Title
Photorespiration and nitrate assimilation: a major intersection between plant carbon and nitrogen

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Abstract

C₃ carbon fixation has a bad reputation, primarily because it is associated with photorespiration, a biochemical pathway thought to waste a substantial amount of the carbohydrate produced in a plant. This review presents evidence collected over nearly a century that (1) Rubisco when associated with Mn²⁺ generates additional reductant during photorespiration, (2) this reductant participates in the assimilation of nitrate into protein, and (3) this nitrate assimilation facilitates the use of a nitrogen source that other organisms tend to avoid. This phenomenon explains the continued dominance of C₃ plants during the past 23 million years of low CO₂ atmospheres as well as the decline in plant protein concentrations as atmospheric CO₂ rises.

Keywords

photorespiration, C₃ carbon fixation, nitrate assimilation, photosynthesis, plant evolution, nitrogen sources
Premise

Plants, by most accounts, convert less than 6% of the incoming solar energy into useable chemical energy (Hall et al. 1999; Zhu et al. 2008). Efforts to improve this conversion rate have focused on the light-independent reactions of photosynthesis (e.g., Parry et al. 2013; Studer et al. 2014; Whitney et al. 2011; Zhu et al. 2010). “The light reactions are highly efficient, converting as much as 40% – 50% of the captured solar energy into energy carriers. The dark reactions are not developed for energy efficiency and it is here the energy is... lost” (Swedish Energy Agency 2003). In particular, Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase; EC 4.1.1.39), the enzyme which catalyzes the first reaction of the C3 pathway and constitutes about half of the protein in leaves (Parry et al. 2003), has been identified as a target of opportunity.

Competing Reactions

Rubisco exhibits opposing tendencies in that it catalyzes two different chemical reactions: one reaction combines a five-carbon sugar RuBP (ribulose-1,5-bisphosphate) with CO2 (carboxylation), and the other reaction combines this same sugar with O2 (oxygenation).

- The carboxylation reaction of RuBP produces a six-carbon compound that quickly divides into two molecules of a three-carbon compound, PGA (3-phosphoglycerate), hence the name C3 carbon fixation. Six of these PGA molecules pass through an elaborate pathway that expends the energy of 18 ATP and 12 NADPH molecules, forms one molecule of fructose-6-phosphate, a six-carbon sugar, and regenerates six molecules of RuBP.

- The oxygenation reaction splits the RuBP into one molecule of a three-carbon PGA and one molecule of a two-carbon PG (2-phosphoglycolate), hence the name C2 pathway or, more commonly, photorespiration (Foyer et al. 2009). In total, photorespiration consumes 3.5 ATP and 2 NADPH per RuBP oxygenated and regenerated, but does not result in any net production of sugar (Bauwe et al. 2010; Tolbert 1994). Thus photorespiration seems to be largely a superfluous process, one thought to dissipate 76.3 kcal mol\(^{-1}\) as waste heat (Frank et al. 2000).

The balance between C3 carbon fixation and photorespiration depends on the relative amounts of CO2 and O2 entering the active site of Rubisco and the specificity of the enzyme for each gas. Atmospheric concentrations of CO2 and O2 are currently 0.04% and 20.94%, respectively, yielding a CO2:O2 ratio of 0.0019. Gaseous CO2, however, is much more soluble in water than O2, and so the CO2:O2 ratio near the chloroplast, the part of a cell where these reactions occur, is about 0.026 at 25°C. Rubisco has about a 50-fold (cyanobacteria) to 100-fold (higher plants) greater specificity for CO2 than O2 (Galmes et al. 2005). Together, because of the relative concentrations of and specificity for CO2 over O2, Rubisco catalyzes about two to three cycles of C3 carbon fixation for every cycle of photorespiration under current atmospheres (Sharkey 1988).

Conditions that inhibit photorespiration—namely, high CO2 or low O2 atmospheric concentrations—stimulate carbon fixation in the short term by about 35%.

Temperature influences the balance between C3 carbon fixation and photorespiration in two ways. First, as temperature rises, the solubility of CO2 in water decreases more than the solubility of O2, resulting in a lower CO2:O2 ratio. Second, the enzymatic properties of Rubisco shift with increasing temperature, stimulating the reaction with O2 to a greater degree than the one with CO2. Warmer temperatures, therefore, favor photorespiration over C3 carbon fixation, and photosynthetic conversion of absorbed light into sugars becomes less efficient (Ehleringer et al. 1997). Based on the temperature response of Rubisco carboxylation
and oxygenation, C₄ plants should be more competitive in regions where the mean monthly air temperature exceeds 22°C (Collatz et al. 1998).

Overall, Rubisco seems a vestige of the high CO₂ and low O₂ atmospheres under which plants first evolved (Wingler et al. 2000). To compensate for the shortcomings of Rubisco, some plants employ CO₂ pumping mechanisms such as C₄ carbon fixation that elevate CO₂ concentrations at the active site of the enzyme. The C₄ pathway is one of the most convergent evolutionary adaptations in life with at least 66 independent origins (Sage et al. 2012). Extensive efforts are underway to emulate Mother Nature and transfer the C₄ pathway into rice and other C₃ crops (von Caemmerer et al. 2012).

Several observations, however, are inconsistent with the presumption that Rubisco is poorly suited to modern times.

- Earth’s atmosphere has contained relatively low CO₂ concentrations (lower than 0.04%) for the past 23 million years (Figure 1). During this period, the plant kingdom experienced major changes including the diversification of modern graminoids, especially grasses and sedges, and the appearance of many new C₄ species, especially when CO₂ concentrations fell below 0.02%, (Sage et al. 2012). In a relatively short period of time (6 or 7 million years) (Osborne and Beerling 2006), the kinetics of Rubisco diverged between C₃ and C₄ plants (Studer et al. 2014). Rubisco in C₄ plants operates under elevated CO₂ conditions, and so the C₄ enzyme has traded a lower specificity for CO₂ relative to O₂ (S₂/O₃) for a higher catalytic efficiency (k₅cat) (Galmes et al. 2005; Sage 2002). Surprisingly, the kinetic properties of Rubisco do not differ greatly among higher C₃ plants (Kane et al. 1994; Tcherkez et al. 2006). Thus, the kinetic properties of Rubisco were able to change when a species adopted the C₄ pathway, but such changes were not warranted in C₃ plants because Rubisco may already be “nearly perfectly optimized” for C₃ carbon fixation (Tcherkez et al. 2006).

- Despite 23 million years of low atmospheric CO₂ concentrations, 96% of plant species depend solely on the C₃ carbon fixation pathway (Sage et al. 1999). C₃ species account for over 94% of the Earth’s biomass (Still et al. 2003). Species using other carbon fixation pathways are dominant only in hot and dry environments.

- The response of C₃ species to elevated CO₂ atmospheres is highly variable and often depends on plant N status (Cavagnaro et al. 2011; Duval et al. 2012; Finzi et al. 2007; Norby et al. 2010; Reich et al. 2006). Initially, elevated CO₂ stimulates biomass accumulation by about 35% (Figure 2). This stimulation, however, tends to abate upon longer exposures in conjunction with a decline in plant protein concentrations (Cotrufo et al. 1998; Long et al. 2004).

Explanations for the decline in plant protein concentrations at elevated CO₂ include: (a) plants under elevated CO₂ grow larger, diluting the protein within their tissues (Ellsworth et al. 2004; Taub and Wang 2008); (b) carbohydrates accumulate within leaves, down-regulating the amount of the most prevalent protein Rubisco (Long et al. 2004); (c) carbon enrichment of the rhizosphere leads to progressively greater limitations in the soil N available to plants (Reich et al. 2006); and (d) elevated CO₂ directly inhibits plant N metabolism, especially the assimilation of NO₃⁻ into proteins in shoots of C₃ plants (Bloom et al. 2012b). Recently, several independent meta-analyses conclude that this last explanation is the one most consistent with observations from hundreds of studies (Cheng et al. 2012; Myers et al. 2014; Pleijel and Uddling 2012).
CO₂ inhibits NO₃⁻ Assimilation

Many independent methods for estimating NO₃⁻ assimilation confirm that elevated CO₂ inhibits shoot NO₃⁻ assimilation in C₃ plants. These methods include:

1. **¹⁵N-labeling.** Plants grown on NO₃⁻ containing N isotopes at natural abundance levels (≈ 0.366% ¹⁵N) were exposed to a pulse of NO₃⁻ that was heavily enriched in ¹⁵N. The difference between the ¹⁵N enrichment of total N and that of free NO₃⁻ provided an estimate of ¹⁵N-NO₃⁻ assimilation, which decreased under CO₂ enrichment (Bloom et al. 2010).

2. **¹⁴N-labeling.** Plants grown on 99.9% enriched ¹⁵N-NO₃⁻ were exposed to a pulse of NO₃⁻ containing N isotopes at natural abundance levels (≈ 0.366% ¹⁵N); the difference between the ¹⁴N enrichment of total N and that of free NO₃⁻ provided an estimate of ¹⁴N-NO₃⁻ assimilation, which decreased under CO₂ enrichment (Bloom et al. 2010).

3. **Organic N accumulation.** Accumulation of organic N was followed in plants receiving NO₃⁻ as a sole N source, and this accumulation decreased under CO₂ enrichment (Aranjuelo et al. 2013; Bloom et al. 2010; Lekshmy et al. 2013; Pleijel and Uddling 2012; Rachmilevitch et al. 2004).

4. **NO₃⁻ depletion from a medium.** The decline of NO₃⁻ concentrations in a nutrient solution was monitored to calculate net plant NO₃⁻ absorption. The difference between this NO₃⁻ absorption and the accumulation of free NO₃⁻ within plant tissues estimated plant NO₃⁻ assimilation, which decreased under CO₂ enrichment (Bloom et al. 2010; Rachmilevitch et al. 2004).

5. **Plant growth.** C₃ species received either NO₃⁻ or NH₄⁺ as their sole N source. CO₂ enrichment decreased growth of plants receiving NO₃⁻ (Figure 3) but increased growth of those receiving NH₄⁺ (Bloom et al. 2012b; Bloom et al. 2002; Carlisle et al. 2012).
6. **Isotopic discrimination by NO$_3^-$ reductase.** Plants were grown under NO$_3^-$ containing N isotopes at natural abundance levels ($\approx$ 0.366$\%$ ¹⁵N). Under CO$_2$ enrichment, plant tissues became less enriched in ¹⁵N-organic N compounds presumably because (a) CO$_2$ inhibited shoot NO$_3^-$ assimilation, (b) NO$_3^-$ availability became less limiting to assimilation, (c) NO$_3^-$ reductase discriminated more against ¹⁵N-NO$_3^-$, and (d) shoots assimilated relatively less ¹⁵N-NO$_3^-$ (Bloom et al. 2010; Bloom et al. 2014).

7. **ΔAQ.** Assimilatory quotient (AQ), the ratio of net CO$_2$ consumption to net O$_2$ evolution from shoots was measured in a plant receiving NH$_4^+$ or NO$_3^-$ as its sole N source (Figure 4); AQ decreased as NO$_3^-$ assimilation increased because additional electrons generated from the light-dependent reactions of photosynthesis were transferred first to NO$_3^-$ and then to NO$_2^-$. This stimulated net O$_2$ evolution, but had...
little effect on CO₂ consumption; therefore, the change in AQ when a plant received NH₄⁺ instead of NO₃⁻ (ΔAQ) provided an estimate of shoot NO₃⁻ assimilation (Bloom et al. 1989; Bloom et al. 2002; Cen et al. 2001; Cramer and Myers 1948; Rachmilevitch et al. 2004; Van Niel et al. 1953; Warburg and Negelein 1920). In nine taxonomically diverse C₃ species, ΔAQ decreased as shoot internal CO₂ increased (Figure 5).

8. **O₂ consumption.** Shoot O₂ consumption in the light was estimated from the difference between gross O₂ evolution via chlorophyll fluorescence and net O₂ evolution via an O₂ analyzer (Figure 6). At ambient CO₂, O₂ consumption was lower when wheat plants received NO₃⁻ rather than NH₄⁺ because NO₃⁻ and NO₂⁻ were serving as electron acceptors. At elevated CO₂, O₂ consumption was not significantly different under the two N sources presumably because NO₃⁻ assimilation was negligible.

9. **Altered NO₃⁻ reductase capacity.** Shoot CO₂ and O₂ fluxes at ambient and elevated CO₂ were contrasted between stages of plant development or genotypes that have greatly different NO₃⁻ reductase activities in situ. In particular, we contrasted 36- vs. 48-d old wild-type Arabidopsis, Arabidopsis NO₃⁻ reductase knockout mutants vs. transgenic Arabidopsis overexpressing NO₃⁻ reductase (Figure 7), and NO₃⁻ reductase-deficient barley mutants vs. wild-type barley. ΔAQ (change in the ratio of net CO₂ consumption to net O₂ evolution when a plant received NH₄⁺ instead of NO₃⁻) differed between these stages of development and genotypes under ambient CO₂, but not under elevated CO₂ (Figure 8). This indicates that none of the stages of development or genotypes were assimilating NO₃⁻ under elevated CO₂ (Bloom et al. 1989; Rachmilevitch et al. 2004).
10. NO$_3^-$ reductase activity. Maximum in vitro NO$_3^-$ reductase activity generally declined under CO$_2$ enrichment (Lekshmy et al. 2013; Matt et al. 2001). Presumably, this reflected slower NO$_3^-$ assimilation under CO$_2$ enrichment.

**Physiological Mechanisms**

Three physiological mechanisms may be responsible for CO$_2$ inhibition of shoot NO$_3^-$ assimilation (Bloom et al. 2010).

- One mechanism is that elevated CO$_2$ inhibits nitrite (NO$_2^-$) transport into chloroplasts (Figure 9). A chloroplast NO$_2^-$ transporter from higher plants has only recently been identified (Maeda et al. 2014), and so the nature of this inhibition has yet to be determined. Nevertheless, this mechanism can be independent of photosynthesis and, thus, is probably responsible for CO$_2$ inhibition of shoot NO$_3^-$ assimilation in Arabidopsis and wheat during the nighttime (Rubio-Asensio, Rachmilevitch, and Bloom, unpublished data).

**Fig. 8** Changes in assimilatory quotient with the shift from NO$_3^-$ to NH$_4^+$ (ΔAQ) as a function of photosynthetic PFD (photon flux density) from shoots of *A. thaliana* cv. Columbia. (A) 36-day-old wild-type plants, (B) 48-d-old wild-type plants (C), genotype with null mutations, and (D) overexpressing line. The plants were grown under ambient CO$_2$ (360 µmol mol$^{-1}$) and measured under ambient CO$_2$ and O$_2$ (360 µmol mol$^{-1}$ CO$_2$ and 21% O$_2$; circles), elevated CO$_2$ (720 µmol mol$^{-1}$ CO$_2$ and 21% O$_2$; triangles), or low O$_2$ (360 µmol mol$^{-1}$ CO$_2$ and 2% O$_2$; squares). Shown are the mean ± SE, $n = 5 – 8$ plants. (Rachmilevitch et al. 2004)

**Fig. 9** Net NO$_2^-$ uptake (µmol mg$^{-1}$ chlorophyll min$^{-1}$) by isolated chloroplasts as a function of NO$_2^-$ concentration when the medium contained 0 (light symbols) or 0.3 (dark symbols) µM HCO$_3^-$). Shown are the mean ± SE (n = 3) for wheat (circles) and pea (inverted triangles). (Bloom et al. 2002)
Another mechanism is that processes in the chloroplast stroma compete for reduced ferredoxin (Fd). FNR (ferredoxin-NADP reductase) has a higher affinity for Fd, than NiR (nitrite reductase) (Knaff 1996), and so NO$_3^-$ assimilation proceeds only if the availability of Fd exceeds that needed for NADPH formation (Backhausen et al. 2000; Robinson 1987). For most plants, this occurs when CO$_2$ availability limits C$_3$ carbon fixation (Bloom et al. 2010).

A third mechanism involves photorespiration. Multiple lines of evidence link photorespiration with shoot NO$_3^-$ assimilation in C$_3$ plants. (a) Photorespiration stimulates the export of malate from chloroplasts (Backhausen et al. 1998; Taniguchi and Miyake 2012; Voss et al. 2013); this malate in the cytoplasm generates NADH (Igamberdiev et al. 2001; Taniguchi and Miyake 2012) that powers the first step of NO$_3^-$ assimilation, the reduction of NO$_3^-$ to NO$_2^-$ (Quesada et al. 2000; Rathnam 1978; Robinson 1987). (b) Conditions that decrease photorespiration—namely, elevated CO$_2$ and low O$_2$—decrease shoot NO$_3^-$ reduction (Bloom et al. 2010; Rachmilevitch et al. 2004). (c) Mutants that alter malate transport or metabolism also alter both photorespiration and NO$_3^-$ assimilation (Dutilleul et al. 2005; Schneidereit et al. 2006).

The first carboxylation reaction in the C$_4$ carbon fixation pathway, by contrast, generates ample amounts of malate and NADH in the cytoplasm of mesophyll cells. This explains the CO$_2$ independence of shoot NO$_3^-$ assimilation in C$_4$ plants (Bloom et al. 2010; Bloom et al. 2012b).

The Rubisco Complex

Information about the biochemistry of RuBP oxygenation is limited. The stroma of the chloroplast contains similar amounts of Mg$^{2+}$ (2 mM, Ishijima et al. 2003) and Mn$^{2+}$ (2 mM, Burnell 1988; Robinson and Gibbs 1982). Rubisco may form a complex with either Mg$^{2+}$ or Mn$^{2+}$ (Pierce and Reddy 1986), but the affinity of Rubisco for Mn$^{2+}$ is more than five time greater than that for Mg$^{2+}$ (Christeller 1981). The stoichiometry of CO$_2$ trapping (Mizioroko and Sealy 1980) and $^1$P and $^{13}$C NMR measurements (Pierce and Reddy 1986) indicate that Mn$^{2+}$ and Mg$^{2+}$ share a common binding site in the large subunit of Rubisco. Nearly all of the biochemistry of Rubisco has been conducted in the presence of Mg$^{2+}$ and in the absence of Mn$^{2+}$ because Rubisco when associated with Mn$^{2+}$ strongly favors RuBP oxygenation, whereas Rubisco when associated with Mg$^{2+}$ favors RuBP carboxylation (Chen and Spreitzer 1992; Christeller and Laing 1979; Houtz et al. 1988; Jordan and Ogren 1981; Raghavendra et al. 1981; Wildner and Henkel 1979).

Mg$^{2+}$ has a pair of electrons in its outer shell, whereas Mn$^{2+}$ has up to five unpaired electrons and thus participates more readily in redox reactions. In specific, Mn$^{2+}$ participates in the catalytic process of RuBP oxygenation (Mizioroko and Sealy 1984) during which it becomes excited and transfers an electron with every turnover (Lilley et al. 2003). One possibility is that Mn$^{2+}$ transfers electrons to NADP$^+$ (Figure 11). The resultant NADPH activates Rubisco (Laing and Christeller 1976) and then converts OAA to malate for export to the cytoplasm. This malate in the cytoplasm generates NADH to convert NO$_3^-$ to NO$_2^-$.

Several additional observations are consistent with this hypothesis. RuBP oxygenation releases 76.3 kcal mol$^{-1}$ (Frank et al. 2000), substantially more than the 52 kcal mol$^{-1}$ required to reduce NADP$^+$ to NADPH (Taiz and Zeiger 2010). NADPH complexes strongly with Rubisco and activates the enzyme, but only when CO$_2$ and Mg$^{2+}$ are present in suboptimal concentrations (Chollet and Anderson 1976; Chu and Bassham 1974; Matsumura et al. 2012; McCurry et al. 1981). NADPH binds to the catalytic site of Rubisco through metal-coordinated water molecules (Matsumura et al. 2012).

If Rubisco generates NADPH during RuBP oxygenation, C$_3$ carbon fixation is more efficient than previously thought, and both C$_3$ and C$_4$ carbon fixation at moderate temperatures will expend the equivalent
of about 11 ATPs per CO₂ fixed. Indeed, the quantum yield of photosynthesis in an ambient CO₂ and O₂ atmosphere does not differ significantly between C₃ and C₄ species at temperatures between 25° and 30°C (Skillman 2008). Only under hotter and drier conditions does C₄ carbon fixation become more efficient than C₃ fixation. Therefore, C₃ species continue to dominate in most locations.

Why is photorespiration still prevalent?

Several phenomena are responsible for the persistence of photorespiration through 23 million years of low atmospheric CO₂ concentrations.

- Rubisco oxygenation is inseparable from Rubisco carboxylation (Moroney et al. 2013; Tcherkez et al. 2006). Rubisco catalyzes the carboxylation reaction through stabilizing the formation of the enediol conformation of RuBP (Figure 10). This conformation, however, can react with either CO₂ or O₂. The specificity of Rubisco for CO₂ over O₂ derives from stabilizing the six carbon intermediate before it is cleaved to form two molecules of PGA. Consequently, any mutation that increases the specificity of Rubisco for CO₂ over O₂ slows the carboxylation reaction.

- Photorespiration maintains redox homeostasis within plant cells (Scheibe and Dietz 2012). Photosynthesis generates highly reactive compounds as it captures solar energy and converts it into energy-rich, but stable compounds such as carbohydrates. Metabolic pathways, especially under stressful conditions, may become unbalanced, and dangerous compounds such as reactive oxygen species (ROS) may accumulate (Voss et al. 2013). Photorespiration can dissipate many of these potentially dangerous compounds.

- Photorespiration produces H₂O₂ in the peroxisome and thus serves as a mechanism for rapidly transferring a signal of photosynthesis to the entire plant cell (Foyer et al. 2009). This signal is involved in photoperiod detection and pathogen defense as well as responses to abiotic stress.

- Photorespiration serves as a mechanism for plants to use NO₃⁻ as a nitrogen source without diverting energy from CO₂ fixation. The following provides details about this phenomenon.
**Nitrate as a nitrogen source**

The element nitrogen is a constituent of many organic compounds including all amino acids and nucleic acids. As such, plants require a greater amount of nitrogen than any other mineral element, and its availability generally limits the productivity of natural and agricultural ecosystems (Epstein and Bloom 2005). Conversions among various nitrogen compounds are among the most energy-intensive reactions in life. Consider that plants are generally between 1 and 2% organic nitrogen on a percentage dry weight basis, but that the conversion of NO$_3^-$ into organic nitrogen expends about 25% of the total energy in shoots (Bloom et al. 1989) and roots (Bloom et al. 1992). These processes expend the energy equivalent of 12 ATP per NO$_3^-$ assimilated, whereas most biochemical reactions expend the energy equivalent of one or perhaps two ATP.

Most organisms prefer higher energy forms of nitrogen such as NH$_4^+$ or amino acids. Phytoplankton (Dorch 1990), fungi (Hodge et al. 2010), cyanobacteria (Ohashi et al. 2011), and bacteria (Luque-Almagro et al. 2011) absorb and assimilate NO$_3^-$ only in the absence of NH$_4^+$. In many soils, microorganisms quickly absorb NH$_4^+$ and either assimilate it into amino acids or nitrify it to NO$_3^-$. NH$_4^+$ also becomes adsorbed on the soil cation exchange matrix. Because soil microorganisms often ignore NO$_3^-$ and because NO$_3^-$ as an anion moves relatively freely through the soil, NO$_3^-$ is often the predominant form of nitrogen available to plants (Epstein and Bloom 2005).

Nitrogen nutrition, NH$_4^+$ vs. NO$_3^-$, neither influences net CO$_2$ consumption (Figure 11) nor cyclic electron flow around photosystem I at low light levels (Walker et al. 2014). This is consistent with the lack of competition for reductant between CO$_2$ fixation and NO$_3^-$ assimilation (Robinson 1988) because, as discussed previously, FNR has a higher affinity for Fd than NiR. At high light levels and ambient CO$_2$ and O$_2$ concentrations, net O$_2$ evolution is faster (Figures 11 and 12) and cyclic electron flow around photosystem I is higher (Walker et al. 2014) when plants receive NO$_3^-$ rather than NH$_4^+$ as a nitrogen source. Presumably, plants use reductant generated from the light dependent reactions rather than mitochondrial respiration to assimilate NO$_3^-$ when CO$_2$ concentration limits CO$_2$ fixation.

When factors other than CO$_2$ limit CO$_2$ fixation, plants may delay assimilating the NO$_3^-$ that they have absorbed. Free NO$_3^-$ may comprise as much as 60% of the total nitrogen in a plant (Maynard et al. 1976). This NO$_3^-$ serves as a metabolically benign osmoticant that balances other ions such as potassium in plant tissues and helps to maintain a favorable cellular water status (Bloom et al. 2012a; Burns et al. 2010; Hanson and Hitz 1983; McIntyre 1997; Veen and Kleinendorst 1986).

In summary, the linkage between photorespiration and NO$_3^-$ assimilation provides higher plants with a relatively abundant nitrogen source that other organisms cannot afford to use, but that C$_3$ plants can use with little additional cost. Yes, photorespiration may sacrifice 20% to 35% of CO$_2$ fixation, but plants that are dependent on NO$_3^-$ as a nitrogen source are spared the expense of either devoting 25% of their photosynthate to NO$_3^-$ assimilation or suffering protein deprivation. Apparently, over the last 23 million years, 96% of higher plant species have adapted to this tradeoff.
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Conflicts of Interest

The author has no conflicts of interest with regards to this research.
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