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NITROGEN INTERACTIONS AND PHOTOSYNTHETIC RESPONSES TO CO_2: WORK PLAN FOR BIOCON EXPERIMENT/PHYSIOLOGICAL MEASUREMENTS AT CEDAR CREEK

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Preface:
Nitrogen plays a critical role in photosynthetic function, which in turn can affect many ecosystem processes through its effects on plant growth and ecosystem carbon cycles. As a result of its central role in photosynthetic enzymes, leaf N status can affect the magnitude of photosynthetic enhancement by elevated CO_2. It is now well-recognized that species responses to elevated CO_2 may be different when species are grown in isolation vs. in a mixed community. Part of this effect may result from effects on leaf N itself as a result of species competition for N in N-limited ecosystems, and part of the effect is simply a function of dilution of leaf nutrients in leaves with greater carbohydrates as a result of elevated CO_2. However, photosynthetic efficiency itself may be affected if N-limited plants reallocate N within leaves away from carboxylation functions under elevated CO_2 compared to ambient plants (Drake et al. 1997). Thus while there is cause to believe that there are interactive effects of N and CO_2 on species photosynthetic physiology, there is little experimental data to support or reject this idea, particularly in realistic ecosystems under field conditions.

Biotic interactions, most notably the presence of N-fixing plants, can affect ecosystem N stocks and carbon cycling via effects of N on photosynthetic function (Chapin et al. 1997, Hooper and Vitousek 1997). If photosynthetic responses of leaves and ecosystems are largely mediated through canopy N, then biotic as well as inorganic N sources will affect the magnitude of these responses. Under elevated CO_2 there is evidence from the Swiss FACE experiment that growth and photosynthetic function are most responsive to CO_2 in species mixtures including N-fixers (Hebeisin et al. 1997, Lüscher et al. 1998, S.P. Long, pers. comm.). However, in that experiment there were confounding management factors and species diversity effects *per se* could not be tested. Still, photosynthetic studies showed that CO_2-induced photosynthetic adjustments in the Swiss FACE experiment were greater under low N and in monocultures than in the mixture of grasses and the N-fixing species clover (S.P. Long, pers. comm.). Effects of species diversity and N-fixers in specific on plant CO_2 responses in interaction with N have important implications for predicting ecosystem responses to elevated CO_2 under a variety of site conditions, and may also temper management for mitigation of ecosystem CO_2 responses.

Objective: Determine Nitrogen and Biodiversity (N-fixer) effects on photosynthetic responses in interaction with elevated CO_2 in the BioCON FACE experiment.

Hypotheses:
1) The magnitude of photosynthetic responses to elevated CO_2 will vary in magnitude according to canopy N status.
2) Photosynthetic acclimation of species will be greatest for N-limited plants, and progressively lower for plants with progressively higher leaf N.
3) Species interactions with legumes will improve N status and hence the photosynthetic response to elevated CO_2.

My specific prediction is that the magnitude of the photosynthetic response to CO_2 will be greatest for C-3 plant species in high N x diversity plots followed by high N monoculture, low N x diversity+N fixer plots, and low N x diversity+N fixer plots (see Figure below).

Design:
The site is the BioCON FACE experiment (Cedar Creek Experiment E141) at the Cedar Creek Natural History Area. The overall experimental design for BioCON is described in the original proposal by Reich et al. and similar to that used in Tilman et al. (1997) except that species are grown in combinations of 1, 4, 9 and 16 species mixtures within high and low N sectors of ambient and elevated CO_2 FACE rings. The specific measurement design will involve temperature and light-controlled measurements of

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photosynthetic responses to CO_2 (A-c_i curves) for each species in a variety of plots. Each species (see list below) will be measured in monoculture stands in high and low N plots under ambient and elevated CO_2. In addition, each species will be measured in 9-species polyculture stands containing no legumes (-N fixer) or containing at least 2 species of legumes (+N fixer). Thus the overall design is 4 C-3 species x 2 CO_2 levels x 2 N levels x 3 diversity levels (monoculture, diversity-N fixer, and diversity+N fixer) x 2 to 3 reps (depending on plot type). The measurement matrix yields a total of 128 A-c_i curves to be measured. In addition, both legume species (see list below) will be measured in monoculture at high and low N and CO_2 and one legume (probably *Lespedeza*) will be also measured in the 9 species diversity +N fixer plots (16 + 12 more A-c_i curves).

Three visits will be made to the site in 1998 (May, July and Aug.) for the purpose of conducting A-c_i curve measurements and conductance measurements under the Ellsworth/TECO project. Early season perennials will be measured in May 1998 as well as some of the species with later phenology. The majority of species will be measured in July except those that show early senescence. For the projected 156 A-c_i curves anticipated to be measured in the experimental design, roughly 25 full working days will be required and at least two gas exchange systems will need to be operated simultaneously, not including equipment problems and inclement weather considerations.

A-c_i curves will be analyzed using the biochemical model of photosynthesis (Farquhar model; see Long 1991, Wullschleger 1993) to determine if adjustment of photosynthetic characteristics has occurred and the nature of these adjustments in all measured treatment combinations. Foliage will be analyzed for N concentration and SLA, and a subset of foliar samples will be run for $\delta^{13}C$ (to determine the c_i/c_a setpoint for photosynthesis) and $\delta^{15}N$ (to see if N transfer from legumes can be inferred). Data will be analyzed for effects of CO_2 on photosynthetic efficiency (initial slope of A-c_i curve as a function of N) under the treatment conditions, and for CO_2, N and legume diversity effects on total N as a determinant of photosynthesis under growth c_a and photosynthetic efficiency. The analysis of A-c_i curves as a function of the experimental treatment will yield dependencies of the initial slope (V_{cmax} from the Farquhar model) and A_{net} at a given c_a as a function of leaf N (see attached figure). To the extent that there are interactions among experimental variables, the effects of these variables on both A_{net} and N will not be additive.

LIST of species for experimentation:
Agropyron repens, C-3 grass (or *Koeleria cristata* ??)
Bromus inermis, C-3 grass

Achillea millefolium, C-3 Forb
Solidago rigida, C-3 Forb

Lespedeza capitata, Legume
Lupinus perennis, Legume

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Figure: A family of A-c_i curves for a C-3 plant in the BioCON experiment illustrating the dependence of curve parameters on leaf N, which in turn is influenced by experimental treatment (+N, +N-fixer, +CO_2 and combinations thereof).