Improving yield potential in crops under elevated CO2: integrating the photosynthetic and nitrogen utilization efficiencies

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Increasing crop productivity to meet burgeoning human food demand is challenging under changing environmental conditions. Since industrial revolution atmospheric CO2 levels have linearly increased. Developing crop varieties with increased utilization of CO2 for photosynthesis is an urgent requirement to cope with the irreversible rise of atmospheric CO2 and achieve higher food production. The primary effects of elevated CO2 levels in most crop plants, particularly C3 plants, include increased biomass accumulation, although initial stimulation of net photosynthesis rate is only temporal and plants fail to sustain the maximal stimulation, a phenomenon known as photosynthesis acclimation. Despite this acclimation, grain yield is known to marginally increase under elevated CO2. The yield potential of C3 crops is limited by their capacity to exploit sufficient carbon. The "C fertilization" through elevated CO2 levels could potentially be used for substantial yield increase. RuBisCO is the rate-limiting enzyme in photosynthesis and its activity is largely affected by atmospheric CO2 and nitrogen availability. In addition, maintenance of the C/N ratio is pivotal for various growth and development processes in plants governing yield and seed quality. For maximizing the benefits of elevated CO2, raising plant nitrogen pools will be necessary as part of maintaining an optimal C/N balance. In this review, we discuss potential causes for the stagnation in yield increases under elevated CO2 levels and explore possibilities to overcome this limitation by improved photosynthetic capacity and enhanced nitrogen use efficiency. Opportunities of engineering nitrogen uptake, assimilatory, and responsive genes are also discussed that could ensure optimal nitrogen allocation toward expanding source and sink tissues. This might avert photosynthetic acclimation partially or completely and drive for improved crop production under elevated CO2 levels.

Keywords: photosynthesis, nitrogen use efficiency, RuBisCO, carbon, nitrogen, elevated CO2, yield

INTRODUCTION

The human population has just crossed the mark of seven billion, and by the middle of this century it is expected to exceed nine billion (Godfray et al., 2010). To sufficiently feed such a large population, considerable stress will be imposed on increasing crop productivity due to a combination of factors, including shortage of arable land, resource constraints of water and nutrients, changing food habits, use of crop produce for biofuel, and rapid global environmental changes. Although, agronomic and breeding efforts in the past five decades have achieved a linear increase in food productivity, a further ability to increase or even sustain the crop yield and quality is uncertain in the face of rapid global environmental change (Rothstein, 2007; Tester and Langridge, 2010). The environmental changes are coincident with increasing biotic and abiotic threats such as heat and water stress, newer insect-pests as well as diseases and rising greenhouse gases including elevated CO2. Among these, atmospheric CO2 levels are increasing linearly over time; present atmospheric CO2 has increased from 280 to 390 μmol mol−1 since 1800, and is expected to double by the end of the twenty-first century (IPCC, 2007). Plants could adapt to these elevated levels through photosynthetic conversion of high CO2 into increased growth and productivity. However, the potential for different plant species to assimilate higher CO2 concentrations and their consequences is not yet fully understood.

Carbon (C) and nitrogen (N) are the key structural elements for plant growth and constitute ~45 and ~5% of plant dry matter, respectively (Ho, 1976; Marschner, 1995). The maintenance of optimum C and N balance (often referred as the C/N ratio) within plants as well as externally in soil or growth media is essential for optimal plant growth and development (Paul and Driscoll, 1997; Martin et al., 2002; Malamy, 2005; Wingler et al., 2006; Zhang et al.,...
Photosynthesis is the process whereby light is harvested by the chloroplast thylakoids of the leaf and other photosynthetic structures. The resultant chemical energy (ATP and NADPH) is used to fix atmospheric CO$_2$, either directly via Rubisco (C$_3$ photosynthesis), or indirectly after primary fixation by phosphoenolpyruvate carboxylase (PEPC). C$_4$ fixed through this mechanism is subsequently re-released into adjacent cells which are not in direct communication with atmospheric CO$_2$ (C$_4$ photosynthesis). The majority of crop species (rice, wheat, grain legumes, canola, and all root crops) and ~85% of terrestrial plants use C$_3$ photosynthesis, while C$_4$ crops are a minority, represented predominantly by maize, sorghum, and sugarcane among economically important crops (Ehleringer et al., 1991). The Rubisco enzyme, which is fundamental to C fixation in both C$_3$ and C$_4$ plants, displays a high affinity to O$_2$, and its inability to distinguish it from the CO$_2$ molecule results in unnecessary O$_2$ uptake, especially under hot and arid conditions. This oxygenation activity produces phosphoglycolate molecules, which are then broken down in a process referred to as photorespiration, an energy-consuming and wasteful process (Kajula et al., 2011). Photorespiration has been identified as the bottleneck preventing C$_3$ plants from achieving full photosynthetic potential due to competition between CO$_2$ and O$_2$ at the C fixation site on the Rubisco enzyme. Whereas, C$_4$ photosynthesis evolved to ameliorate photorespiration by utilizing two distinct cell types not
In contrast, as C3 plants are not photosynthetically saturated, the ratio of CO2 to O2 at the site of fixation in the chloroplast, favoring carboxylation over oxygenation of Rubisco, enables photosynthetic rates to be increased in C3 plants. The increased concentration of CO2 at the site of Rubisco activity maximizes photosynthetic efficiency. These evolutionary adaptations in C4 plants provide an advantage over C3 photosynthesis while potentially improving water and nutrient use (Kajala et al., 2011). Zhu et al. (2008) reported a 60% increase in maximum photosynthetic efficiency in C4 plants compared to C3 plants. C4 plants can photosynthesize with ~50% greater water use efficiency, as C4 photosynthesis can assimilate an equivalent amount of CO2 with only half the stomatal conductance (Sage and Kubien, 2003; von Caemmerer and Furbank, 2003). Under N-limited conditions, C4 plants also out-compete C3 plants, as they require less Rubisco to harness a similar amount of C due to increased photosynthetic efficiency (Sage and Kubien, 2003).

Since C4 plants are photosynthetically saturated at current CO2 conditions, predicted rises in atmospheric CO2 would have no major impact on their C fixation rate, biomass production, and yield (Figure 2; Cure and Acock, 1986; Ainsworth and Long, 2005). In contrast, as C3 plants are not photosynthetically saturated at present CO2 levels, photosynthesis, biomass, and subsequent yields should increase with elevated atmospheric CO2. The understanding of the biochemical and molecular nature of C3 and C4 photosynthesis provides a valuable tool for crop improvement in the twenty-first century, particularly with respect to improving C assimilation in C3 plants and reducing the impact of photosynthetic acclimation.

**IMPACTS OF ELEVATED CO2**

**LEAF PHOTOSYNTHESIS, GROWTH, AND YIELD**

The present atmospheric CO2 concentration of 390 μL CO2 L−1 limits the rate of photosynthesis in C3 plants (Farquhar et al., 1980; Farquhar and Sharkey, 1982), and presumably lower concentrations of CO2 in the recent past were even more limiting. Laboratory and field studies have shown that photosynthetic rates of C3 plants were approximately doubled when plants grown at about 380 μL CO2 L−1 were exposed to 700 μL CO2 L−1 (Ainsworth and Long, 2005). This increase in photosynthetic rate as atmospheric CO2 rises is primarily due to increases in Rubisco carboxylation capacity. Rubisco has an affinity for O2 as well as CO2 (Badger and Price, 2003); consequently, at 21% O2 and 390 μL CO2 L−1, a considerable amount of energy is wasted in the photosrespiratory carbon oxidation cycle (PCO). This reduces photosynthetic rates by about 40% from the optimum level (Sharkey, 1985). Increasing the ambient CO2 concentration increases the ratio of CO2 to O2 at the site of fixation in the chloroplast, favoring PCR over PCO, and thus photosynthetic rates are increased in C3 plants. The limitation of photosynthesis imposed by Rubisco is referred to as the limitation due to supply and utilization of CO2 (Farquhar and Sharkey, 1982). Two other limitations were also identified: the supply and utilization of light and the utilization of triose phosphate. The former can be caused by low photon flux densities or inability to convert light energy to chemical energy. Triose phosphate is the end product of photosynthesis and can be formed into starches and sugars or utilized as a direct source of chemical energy. Limitation occurs when there are insufficient sinks for sucrose (Stitt and Schulze, 1994), thus reducing conversion to sugar and inhibiting photosynthesis. These three limitations to leaf photosynthesis were first identified as responses that were grown at a given CO2 concentration and then transferred to different CO2 concentration during measurement of photosynthesis (Drake et al., 1997). However, when plants are exposed to high CO2 for extended period, the photosynthetic rates slow down due to the so-called “acclimation” response (Long et al., 2004; Reich et al., 2006). This is thought to result from direct effects of sucrose on the transcription of genes encoding proteins involved in CO2 fixation and electron transport activity (Moore et al., 1999).

The effect of elevated CO2 on plant growth and yield has been studied in both controlled and field conditions, with the latter referred to as the Free Air Carbon dioxide Enrichment (FACE) system. The controlled conditions might produce larger artifacts, whereas FACE produces an environment similar to field conditions. The differential plant response under the two conditions has been reported. For example, Ainsworth et al. (2008) suggested
a 14% yield increase in FACE and a 31% increase in controlled conditions in different plant species when CO$_2$ was raised from 350 to 500 ppm (Aoki et al., 2003). Generally, elevated CO$_2$ increases photosynthesis, resulting in increased dry matter accumulation, leaf area, and plant height in trees and shrubs and to some extent in C$_3$ plants (Figure 2; Ainsworth and Long, 2005). The yield increase in C$_4$ crops under elevated CO$_2$ is variable and dependent on other environmental factors such as water, temperature, and soil N (Ainsworth and Long, 2005). Irrespective of photosynthetic machinery, a yield increase requires a concomitant increase in sink capacity to match the source activity. The initial response of C$_3$ plants to elevated CO$_2$ is an increase in photosynthetic rate; however, due to the acclimation phenomenon this stimulation is not always maintained at the maximal level when plants are exposed to elevated CO$_2$ for a longer period. This partial reversal of photosynthesis and settling at lower than maximal level could be ascribed to (i) reduced stomatal conductance resulting in depletion of intercellular CO$_2$, leading to reduced CO$_2$ supply to the photosynthetic machinery; and (ii) reduced rates of electron transport to Rubisco carboxylation (Figure 1 and also discussed in the following sub-section). Lower activation state and reduced concentration of Rubisco leads to changes in C assimilation and alters the whole plant N metabolism. Thereby, biochemical adjustments occur from the cellular to whole plant level in response to elevated CO$_2$, accompanied by growth, development, and yield changes.

MOLECULAR CHANGES IN PLANTS
Rubisco is the rate-limiting enzyme in photosynthesis and its synthesis and degradation is affected by environmental factors such as temperature, light intensity, soil N, and atmospheric CO$_2$. Prolonged exposure to elevated CO$_2$ results in reduced Rubisco content and Rubisco activity (Moore et al., 1999; Ainsworth and Long, 2005; Seneweeru et al., 2011). A concomitant reduction in the transcript level of genes encoding proteins involved in photosynthesis, including small subunit of Rubisco (RbcS), large subunit of Rubisco (RbcL), and Rubisco activase (Rca), has been observed in different plants (Nie et al., 1995; Cheng et al., 1998; Moore et al., 1998, 1999; Stitt and Krapp, 1999). In contrast, in expanding rice leaf blades there was no significant difference in RbcS transcript level between ambient and elevated CO$_2$ levels (Aoki et al., 2003). This can be correlated with changes in Rubisco concentration during leaf development, with a rapid increase in Rubisco protein during leaf expansion, reaching a maximum when the leaf is fully expanded and a gradual decline with the onset of leaf senescence (Seneweeru and Conroy, 2005; Imai et al., 2008). The decline in Rubisco in both Rubisco and subsequent photosynthesis acclimation in plants under elevated CO$_2$ could be attributed to two processes. It could be due to carbohydrate sink limitation since plants grown under CO$_2$ enrichment initially assimilate more CO$_2$ than they can incorporate in their sink tissues, and as a feedback response plants diminish CO$_2$ assimilation by reducing Rubisco and other proteins (Long et al., 2004). Previous reviews have reported that feedback repression of the RbcS and RbcL genes by soluble carbohydrates accumulation leads to a decline in Rubisco protein levels (Moore et al., 1999). Alternatively the C/N ratio usually increases under elevated CO$_2$ (Geiger et al., 1999; Luo et al., 2004; Taub and Wang, 2008; Bloom et al., 2010), since N is a key constituent of Rubisco and it becomes a rate-limiting factor for Rubisco synthesis (Nakano et al., 1997; Seneweeru et al., 2011).

**NUTRITIONAL CHANGES IN PLANTS**
Elevated CO$_2$ stimulates higher photosynthesis and an increased growth rate, which is required to match with an increased demand for nutrients. This may vary between plant species, nutrient availability, and the nutrient element in question. Among different nutrient elements, maintaining the C/N balance is important for optimal plant growth. For instance, under a higher C/N ratio in soil or growth media, there is a reduced uptake of N in plants, leading to reduced grain quality in cereals due to lower grain protein content. In cereals such as wheat, rice, and barley, a decrease of up to 15% grain protein was observed under elevated CO$_2$, with an overall decrease in amino acid concentrations (Taub et al., 2008; Wiser et al., 2008; Hög et al., 2009). A decrease in cereal grain quality and a reduced protein composition may have serious health and economic implications. The spatial leaf N content has a strong correlation with Rubisco content in rice leaves, suggesting their inter-dependency with net photosynthetic rates (Seneweeru, 2011). Leaf N allocation clearly declines under elevated CO$_2$, accompanied by lower chlorophyll content, as both are closely linked (Figure 1; Conroy and Hocking, 1993; Nakano et al., 1997; Ainsworth and Long, 2005; Leakey et al., 2009), also discussed in a later section. Other macro- and micro-nutrient concentrations change under elevated CO$_2$ conditions, though with lesser implications compared to N (Hög et al., 2009; Kirn et al., 2010). Potassium and phosphorous contents can increase or decrease depending upon growth conditions. Significantly lower levels of sodium, calcium, magnesium, sulfur, iron, zinc, manganese, and aluminum contents have been observed in wheat grain under elevated compared to ambient CO$_2$ (Hög and Fangmeier, 2008).

**STRATEGIES FOR IMPROVING PHOTOSYNTHETIC RATES IN C$_3$ PLANTS**
Increase in net photosynthesis per unit leaf area is important for increasing crop production to meet the world food demand. To improve photosynthesis rates in C$_3$ plants several approaches have been used, for example introducing C$_4$ like characteristics into C$_3$ cells (Kajala et al., 2011; Miyao et al., 2011; Peterhansel, 2011); introducing a CO$_2$/HCO$_3$ pump protein into chloroplast membranes from cyanobacteria (Price et al., 2008); introducing new catalytic pathways into plants that bypass the photosynthetic recycling Rubisco oxygenation product, 2-phosphoglycolate, and concomitantly releasing CO$_2$ into the stroma (Kebeish et al., 2007); and also improving the Rubisco kinetic characteristics. Some opportunities to improve photosynthetic efficiency in C$_3$ plants are discussed here.

C$_4$ photosynthesis has been identified to be evolving independently at least 66 times in 19 different families of angiosperms (Sage et al., 2011) with 21 of these lineages displaying the intermediate C$_4$/C$_3$ photosynthetic characteristics (Brown and Hattersley, 1983; Edwards et al., 2004). The evolution of C$_4$ from C$_3$ photosynthesis involves a number of intermediate steps, while the enzymes and structures present in C$_4$ plants are also present in
C₄ plants in some form (Elmeringer et al., 1991). This is advantageous for plant biologists attempting to engineer C₄ pathways in C₃ plants, through the identification of genotypes expressing some degree of cellular similarities to C₄ plants, such as high numbers of chloroplasts in the BSC, and separation of MC by only a single cell (Turban et al., 2009). Partial C₄ cycles genes have been introduced into rice, potato, and tobacco (Kajala et al., 2011) without incorporating the complete Kranz anatomy, which would require targeting multiple genes. The Kranz anatomy of C₄ plants is generally considered to be too complex to engineer into C₃ cells. However, two species of the family Chenopodiaceae were found to have a C₄ photosynthesis system contained within a single chlorenchyma cell in the absence of Kranz anatomy. The cells performed the same role as Kranz anatomy by partitioning themselves into two cyttoplasmic compartments (Edwards et al., 2004). Each of these cells performs a function analogous to the MC and BSC in Kranz anatomy, serving to concentrate C around Rubisco. This has provided hope that C₄ like photosynthesis can be introduced into C₃ plants in the absence of full Kranz anatomy. Specific genes have been suggested by Miyao (2003) in C₃ plants very similar to those in C₄, however, their expression level is very low are thought to serve housekeeping functions (Kajala et al., 2011). Overexpression of native C₃ genes or homologous C₄ genes could possibly be useful for improving photosynthetic efficiency in C₃ plants. Attempts have been made to engineer single-celled and two-celled photosynthetic pathways with expression of specific genes into rice (Kajala et al., 2011; Miyao et al., 2011). Four C₄ genes, PEPC, malate dehydrogenase (MDH), NADP-malic enzyme (NADP-ME), and NADP-malate dehydrogenase (NADP-MDH) have been engineered in rice (Tanguchi et al., 2008; Miyao et al., 2011). However, a functional C₄ cycle in leaves of C₃ species has not yet achieved. In addition, the negative effects of engineering C₄ genes in C₃ plants have been reported, such as overexpression of maize NADP-ME in rice that led to enhanced photosynthesis and plastidic effects (Tsuchida et al., 2001), stunted transgenic plants due to generation of futile cycles and improper croseration of regulation of genes (Tanguchi et al., 2008; Kajala et al., 2011). To achieve C₄ photosynthetic pathway operatively in C₃ plants is an enormous challenge and would require: careful selection and engineering of multiple genes encoding for both C₄ photosynthetic genes and transporters of C₄ metabolites, driving the optimal expression of genes, site-specific expression of selected genes such as in the MC or BSC, choice of coding sequence since C₄ genes have acquired changes in coding regions during evolutionary process, and proper regulation of C₄ enzymes (Kajala et al., 2011; Miyao et al., 2011; Peterhansel, 2011).

Cyanobacteria are a phylum of bacteria that obtain energy through photosynthesis and are the ancestors of chloroplasts in eukaryotic cells (Raven and Allen, 2003). Cyanobacteria are highly efficient for producing biomass from inorganic C (Nogales et al., 2012). As a photosynthetic organism, cyanobacteria have evolved a very efficient mechanism for converting CO₂ to Rubisco CO₂, an important step in transporting C into the chloroplast stroma. The carbon concentrating mechanism (CCM) of cyanobacteria delivers several-fold higher CO₂ to Rubisco sites compared to C₃ photosynthesis. There have been a number of attempts made to introduce CCM into C₃ plants, but so far limited progress has been made (Hibberd et al., 2008; Peterhansel et al., 2008). A cyanobacterial gene rpsG has been linked to HCO₃⁻ accumulation within cyanobacteria, and when expressed in transgenic Arabidopsis and tobacco resulted in a significant increase in photosynthetic rates (Lieman-Hurwitz et al., 2003). The expression of such genes in crop plants could lead to significant yield increases by developing a C₄-like C₃ concentration mechanism within plants currently exhibiting C₃ anatomy. Only a small subset of genes would need to be transferred to C₃ crop species, and specialized anatomy and morphology may not be required; engineering such changes is within the scope of the current genomic technology.
N. infibus (Bloom et al., 2002, 2010; McDonald et al., 2002; Luo et al., 2004; Taub and Wang, 2008).

The decrease in N content in plants grown under elevated CO2 aggravates N-limiting conditions in the following years, as plant leaves senescence and drops to the soil, thus increasing microbial immobilization of N. Due to a high C:N ratio, the availability of N to plants further declines as more N is fixed in soil microbes. Consequently, this leads to progressive N limitation in most agricultural cropping systems (Ball, 1997; Luo et al., 2004). This suggests that N supply needs to be matched with higher C assimilation under elevated CO2, requiring new N management strategies in agriculture. Legumes have the potential to respond maximally to higher CO2 due to their N-fixing capacity by overexpression of under elevated CO2, requiring new N management strategies in agriculture. Legumes have the potential to respond maximally to higher CO2 due to their N-fixing capacity. This improved N assimilation has increased photosynthetic stimulation and higher productivity in legumes compared to non-legumes under elevated CO2 (Zanetti et al., 1996; Ainsworth et al., 2002; Rogers et al., 2006). Introducing N-fixation capabilities in non-leguminous plants has always been an attractive prospect, which could close the N acquisition gap, allowing efficient CO2 capture and maximizing yield gains under elevated atmospheric CO2. Otherwise, in non-leguminous plants additional N fertilization would be required to obtain similar yield benefits, which might not be economically and environmentally feasible. Maximization of plant growth under elevated CO2 conditions without additional N application would result in yield increases at no additional cost of fertilizer or risk to the environment. There is a large opportunity to efficiently utilize the existing N supply in most agricultural soils given that most cereal crops have a NUE of less than 40%. Therefore, over 60% of soil N is lost through a combination of leaching, surface runoff, de-nitrification, volatilization, and microbial consumption. It is estimated that a 1% increase in NUE could save ~$1 billion annually. Hence, developing crop varieties with a higher NUE would minimize the loss of N, reduce environmental pollution and decrease input cost (Kant et al., 2011). NUE has been defined in several ways (Good et al., 2004); the most simple and practical is yield per unit of N available in the soil. Coordinated efforts are required to increase N uptake, assimilation, and/or remobilization efficiency for improved NUE. During vegetative growth, N uptake is dedicated to storage and assimilation into amino acids where developing leaves and shoots act as sinks for N. During reproductive development, N assimilation and remobilization becomes more prominent, and leaves and shoots act as an N source, supplying amino acids for reproductive organs.

Attempts have been made to manipulate the expression of different nitrate and ammonium transporters and assimilatory genes, mostly in model plants and some crop plants (Good et al., 2004; Kant et al., 2011). Higher or lower N contents led by overexpression or mutation of genes for N transporters have been reported in several studies in Arabidopsis (Geelen et al., 2000; De Angeli et al., 2006; Chopin et al., 2007). However, evidence of improved yield or NUE in crop plants attributed to modification of N responsive genes is limited, with little improvement in some traits. For example, transgenic wheat plants displayed enhanced N assimilation capacity by overexpression of Glutamine Synthetase (GS1; Habash et al., 2001). Overexpression of the GS1.3 gene in maize resulted in an increase of 30% kernel number (Martin et al., 2006). The limited benefits of modifications of such genes could be ascribed to (i) lack of suitable combinations of promoters and regulatory elements for specific expression of the target genes that can match with a certain growth stage, plant tissue type, or environmental conditions, and (ii) limited sink capacity in crop plants to assimilate and utilize additional N for increased growth and yield. Additional C skeleton and C assimilation would be required to expand sink capacity where surplus N can be incorporated. Overexpression of genes for N uptake, transport, and assimilation would ensure increased availability of N content and amino acids utilized for photosynthetic machinery which mainly control plant growth and development. Simultaneously, elevated atmospheric CO2 would ensure adequate C supply for enhanced plant growth. Hence, orchestrating coordinated efforts for growing C3 plants with increased NUE and better C assimilation capacity under elevated CO2 would be an effective strategy for avoiding CO2 or photosynthesis acclimation, leading to higher growth rates, yield, and quality in cereals.

CONCLUDING REMARKS

Plant growth is typically stimulated at elevated CO2, but often decreases with time, due to relaxation of photosynthesis to a lower rate under exposure to elevated CO2 over longer periods. The sustained and maximal stimulation of growth at elevated CO2 requires acquisition of additional N to maximize increased C assimilation. Coordinated efforts for increasing photosynthetic efficiency, enhancing sink capacity, and improving N uptake would potentially increase grain yield under rising atmospheric CO2. A marginal increase in crop growth and yield has been reported in several FACE experiments. Nevertheless, improving NUE and N uptake in crop plants could partially avert the limitations of both photosynthetic acclimation and reduced grain quality under elevated CO2 levels. The major private plant biotechnology companies are attempting to develop improved NUE transgenic lines in their research and development strategies. This would be an effective method and would reinforce their strategy for improved grain quality under commonly accepted climate change scenarios. In the past 15 years (1996–2010), the accumulated global land area for transgenic crops exceeded one billion hectares grown by over 15 million farmers (James, 2010). The use of genetically engineered crops has increased farmer profits, reduced herbicide and pesticide usage, and reduced chemical impact on the environment, which has mainly been achieved through single gene modifications. However, the traits of improving NUE and enhanced crop response to elevated CO2 are more complex and would require stacking of multiple modified genes. Efficient management of ammonium and nitrate application could also facilitate benefits of increased yield and sustained grain quality under forecasted atmospheric CO2 elevation. However, careful manipulations of N-responsive genes provide the greatest global advantages, since additional nitrogenous fertilizers pose undesirable economic and environmental threats.

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