Contrasting Growth Response of N_2-Fixing and Non-N_2-Fixing Plants to Elevated CO_2 Depends on Soil N Supply

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Introduction

Rising atmospheric carbon dioxide (CO_2) concentration and increasing inputs of fixed forms of nitrogen (N) into the global N cycle are predicted to have profound effects on ecosystems. While numerous studies document the response of plants to these factors independently, fewer evaluate the combined effects of elevated CO_2 and increased soil N supply, which likely interact in complex ways and differently at different scales. Plant responses to elevated CO_2 are fundamentally mediated by photosynthesis and a suite of physiological, morphological and growth changes. Typical increases in photosynthetic rates and biomass accumulation in elevated compared to current ambient CO_2 concentrations have ranged between 20 and 50% in crops.

The variation in growth and photosynthetic enhancements under elevated CO_2 may be associated with the differential responses of species to other limiting resources such as nutrients, water, and light. Since available N already limits productivity in most ecosystems, and because tissue N is a major determinant of photosynthesis, low N may reduce potential photosynthetic rate and growth enhancements under elevated CO_2, and thus limit the ability to incorporate additional carbon. Some simulation models suggest that growth responses to elevated CO_2 concentrations are constrained by N limitation, although actual evidence is mixed. Our objective was to consider the role of symbiotic N_2 fixation in the CO_2 response and to evaluate potential interactive plant responses to elevated atmospheric CO_2 and enriched N addition by combining measures of net photosynthesis and whole-plant growth with estimates of N derived from symbiotic N_2 fixation in N_2-fixing and non-fixing species. We used plant species native to the Upper Midwest USA in this experiment.

Methods

Seeds of wild lupine and yarrow were sown in Nymore sand contained in plastic pots. Lupine was inoculated with appropriate rhizobia. Plants were grown in growth chambers programmed to mimic day length at 45˚ N latitude from May 20 until July 30, with light intensity of about 1100 mol m^{-1} s^{-1} and either 365 or 700 mg L^{-1} CO_2 . Nitrogen treatments were calculated so that additions were equivalent to rates of 0, 4, 8 12, 16, or 20 g N m^{-2} yr^{-1} based on a 12-week growing season. Applications were made every third day as a solution of ^{15}N-enriched NH_4NO_3 with ammonium and nitrate equally labeled at 5.7 atom percent ^{15}N. Initial soil pH was 5.3, Bray-extractable P was 61 mg P kg^{-1} soil, and 1*M* ammonium acetate-extractable cations were 51 mg K kg^{-1} soil, 328 mg Ca kg^{-1} soil and 50 mg Mg kg^{-1} soil. Final harvest was at 56 days after sowing when flowering began.

Results and Conclusion

Total plant biomass of lupine increased on average 80% under elevated compared to ambient CO_2 and N additions did not affect biomass at either CO_2 concentration (Fig. 1). In contrast, total plant biomass of yarrow increased faster with CO_2 enrichment under elevated than ambient N, ranging from no difference in low N soil to a 25% increase at the highest levels of N (Fig 1). Across the wide range of N additions, whole plant N concentration in lupine did not change with either CO_2 enrichment or N addition (Fig. 2). In contrast, whole plant N concentration in yarrow decreased 20% in elevated compared to ambient CO_2-grown plants and N concentration increased linerarly with increasing N addition (Fig. 2).

Importantly, the dependence of lupine on N_2 fixation increased with higher CO_2, in response to improved growth potential (Fig. 3), and this increased dependence did not disappear as inorganic N supplies increased, within the rates used here. Variations in the magnitude of this response likely correlate with the availability of other resources such as soil moisture, or levels of other nutrients like P, Mo, or Fe, which are critical for and often limit N_2 fixation. It is clear that the relationship among plant species in mixed communities, such as is found in many native plant communities, grasslands, and pastures, will change, at least in the short term under higher atmospheric CO_2.

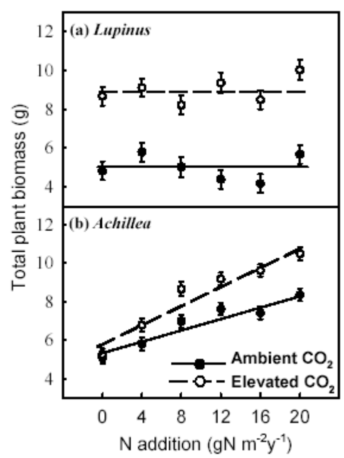

Figure 1. Response of lupine and yarrow plant biomass to increased CO_2 in the atmosphere and to available N.

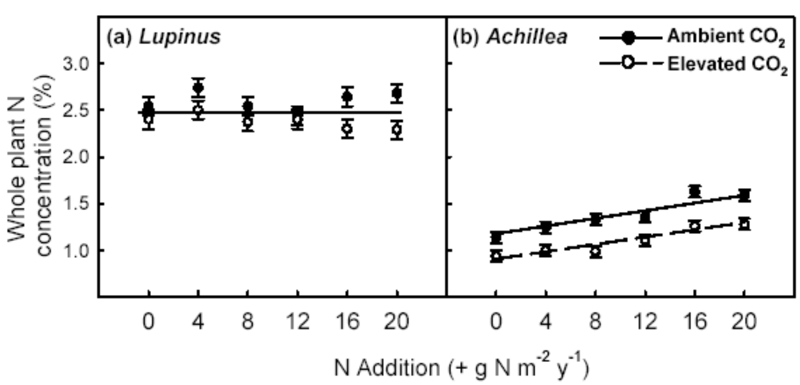

Figure 2. Response of lupine and yarrow plant N concentration to increased CO_2 in the atmosphere and to available N.

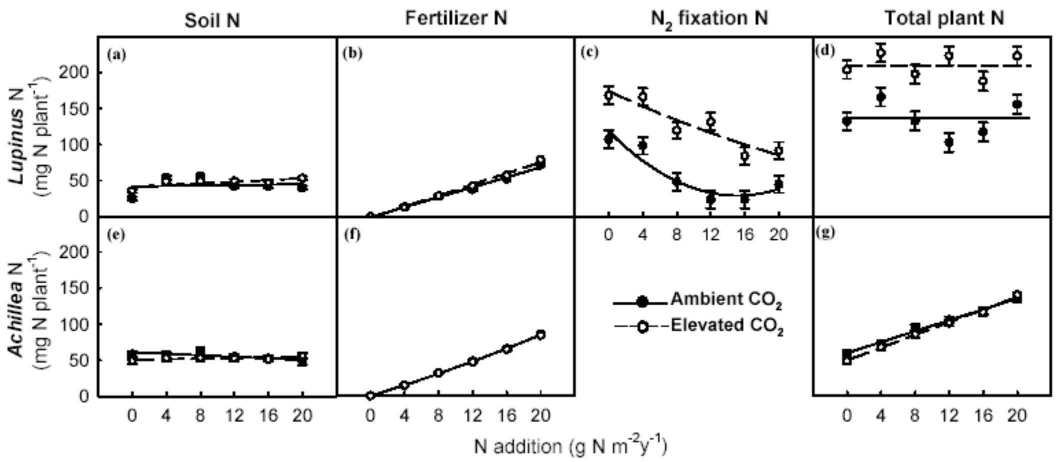

Figure 3. Sources of N in lupine and yarrow under different inorganic N supply and atmospheric CO_2 levels.

Dinitrogen Fixation in Illinois Bundleflower

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Introduction

Legumes have the potential to increase forage production and quality in warm-season pastures and to serve as an ecologically sustainable source of N. Fixed N can be transferred from legumes to companion grasses, reducing the need for application of fertilizer N. Agroecosystems dependent on legume-fixed N rather than fertilizer N tend to have improved N balances and reduced leaching losses. The use of perennial species rather than annual species provides additional benefits of reduced erosion and improved soil nutrient cycling. However, in the northern USA, warm-season grasses are not compatible with alfalfa or other cool-season legumes, due to differing biomass accumulation patterns. On the other hand, many native warm-season legumes are not persistent when grown in mixtures with grasses.

Illinois bundleflower, an herbaceous perennial legume native to the central USA as far north as Minnesota and North Dakota, may fulfill the need for a persistent, high-quality warm-season forage legume. According to preliminary work in Minnesota by Lee DeHaan towards developing varieties of Illinois bundleflower adapted to the north-central USA, northern accessions of the species produce much of their biomass between July and August, when productivity of cool-season grasses and legumes in the region is low. In addition to its value as a forage crop, Illinois bundleflower produces large yields of seeds with high protein concentration. Given the growing interest in Illinois bundleflower as a forage and grain legume, it is important to obtain information on its N_2 fixation capability.

Methods

Experiments were conducted at three Minnesota locations: at Becker on a Hubbard loamy sand, at Rosemount on a Waukegan silt loam, and at Lamberton on a Normania clay loam. Soil fertility was modified according to soil test results at each location. Three accessions of Illinois bundleflower from the University of Minnesota Perennial Native Legume collection were grown. Accessions were selected for winter survival, maturation, height, and seed yield characteristics using the data from DeHaan's evaluation of phenotypic diversity among accessions of Illinois bundleflower from the north-central USA. Wild senna [*Senna hebecarpa*], a warm-season perennial legume native to the northeastern and east-central USA, was grown as the non-N_2-fixing reference plant for use in the ^{15}N methodologies. In Minnesota, it has similar emergence times and biomass accumulation patterns to Illinois bundleflower. Seed was planted at all locations in spring 2000.

We used three methods to estimate N_2 fixation: ^{15}N natural abundance, ^{15}N isotope enrichment, and total N difference. Plants were harvested at maximum aboveground biomass, which occurs at approximately 10% seedpod fill, before significant leaf loss. Harvest dates were mid August to mid September in 2000 and 2001. We also determined nodule occupancy at each location using PCR.

Results and Conclusions

The PCR results revealed that at both Becker and Rosemount, 26 of the 30 isolates per location were derived from a single inoculant strain. In contrast, 13 of the 28 isolates from Lamberton represented multiple indigenous strains, while the others were derived from the single inoculant strain found at Becker and Rosemount. Estimated N_2 fixation was considerably higher at Lamberton than at the other locations, which suggests that the single inoculant strain that was most competitive may not provide optimal N_2 fixation rates.

Herbage yield averaged across accessions ranged from 1.0 Mg ha^{-1} to 3.7 Mg ha^{-1} in yr 1, and 3.0 Mg ha^{-1} to 8.3 Mg ha^{-1} in year 2. Accessions differed in herbage yield, aboveground N yield, and N_2 fixed at certain locations in year 1, but did not differ among the locations in year 2. Estimates of percentage of N derived from the atmosphere (%Ndfa) varied with location but not with accession in either year. Differences in N_2 fixed among accessions in year 1 were therefore due to differences in N yield rather than to %Ndfa. The ^{15}N natural abundance method gave consistently lower estimates of %Ndfa than the ^{15}N enrichment method. In year 1, N_2 fixation estimates ranged from 0 to 30 kg ha^{-1} N (^{15}N natural abundance method), 11 to 43 kg ha^{-1} (^{15}N enrichment method), and 0 to 50 kg ha^{-1} N (total N difference method), and in year 2 these estimates at two locations were 60 to 67 kg ha^{-1} N, 79 to 127 kg ha^{-1} N, and 67 to 142 kg ha^{-1} N, respectively. No N_2 was fixed in year 2 at Rosemount, possibly due to adverse weather or to S and/or Mo deficiency.

We conclude that Illinois bundleflower can produce reasonable herbage yields in southern Minnesota, provided that appropriate rhizobia are present and that nutrient supply does not limit growth.

Strategic Reductions in Nitrate Leaching Using Alfalfa
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Introduction

Long-term environmental impacts of agricultural activities on ground and surface water quality are of major concern to society. For example, high levels of nitrate (NO_3^-) loading from the Mississippi River, which drains the bulk of the agricultural area in the central USA, may be a primary contributor to the hypoxic zone appearing annually in the Gulf of Mexico. In addition, human health may be impaired by NO_3^- in drinking water.

Leaching of excess or non-utilized NO_3^- below the plant root zone depends on both soil solution NO_3^- concentration and amount of water percolation. Soil characteristics (texture, structure, depth, organic matter content) affect water percolation rates. Weather, including irrigation events in agricultural settings, interacts with crop water use to affect percolation volumes and timing.

Plant species differ in N requirements and uptake potentials, which moderates the quantity of NO_3^- available for leaching. Annual summer crops such as corn and soybean need to be reestablished yearly, and there is a relatively limited period between rapid crop growth in late spring and senescence in the late summer when available NO_3^- is absorbed by plants. Additionally, their root systems are generally shallow (<1.5 m), limiting access to only the upper portions of the soil solution. Established stands of cool-season perennial species, such as alfalfa, begin to actively absorb water and NO_3^- early in the growing season and continue later in the year than annual summer species. Because their root systems often are deeper and can access soil solution to greater depths and over a longer time than annual crops, these perennials have more opportunity to remove NO_3^- from percolating water. Our objective was to evaluate how conversion of strategically selected land to alfalfa might reduce NO_3^- leaching in Midwestern landscapes. Such conversion might also improve the profitability of dairy farming, due to reduced alfalfa hay prices.

Methods

Model simulations were made using the GLEAMS model (version 3.0) to predict NO_3^- leaching below the root zone under various management and weather conditions. Results were generalized over larger study areas using GIS software. Three study areas were selected in the Midwestern USA from Nebraska to Illinois. These areas are predominantly agricultural, where annual cropping systems, primarily corn-soybean rotation and continuous corn, dominate the landscape. The mean annual precipitation in these transects ranges from 640 mm yr^{-1} in the west (NE), where irrigation is often necessary for optimum yields, to 940 mm yr^{-1} in the east (IL), where rainfed agriculture is typical. Continuous corn and corn-soybean rotations were used in the model as the representative annual crops, and alfalfa was used as the perennial crop. Soil maps from the STATSGO database, at a mapping scale of 1:250,000, were used for extracting soil characteristics. Topology and attribute data were obtained from the USDA-NRCS Soil Survey Division. From these statewide coverages, representative transects averaging about 23,000 km^2 were delineated and displayed for this modeling simulation. Following model calibration with field data from the region, the model was applied to 40-ha sample areas in each soil type identified in each transect using 20 years of weather data (1980-1999) from the closest available station based on quadrant location within the transect.

Results and Discussion

Predicted leaching for this 20-yr precipitation record was highest under continuous corn for soils coarser than fine sandy loam (>27 kg N ha^{-1} yr^{-1}). Predicted leaching was lowest under fine-textured soils (silt loam or finer) for all crops, but lowest overall under alfalfa regardless of soil type (3 to 10 kg N ha^{-1} yr^{-1}). The predicted losses under alfalfa may be exaggerated, because we limited active rooting depth to 1.5 m in these simulations. Critical areas or "hot spots" were apparent in all three areas under annual crops, but were absent under alfalfa for the same conditions; one of the more noticeable areas was in Nebraska under continuous corn on a coarse sandy soil, where predicted losses were 30 to 40 kg N ha^{-1} yr^{-1}. Extensive leaching was predicted in select areas of Iowa and Illinois for annual crops, but with a greater extent under continuous corn, especially in Illinois with its uniformly greater precipitation. There was generally a 20 kg N $ha^{-1}yr^{-1}$ difference in predicted NO_3^- leaching losses between perennial and annual crops in Iowa and Illinois for this precipitation record.

Conversion of selected areas of annual crop in each transect (3% of the area in NE and IA, 13% for IL) to alfalfa resulted in a reduction in predicted NO_3^- leaching of between 1400 and 5600 Mg N yr^{-1} from continuous corn and between 600 and 2700 Mg N yr^{-1} from corn-soybean rotations. This reduction is partly attributable to alfalfa's deeper root system and higher N-removal capacity, and partly to the reduction in external N inputs that accompanies the transition to a crop that requires no commercial fertilizer application. A more aggressive conversion (roughly 23% for IA and IL, and 47% for NE) could reduce the predicted mass of NO_3^- losses by 6100 to 8600 Mg N yr^{-1} from continuous corn and 1300 to 3900 Mg N yr^{-1} from corn-soybean rotations.

Conclusion

Most perennial forages have limited lifespan. The land manager will need to be particularly careful to avoid NO_3^- leaching when establishing a new stand or when rotating to an annual crop. Appropriate legume N credits should be used to reduce subsequent fertilizer N applications or effective diagnostic tests (such as the pre-sidedress soil NO_3^- test) should be employed to determine the need for fertilizer N. This has proven successful in limiting NO_3^- losses during rotation from alfalfa to corn. We do not recommend that perennial forages on these sensitive sites be harvested by grazing, as the preponderance of literature shows that grazing increases the potential for NO_3^- leaching.

Questions arise about how to determine which "hot spots" should be converted to perennial crops and how to achieve the conversion. Clearly, when those soils overlay surficial drinking water aquifers or are tile drained, it is in the public interest to limit NO_3^- leaching. Motivation could be provided by persuasion, peer pressure, a subsidy to protect the public resource (such as the Conservation Security Program provides), or regulation. In any case, our research confirms work by others that the use of simulation models and GIS is a powerful tool to strategically target an environmental protection program.