http://dx.doi.org/10.1046/j.1365-3040.1999.00386.x

[9] E. P. McDonald, J. E. Erickson and E. L. Kruger., "Can Decreased Transpiration Limit Plant Nitrogen Acquisition in Elevated CO_2?" *Functional Plant Biology*, Vol. 29, No. 9, 2002, pp. 1115-1120. http://dx.doi.org/10.1071/FP02007

[10] H. Shimono and J. A. Bunce, "Acclimation of Nitrogen Uptake Capacity of Rice to Elevated Atmospheric CO_2 Concentration," *Annals of Botany*, Vol. 103, No. 1, 2009, pp. 87-94. http://dx.doi.org/10.1093/aob/mcn209

[11] S.-Y. Kim, R. C. Sicher, H. Bae, D. C. Gitz, J. T. Baker, D. J. Timlin and V. R. Reddy, "Canopy Photosynthesis, Evapotranspiration, Leaf Nitrogen, and Transcription Profiles of Maize in Response to CO_2 Enrichment," *Global Change Biology*, Vol. 12, No. 3, 2006, pp. 588-600. http://dx.doi.org/10.1111/j.1365-2486.2006.01110.x

[12] A. D. B. Leakey, M. Uribelarrea, E. A. Ainsworth, S. L. Naidu, A. Rogers, D. R. Ort and S. P. Long, "Photosynthesis, Productivity, and Yield of Maize Are Not Affected by Open-Air Elevation of CO_2 Concentration in the Absence of Drought," *Plant Physiology*, Vol. 140, No. 2, 2006, pp. 779-790. http://dx.doi.org/10.1104/pp.105.073957

[13] P. V. Vara Prassad, K. J. Boote and L. H. Allen Jr., "Adverse High Temperature Effects on Pollen Viability, Seed-Set, Seed Yield and Harvest Index of Grain-Sorghum [*Sorghum bicolor* (L.) Moech] Are More Severe at Elevated Carbon Dioxide Due to Higher Tissue Temperatures," *Agricultural and Forest Meteorology*, Vol. 139, No. 3-4, 2006, pp. 237-251. http://dx.doi.org/10.1016/j.agrformet.2006.07.003

[14] J. A. Bunce, "What Is the Usual Internal Carbon Dioxide Concentration in C_4 Species under Midday Field Conditions?" *Photosynthetica*, Vol. 43, No. 4, 2005, pp. 603-608. http://dx.doi.org/10.1007/s11099-005-0094-y

[15] R. J. C. Markelz, R. S. Strellner and A. D. B. Leakey, "Impairment of C_4 Photosynthesis by Drought Is Exacerbated by Limiting Nitrogen and Ameliorated by Elevated $[CO_2]$ in Maize," *Journal of Experimental Botany*, Vol. 62, No. 9, 2011, pp. 3235-3246. http://dx.doi.org/10.1093/jxb/err056

[16] R. Manderscheid, M. Erbs and H.-J. Weigel, "Interactive Effects of Free-Air CO_2 Enrichment and Drought Stress on Maize Growth," *European Journal of Agronomy*, Vol. 43, 2012, pp. 97-107. http://dx.doi.org/10.1016/j.eja.2012.05.011

[17] D. J. Watson, "The Physiological Basis of Variation in Yield," *Advances in Agronomy*, Vol. 4, 1952, pp. 101-145. http://dx.doi.org/10.1016/S0065-2113(08)60307-7

[18] H. H. Rogers, G. E. Bingham, J. D. Cure, J. M. Smith and K. A. Surano, "Responses of Selected Plant Species to Elevated Carbon Dioxide in the Field," *Journal of Environmental Quality*, Vol. 12, No. 4, 1983, pp. 569-574. http://dx.doi.org/10.2134/jeq1983.00472425001200040028x

[19] A. D. B. Leaky, C. J. Bernacchi, F. G. Dohleman, D. R. Ort and S. P. Long, "Will Photosynthesis of Maize (*Zea*

mays) in the US Corn Belt Increase in Future [CO_2] Rich Atmosphere? An Analysis of Diurnal Courses of CO_2 Uptake under Free-Air Concentration Enrichment (FACE)," *Global Change Biology*, Vol. 10, No. 6, 2004, pp. 951-962. http://dx.doi.org/10.1111/j.1529-8817.2003.00767.x

[20] J. S. Boyer, "Leaf Enlargement and Metabolic Rates in Corn, Soybean, and Sunflower at Various Leaf Water Potentials," *Plant Physiology*, Vol. 46, No. 2, 1970, pp. 233-235. http://dx.doi.org/10.1104/pp.46.2.233

[21] Y. Assefa, K. L. Roozenboom, S. A. Staggenborg and J. Du, "Dryland and Irrigated Corn Yield with Climate, Management, and Hybrid Changes from 1939 through 2009," *Agronomy Journal*, Vol. 104, No. 2, 2012, pp. 473-482. http://dx.doi.org/10.2134/agronj2011.0242

[22] E. P. Wilhelm, R. E. Mullen, P. L. Keeling and G. W. Singletary, "Heat Stress during Grain Filling in Maize: Effect on Kernel Growth and Metabolism," *Crop Science*, Vol. 39, No. 6, 1999, pp. 1733-1741. http://dx.doi.org/10.2135/cropsci1999.3961733x

[23] USDA Economics, "Statistics and Market Information System," 2013. http://usda.mannlib.cornell.edu/MannUsda/