Carbon Dioxide Enrichment Inhibits Nitrate Assimilation in Wheat and Arabidopsis

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resurvey of *Lacerta vivipara* revealed 14 extinct sites out of 46 (30%), which are predicted quite precisely by the model ($\chi^2 = 24.4$, $P < 0.001$). In Australia, the model pinpoints 2009 extinctions of *Liopholis slateri* ($\chi^2 = 17.8$, $P < 0.00001$) and 2009 extinctions of *Liopholis kintorei* ($\chi^2 = 3.93$, $P = 0.047$). In Africa, analysis of Gerrhosauridae and Cordylidae at 165 sites predicts <1% extinctions, and yet the model pinpoints the single extinction reported by 2009 (exact P-value = 0.006). We temper this value with extinction projections of 23% for 2009 at Malagasy Gerrhosauridae sites, which is validated by the observed 21% levels of local extinction across several lizard families in Madagascar nature reserves (*23*).

Thermoconforming lizards have been posited (*31*) to be more vulnerable to climate change relative to heliotherms. Even though $\overline{T}_b$ of thermoconformers (27.5°C ± 1.8°) is significantly less than $\overline{T}_b$ of heliotherms (33.5°C ± 1.3, $t = 2.66$, $P < 0.02$, $n = 34$ families; Table 1), PICs show that extinction risk was unrelated to thermoregulatory mode (fig. S8), but was significantly increased by low $\overline{T}_b$, low h_r, and high $\overline{T}_{max}$. The similar level of local extinctions in 2009 for Malagasy thermoconformers (21%, $n = 63$) and heliotherms [21%, $n = 34$; (*23*)] supports this view. Evolved changes in thermoregulatory mode, T_b, h_r, lay date, and habitat preference set risk as T_{max} rises, but owing to trade-offs, T_b and h_r cannot be simultaneously maximized, hence extinction risk is independent of mode (fig. S8). Moreover, extinction risk is not higher for conformers because heliotherms inhabit equatorial regions (i.e., sub-Saharan Africa) that are unavailable to thermoconformers [a factor not considered by (*31*) or other models (*10*)], and these areas are warming rapidly (Fig. 3).

Our model, based on T_b, h_r in activity during reproduction, and timing of breeding, assesses salient adaptations that affect thermal extinctions. Concordant verification of 2009 levels of local lizard extinction in North and South America, Europe, Africa, and Australia confirm that extinctions span tropical, temperate, rainforest, and desert habitats. Estimates of evolutionary rates required to keep pace with global change indicate that sustained and intense selection compromises population growth rates, precipitating extinctions. Probability of local extinction is projected to result in species extinction probabilities of 6% by 2050 and 20% by 2080 (table S8). Range shifts only trivially offset losses, because widespread species with high T_b shift to ranges of endemics, thereby accelerating their demise. Although global efforts to reduce CO_2 may avert 2080 scenarios, 2050 projections are unlikely to be avoided; deceleration in $\dot{T}_{max}$ lags atmospheric CO_2 storage by decades (*4*). Therefore, our findings indicate that lizards have already crossed a threshold for extinctions.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/328/5980/894/DC1
Materials and Methods
Figs. S1 to S9
Tables S1 to S8
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Carbon Dioxide Enrichment Inhibits Nitrate Assimilation in Wheat and *Arabidopsis*

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The concentration of carbon dioxide in Earth's atmosphere may double by the end of the 21st century. The response of higher plants to a carbon dioxide doubling often includes a decline in their nitrogen status, but the reasons for this decline have been uncertain. We used five independent methods with wheat and *Arabidopsis* to show that atmospheric carbon dioxide enrichment inhibited the assimilation of nitrate into organic nitrogen compounds. This inhibition may be largely responsible for carbon dioxide acclimation, the decrease in photosynthesis and growth of plants conducting C_3 carbon fixation after long exposures (days to years) to carbon dioxide enrichment. These results suggest that the relative availability of soil ammonium and nitrate to most plants will become increasingly important in determining their productivity as well as their quality as food.

The concentration of CO_2 in Earth's atmosphere has increased from about 280 to 390 μmol CO_2 per mol of atmosphere (μmol mol^{-1}) since 1800, and predictions are that it will reach between 530 and 970 μmol mol^{-1} by the end of the 21st century (*1*). Plants could mitigate these changes through photosynthetic conversion of atmospheric CO_2 into carbohydrates and other organic compounds, yet the potential for this mitigation remains uncertain. Photorespiration is the biochemical pathway in which the chloroplast enzyme Rubisco catalyzes the oxidation of the high-energy substrate RuBP rather than catalyzes the carboxylation of RuBP through the C_3 carbon-fixation pathway (*2*). Elevated CO_2 (or

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low O_2) atmospheric concentrations decrease rates of photorespiration and initially enhance rates of photosynthesis and growth by as much as 35% in most plants (C_3 plants). This enhancement, however, diminishes over time (days to years), a phenomenon known as CO_2 acclimation (*3*, *4*). Most studies suggest a strong link between CO_2 acclimation and plant nitrogen status [for example, (*5*)].

Nitrogen is the mineral element that organisms require in greatest quantity (*6*). The primary source of N for terrestrial plants is soil inorganic N in the forms of nitrate (NO_3^-) and ammonium (NH_4^+). Root absorption of NO_3^- and NH_4^+ from the soil and assimilation of NO_3^- and NH_4^+ into organic N compounds within plant tissues have a large influence on primary productivity. The assimilation of NO_3^- involves the sequential conversion of NO_3^- into NO_2^-, then into NH_4^+, then into glutamine, and finally into other organic N compounds. The first step of this process occurs in the cytosol, and the subsequent ones occur within chloroplasts or plastids.

Previously, we reported that atmospheric CO_2 enrichment does not stimulate the growth of wheat plants receiving NO_3^- as a sole N source to the same extent as those receiving NH_4^+ (*7*). This result, as well as gas exchange measurements of wheat and *Arabidopsis*, suggested that elevated CO_2 (or low O_2) atmospheric concentrations, which are conditions that decrease photorespiration, inhibit NO_3^- assimilation in the shoots of C_3 plants (*7*, *8*). In the present study, we assessed the influence of elevated CO_2 and sometimes low O_2 atmospheric concentrations on NO_3^- assimilation in wheat and *Arabidopsis* using several independent methods.

Our first method, NO_3^- depletion, involved growing plants under ambient CO_2 and O_2 conditions and depriving them of NO_3^- nutrition until their tissue NO_3^- contents decreased to low steady levels (*9*). The shoots of these NO_3^--depleted plants were then subjected to an ambient or elevated CO_2 atmospheric concentration and an ambient or low O_2 atmospheric concentration. The roots then received a pulse of NO_3^- in the nutrient medium. The decline of NO_3^- concentrations in the medium provided an estimate of net plant NO_3^- absorption, and the difference between this net NO_3^- absorption and the accumulation of free NO_3^- within the plants provided an estimate of plant NO_3^- assimilation (*8*).

By the NO_3^--depletion method, wheat assimilated nearly all of the NO_3^- that its roots absorbed, whereas *Arabidopsis* assimilated less than half of the NO_3^- that its roots absorbed (Fig. 1). Estimates of NO_3^- absorption via this method were slower than estimates via the isotopic methods (^{15}N and ^{14}N labeling) that are described below. The NO_3^--depletion method deprives plants of NO_3^- for several days, and this has been shown to down-regulate the expression of several NO_3^- transporters (*10*). In contrast, the isotopic methods maintain a constant NO_3^- concentration in the medium and would not alter the expression of transporters.

The NO_3^--depletion method showed that an elevated CO_2 atmospheric concentration around the shoots decreased the rate of NO_3^- assimilation (Fig. 1). A low O_2 atmospheric concentration also decreased the rate of NO_3^- assimilation, but the decrease in *Arabidopsis* was not statistically significant. By this method, as in the isotopic methods described below, NO_3^- absorption varied with elevated CO_2 and low O_2 in a pattern that was similar to NO_3^- assimilation.

Our second method for assessing NO_3^- assimilation, ^{15}N labeling, entailed growing plants under ambient CO_2 and O_2 conditions in a hydroponic medium containing 0.2 mM NO_3^- at natural abundance levels of N isotopes (≈0.366% ^{15}N). We then shifted the plants to an ambient or elevated CO_2 atmospheric concentration and an ambient or low O_2 atmospheric concentration and to a root medium containing 0.2 mM NO_3^- that was 25%-enriched in ^{15}N-NO_3^-. After a 12-hour labeling period, we analyzed the plant tissues for ^{15}N enrichment of total N and free NO_3^-; the ^{15}N enrichment of total N provided an estimate of net ^{15}N absorption, and the difference between the ^{15}N enrichment of total N and that of free NO_3^- provided an estimate of $^{15}NO_3^-$ assimilation.

According to ^{15}N labeling, wheat and *Arabidopsis* assimilated about two-thirds of the ^{15}N-NO_3^- they absorbed (Fig. 1). In wheat, net $^{15}NO_3^-$ absorption and assimilation were significantly greater under ambient CO_2 and O_2 atmospheric concentrations than under an elevated CO_2 or low O_2 concentration. In *Arabidopsis*, net $^{15}NO_3^-$ assimilation was significantly greater under an ambient CO_2 and O_2 atmospheric concentration than under an elevated CO_2 concentration.

In our third method, ^{14}N-NO_3^- labeling, we grew plants under ambient CO_2 and O_2 conditions in a hydroponic medium that contained 99.9% enriched ^{15}N-NO_3^- as the sole N source. When the wheat and *Arabidopsis* plants were about 14 and 36 days old, respectively, the shoots were exposed to an ambient or elevated CO_2 atmospheric concentration and an ambient or low O_2 atmospheric

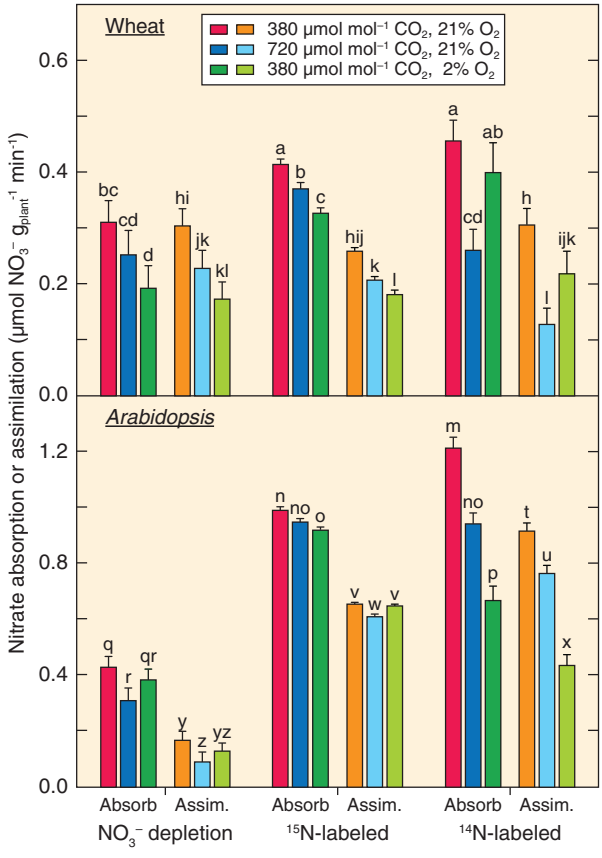

Fig. 1. Three methods for assessing nitrate absorption (Absorb) and assimilation (Assim.) in wheat and *Arabidopsis* plants where the shoots were exposed to atmospheres containing 380 µmol mol^{-1} CO_2 and 21% O_2, 720 µmol mol^{-1} CO_2 and 21% O_2, or 380 µmol mol^{-1} CO_2 and 2% O_2. Shown are means ± SE (n = 6 to 18) in µmol NO_3^- per gram plant per minute. Within a species and for absorption separately from assimilation, bars labeled with different letters differ significantly ($P < 0.05$). Data for the NO_3^- depletion method include those from an earlier study (*8*).

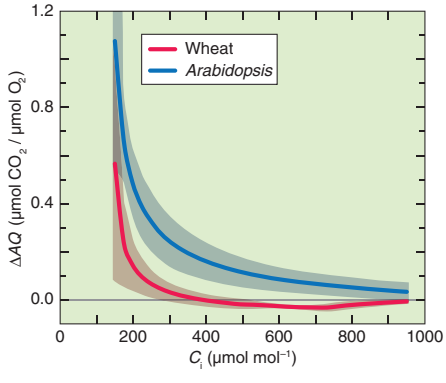

Fig. 2. The ΔAQ, the change in the ratio of shoot CO_2 consumption to O_2 evolution with a shift from NO_3^- to NH_4^+ nutrition, as a function of shoot internal CO_2 concentration (C_i) in wheat and *Arabidopsis*. An instrumental system described previously (*12*) monitored shoot gas fluxes. A biochemical model of photosynthesis (*33*, *34*), which we fitted to the data, interpolated the values at regular C_i intervals. Shown are the means ± SE (n = 8 for wheat and 4 for *Arabidopsis*).

concentration. After a few hours under these atmospheric conditions, the roots received a pulse of NO_3^- containing the isotopes at their natural abundance levels of nitrogen (99.633% ^{14}N). We estimated ^{14}N-NO_3^- absorption and assimilation from the decreases in the ^{15}N enrichment of total N and free NO_3^- in plant tissues after a 12-hour exposure to ^{14}N-NO_3^-.

Differences in atmospheric CO_2 or O_2 concentration produced distinct patterns of the ^{14}N labeling (Fig. 1). Wheat and *Arabidopsis* assimilated about two-thirds of the ^{14}N-NO_3^- they absorbed. In both species, an elevated CO_2 or low O_2 atmospheric concentration significantly decreased $^{14}NO_3^-$ assimilation.

Our fourth method for assessing NO_3^- assimilation depended on the assimilatory quotient (*AQ*), the ratio of net CO_2 consumption to net O_2 evolution from shoots during photosynthesis. Values of *AQ* decrease as NO_3^- assimilation increases, because additional electrons generated from the light-dependent reactions of photosynthesis are transferred first to NO_3^- and then to NO_2^-. This stimulates net O_2 evolution but has little effect on CO_2 consumption (*7*, *8*, *11*–*13*). The Δ*AQ*—the difference in the *AQ* between plants receiving NH_4^+ as the sole N source and those receiving NO_3^-—is strongly correlated with shoot NO_3^- assimilation. For example, Δ*AQ* did not deviate significantly from zero in plants with relatively low NO_3^- reductase activities (that is, *Arabidopsis* knockout mutants and 48-day-old wild-type *Arabidopsis*), whereas Δ*AQ* was positive in plants with significant NO_3^- reductase activities (that is, wild-type wheat, transgenic *Arabidopsis* that overexpresses NO_3^- reductase, and 36-day-old wild-type *Arabidopsis*) (*8*). Rates of photorespiration do not influence *AQ* or Δ*AQ*, because this process changes neither net CO_2 consumption nor net O_2 evolution (*2*).

During these gas-exchange measurements, we exposed the shoots of wheat and *Arabidopsis* to various atmospheric CO_2 concentrations. To account for differences in stomatal conductance, we expressed shoot CO_2 and O_2 fluxes as a function of apparent shoot internal CO_2 concentrations (C_i) that we calculated from water vapor exchange. With increasing C_i, the Δ*AQ* in both species declined from a positive value to one that was not significantly different from zero (Fig. 2), indicating that NO_3^- assimilation was significant at subambient and ambient CO_2 concentrations but was negligible at elevated CO_2 concentrations.

Our fifth method relied on the isotopic discrimination of NO_3^- reductase. When both isotopic forms of NO_3^- are readily available, this enzyme preferentially converts ^{14}N-NO_3^- into organic N compounds by about 15 per mil (‰) (*14*), and so organic N compounds in plant tissues are more depleted in ^{15}N than the N compounds in the growth medium are. In contrast, when NO_3^- availability limits assimilation, this enzyme discriminates less against ^{15}N-NO_3^- and assimilates relatively more ^{15}N-NO_3^-, and so organic N compounds in plant tissues become more enriched in ^{15}N.

We grew wheat and *Arabidopsis* for 14 and 22 days, respectively, in a medium that contained 0.2 or 1.0 mM NO_3^- ($\delta^{15}N = -4$‰) as the sole N source and under an ambient or elevated CO_2 atmospheric concentration. The difference between total plant N and free NO_3^- in the tissues provided an estimate of organic N. Wheat shoot growth did not respond to any of the treatments, whereas *Arabidopsis* shoot growth was greater at the higher NO_3^- level but did not respond to CO_2 treatment (Fig. 3). Shoot NO_3^- contents were higher in plants that were grown at the higher NO_3^- level, and shoot organic N contents decreased under CO_2 enrichment, although the decrease in wheat grown at 1.0 mM was not statistically significant (Fig. 3).

Shoot $\delta^{15}N$ of organic N (Fig. 3) and plant NO_3^- assimilation rate assessed via the isotopic methods (Fig. 1) were lower in wheat than in *Arabidopsis*. In both species, $\delta^{15}N$ of shoot organic N decreased in plants grown at the higher NO_3^- level or under CO_2 enrichment, although the decrease with CO_2 in *Arabidopsis* that was grown at 1.0 mM was not statistically significant (Fig. 3). All of these results are consistent with NO_3^- assimilation discriminating more against ^{15}N-NO_3^- when the availability of NO_3^- at the sites of NO_3^- reduction was higher, as a consequence of either slower NO_3^- assimilation in a species (wheat versus *Arabidopsis*), increased NO_3^- supply (1.0 versus 0.2 mM), or decreased NO_3^- assimilation (elevated versus ambient CO_2).

In this study, five independent methods affirm that CO_2 enrichment inhibits NO_3^- assimilation in wheat and *Arabidopsis* plants. The predominant form of N available to plants in most environments is NO_3^- (*6*); therefore, CO_2 inhibition of NO_3^- assimilation would lead to lower organic N production. Indeed, this could be responsible for the 7.4 to 11% decrease in wheat grain protein (*15*, *16*) and the 20% decrease in total protein content of *A. thaliana* (Columbia) (*17*) observed under CO_2 enrichment in FACE (free-air CO_2 enrichment) experiments. Because the influence of CO_2 enrichment on leaf organic N contents is highly correlated with its influence on photosynthesis and growth (*5*), it is reasonable to assume that CO_2 inhibition of NO_3^- assimila-

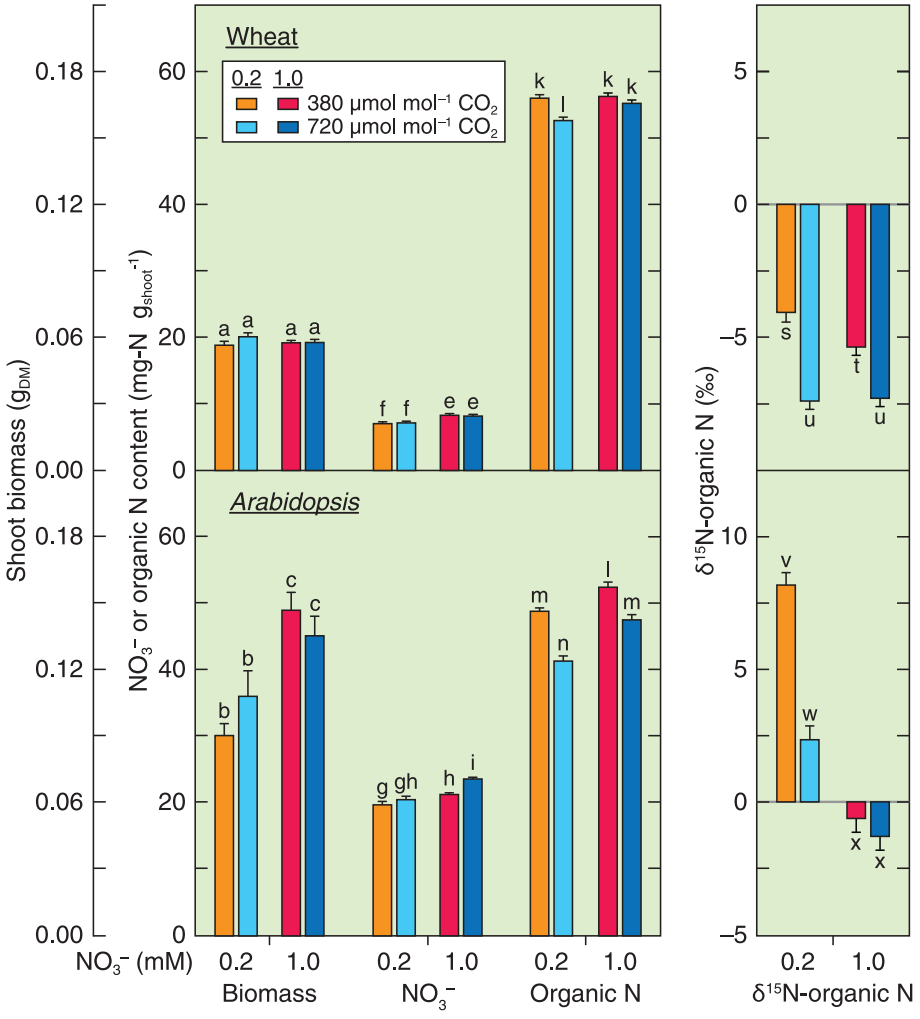

Fig. 3. Shoot biomass, NO_3^- content, organic N content, and $\delta^{15}N$ of organic N in wheat (upper panels) and *Arabidopsis* (lower panels) grown at 0.2 or 1.0 mM NO_3^- and 380 or 720 µmol mol^{-1} CO_2. Shown are means ± SE (n = 6 to 12). For each parameter, bars labeled with different letters differ significantly ($P < 0.05$).

tion and the resultant decline in plant organic N contents play a major role in the phenomenon of CO_2 acclimation, the decline of photosynthesis, and growth of C_3 plants after long exposures (days to years) to CO_2 enrichment.

The extent to which plants use NO_3^- versus NH_4^+ as N sources varies over seasons, years, locations, and species (*6*). This variation in the relative dependence on NO_3^- could explain the observed variation in CO_2 acclimation. Net primary productivity diminished under CO_2 enrichment in an annual California grassland for which NO_3^- was the predominant N source (*18*), presumably because NO_3^- assimilation was inhibited and plant organic N compounds became limiting. In contrast, *Scirpus olneyi*, the prominent C_3 plant in the Chesapeake Bay marsh, which is an NH_4^+-dominated ecosystem, showed little CO_2 acclimation. Even after a decade of treatment, photosynthesis and growth of this species remained about 35% greater under CO_2 enrichment (*19*), with little change in N contents (*20*).

Root NO_3^- absorption and plant NO_3^- assimilation were generally correlated in the N-depletion and isotopic methods, yet differences in the responses to elevated CO_2 or low O_2 atmospheric concentrations were sometimes significant for assimilation but not for absorption (Fig. 1). Moreover, CO_2 enrichment decreased shoot organic N contents, but did not change or even increased shoot NO_3^- contents (Fig. 3). CO_2 enrichment also increased ^{15}N isotope discrimination during NO_3^- assimilation (Fig. 3), indicating that NO_3^- availability became less limiting to assimilation. Finally, changes in atmospheric CO_2 concentration influenced shoot NO_3^- assimilation within minutes (time response of Fig. 2 not shown). These CO_2 changes also influenced transpiration rapidly, but root NO_3^- and NH_4^+ absorption from well-mixed hydroponic solutions is independent of transpiration (*21*). Together, these results indicate that elevated CO_2 or low O_2 atmospheric concentrations inhibited NO_3^- assimilation and that assimilation controlled root absorption, rather than elevated CO_2 or low O_2 atmospheric concentrations influencing root NO_3^- absorption directly.

One physiological mechanism that may be responsible for the relationship between elevated CO_2 or low O_2 atmospheric concentrations and NO_3^- assimilation involves the first biochemical step of NO_3^- assimilation, the conversion of NO_3^- to NO_2^- in the cytoplasm of leaf mesophyll cells. Photorespiration stimulates the export of malic acid from chloroplasts (*22*) and increases the availability of the reduced form of nicotinamide adenine dinucleotide (NADH) in the cytoplasm (*23*) that powers this first step (*24*, *25*). Elevated CO_2 or low O_2 atmospheric concentrations decrease photorespiration and thereby decrease the amount of reductant available to power NO_3^- reduction. In contrast, the C_4 carbon fixation pathway generates ample amounts of malic acid and NADH in the cytoplasm of mesophyll cells. This may explain why shoot NO_3^- assimilation is relatively independent of CO_2 concentrations in C_4 plants (*26*) and limited to the mesophyll (*27*).

Another physiological mechanism that may link NO_3^- assimilation and elevated CO_2 is NO_2^- translocation from the cytosol into the chloroplast. Six transporters of the *Narl* family are involved in NO_2^- translocation from the cytosol into the chloroplast in *Chlamydomonas*, and some of these transport both NO_2^- and HCO_3^- (*28*). We have shown that HCO_3^- inhibits NO_2^- influx into isolated wheat and pea chloroplasts (*7*), indicating that an analogous system is operating in higher plants. Slower NO_2^- influx into the chloroplast under CO_2 enrichment would decrease NO_3^- assimilation.

A third physiological mechanism linking CO_2 enrichment and NO_3^- assimilation involves competition for reductant in the chloroplast stroma. Several processes within the stroma—C_3 carbon fixation, the reduction of NO_2^- to NH_4^+, and the incorporation of NH_4^+ into amino acids—require reduced ferredoxin generated by photosynthetic electron transport. Key enzymes in these processes have different affinities for reduced ferredoxin: FNR (ferredoxin-NADP reductase) has a Michaelis constant K_m of 0.1 μM, NiR (nitrite reductase) has a K_m of 0.6 μM, and GOGAT (glutamate synthase) has a K_m of 60 μM (*29*). As a result, NO_3^- assimilation may proceed only if the availability of reduced ferredoxin exceeds that needed for the formation of the reduced form of nicotinamide adenine dinucleotide phosphate (NADPH) (*24*, *30*). For most plants, this occurs when CO_2 availability limits C_3 carbon fixation (*7*).

The phenomenon of CO_2 acclimation may have several explanations. According to the carbohydrate sink limitation hypothesis, plants under CO_2 enrichment initially assimilate more CO_2 into carbohydrates than they can incorporate into their growing tissues; in response, they diminish CO_2 assimilation by decreasing their levels of Rubisco and other proteins (*3*). An alternative explanation is the progressive N limitation hypothesis in which shoots accumulate carbohydrates faster than plants can acquire N, making leaf N contents decrease (*4*, *31*, *32*). As these leaves senesce and drop to the ground, plant litter quality declines, microbial immobilization of soil N increases because of the high C-to-N ratios in the litter, soil N availability to plants further diminishes because more soil N is tied up in microorganisms, plants become even more N limited, plant protein levels decline, and plant processes including photosynthesis and growth slow down.

Both of these hypotheses about CO_2 acclimation fit nicely into the framework of our results. The decline in Rubisco predicted by the carbohydrate sink hypothesis might derive from CO_2 inhibition of NO_3^- assimilation and the subsequent decline in plant organic N compounds (Fig. 3). The decline in leaf N contents predicted by the progressive N limitation hypothesis might derive from CO_2 inhibition of NO_3^- assimilation and the subsequent decline in plant NO_3^- absorption (Fig. 1).

Our findings have implications for food production. Nitrate is the most abundant form of N in agricultural soils (*6*). As atmospheric CO_2 concentrations rise and NO_3^- assimilation diminishes, crops will become depleted of organic N compounds (see Fig. 3), including protein, and food quality will suffer. Increasing nitrogen fertilization might compensate for slower NO_3^- assimilation rates (Fig. 3), but such fertilization rates might not be economically or environmentally feasible. Greater reliance on NH_4^+ fertilizers and inhibitors of nitrification (microbial conversion of NH_4^+ to NO_3^-) might avoid the bottleneck of NO_3^- assimilation, but would require sophisticated fertilizer management to prevent NH_4^+ toxicity, which occurs when free NH_4^+ accumulates in plant tissues if they absorb more of this compound than they can assimilate into amino acids. To address these issues, a better understanding of plant NH_4^+ and NO_3^- assimilation is critical.

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References

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Resource Management Cycles and the Sustainability of Harvested Wildlife Populations

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Constant harvest policies for fish and wildlife populations can lead to population collapse in the face of stochastic variation in population growth rates. Here, we show that weak compensatory response by resource users or managers to changing levels of resource abundance can readily induce harvest cycles that accentuate the risk of catastrophic population collapse. Dynamic system models incorporating this mix of feedback predict that cycles or quasi-cycles with decadal periodicity should commonly occur in harvested wildlife populations, with effort and quotas lagging far behind resources, whereas harvests should exhibit lags of intermediate length. Empirical data gathered from three hunted populations of white-tailed deer and moose were consistent with these predictions of both underlying behavioral causes and dynamical consequences.

One of the most central problems in ecology is what causes some harvested populations to collapse, whereas others are able to withstand exploitation (*1*–*4*)? Population collapses in many fisheries have encouraged substantial theoretical work on the challenging problem of optimal harvesting policy in response to demographic and environmental stochasticity (*1*–*8*). This has led to several sophisticated optimal harvest models supporting constant harvest mortality rates, threshold harvesting policies, or no-take reserves. Although these policies are sometimes feasible, in reality many management agencies have limited ability to control the number of resource users or harvest effort. This is particularly true of recreational harvesting, because of the open-access philosophy underlying sport fisheries and wildlife hunting. Even when harvest levels are directly set by regional managers, such control is often in the form of ad hoc quotas that vary from year to year. Modern harvesting theory is based on coupling harvest with dynamic variation in resource abundance. Here we show that weak compensatory response by harvesters or resource managers can itself generate cyclic variation in resources, exacerbating the risk of collapse. Weak harvest regulation contributes to the problem rather than providing an acceptable management solution to resource fluctuation.

To consider this issue, we developed a dynamical system model in discrete time (*9*), based on simple intuitive assumptions about human behavior, combined with mass action principles commonly applied in ecological models (*10*–*16*). The model assumes that harvesting is open access, meaning that there is no governmental restriction of harvest effort, but annual quotas are used to constrain the maximum harvest. Harvesters share information about their experiences during hunts or fishing trips, just as people talk about other important aspects of their lives. Mass action principles accordingly guide the sharing of social information, based on the probability of communication among networking members of a finite population of potential harvesters. Hence, we predict that the rate of change in effort from year to year should be a positive function of resource abundance but a negative function of current effort (*9*).

We assume that a similar mix of positive and negative feedbacks influences quota levels set by resource managers. High levels of resource abundance should encourage increasing quotas if managers are sensitive to meeting the rising expectations of harvesters, whereas declining resource levels should encourage the opposite response. Our model assumes that managers make such responses in incremental fashion, applying small percentage increases or decreases to the previous year's level in making their an-

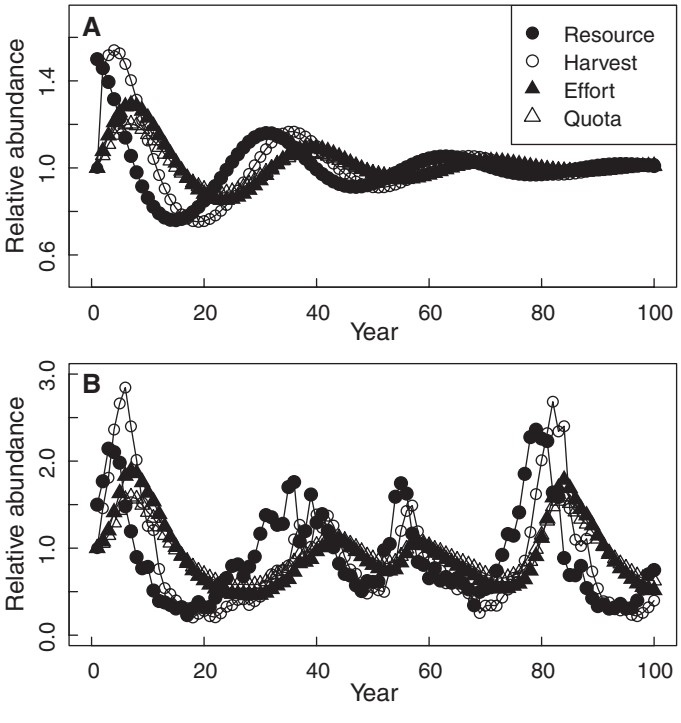

Fig. 1. Predicted time series for the proposed dynamic harvest-effort-quota system, for a locally stable set of parameters (a = 0.3, K = 4, q = 0.0001, c = –0.1, w = 0.2, u = 0.00002, f = –0.05, i = 0.15, j = 0.1) (*9*) (**A**) without any environmental stochasticity and (**B**) with the standard deviation in environmental stochasticity (ε) = 0.20. To simplify plotting on a single set of axes, variables were normalized by dividing yearly values by equilibrium values.

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