Oecologia (2006) 149:519–525
DOI 10.1007/s00442-006-0458-4

GLOBAL CHANGE ECOLOGY

Elevated [CO_2] and increased N supply reduce leaf disease and related photosynthetic impacts on *Solidago rigida*

Joachim Strengbom · Peter B. Reich

Received: 22 June 2005 / Accepted: 3 May 2006 / Published online: 31 May 2006

Abstract To evaluate whether leaf spot disease and related effects on photosynthesis are influenced by increased nitrogen (N) input and elevated atmospheric CO_2 concentration ([CO_2]), we examined disease incidence and photosynthetic rate of *Solidago rigida* grown in monoculture under ambient or elevated (560 μmol mol^{-1}) [CO_2] and ambient or elevated (+4 g N m^{-2} $year^{-1}$) N conditions in a field experiment in Minnesota, USA. Disease incidence was lower in plots with either elevated [CO_2] or enriched N (−57 and −37%, respectively) than in plots with ambient conditions. Elevated [CO_2] had no significant effect on total plant biomass, or on photosynthetic rate, but reduced tissue%N by 13%. In contrast, N fertilization increased both biomass and total plant N by 70%, and as a consequence tissue%N was unaffected and photosynthetic rate was lower on N fertilized plants than on unfertilized plants. Regardless of treatment, photosynthetic rate was reduced on leaves with disease symptoms. On average across all treatments, asymptomatic leaf tissue on diseased leaves had 53% lower photosynthetic rate than non-diseased leaves, indicating that the negative effect from the disease extended beyond the visual lesion area. Our results show that, in this instance, indirect effects from elevated [CO_2], i.e., lower disease incidence, had a stronger effect on realized photosynthetic rate than the direct effect of higher [CO_2].

Keywords Carbon dioxide concentration · Global change · Nitrogen deposition · Photosynthesis · Plant pathogens

Communicated by Christian Körner

J. Strengbom · P. B. Reich
Department of Forest Resources,
University of Minnesota, 1530 Cleveland Ave N,
St Paul, MN 55108, USA

Present address: J. Strengbom (✉)
Evolutionary Biology Centre, Plant Ecology,
Uppsala University, 752 36 Uppsala, Sweden
e-mail: Joachim.Strengbom@ebc.uu.se

Introduction

Pathogenic fungi may have a profound impact on plant communities by influencing various ecosystem processes such as primary productivity (Mitchell 2003a) and plant community structure (Strengbom et al. 2002). Human related activities are known to increase atmospheric CO_2 concentration ([CO_2]) (Houghton et al. 2001) and the rate of nitrogen (N) deposition (Vitousek et al. 1997), which independently or in combination are likely to have large effects on structure and function in terrestrial plant communities. In the present study, we address how elevated [CO_2] and increased N supply in a field experiment in Minnesota, USA, may influence foliar disease severity (proportion leaf area diseased) and incidence (proportion of leaves diseased) on the herb *Solidago rigida*, how foliar disease influences photosynthetic rate, and if the effect from the disease on photosynthetic rate differs with level of [CO_2] and N supply. Increased knowledge of how interactions between plants and pathogens may vary with changes in these abiotic global change factors may be required to accurately predict their effects on plant ecosystem functioning and structure in the future. Although it is well established that leaf diseases

reduce the photosynthetic capacity of plants (Hibberd et al. 1996a; de Jesus et al. 2001; Lopes and Berger 2001; Erickson et al. 2003; Robert et al. 2005) and that elevated [CO_2] and increased N input may influence the photosynthetic rates of plants (Curtis 1996; Long et al. 2004), we do not know of any studies that have examined how negative effects on photosynthetic rates from pathogenic fungi are affected by simultaneous increase in [CO_2] and N supply.

Response of pathogenic fungi

Plant susceptibility to pathogenic fungi most commonly increases with increased N supply (Jarosz and Burdon 1988; Paul 1990; Nordin et al. 1998; Strengbom et al. 2002), but decreased disease incidence or severity have also been reported (Huber and Watson 1974), and the response may depend on functional type of the fungus (necrotrophic or biotrophic), and species identity of both host plant and pathogen (Hoffland et al. 2000; Mitchell et al. 2003b). Increased susceptibility may result from higher leaf [N] (Nordin et al. 1998; Strengbom et al. 2002) that, sensu Schoeneweiss (1975), predisposes the plants to higher susceptibility.

Elevated [CO_2] typically decreases leaf [N] (Cotrufo et al. 1998; Yin 2002; Ainsworth and Long 2005). Therefore, according to the N predisposition hypothesis, disease level should be lower under elevated [CO_2] than under ambient conditions. However, in an earlier study at our experimental site, Mitchell et al. (2003b) found no support for the hypothesis that elevated [CO_2] should decrease foliar diseases among C_3 plants. Negative effects from lower leaf [N] may be balanced or even overridden by a positive effect from high C availability, as fungal growth may be C limited (Manning and von Tiedemann 1995; Hoffland et al. 1999). Because the response of foliar diseases to elevated [CO_2] may be either positive or negative, it may be difficult to make a priori generalizations of the response. However, disease severity and incidence should increase under elevated [CO_2] when fungi are more limited by carbon availability than that of plant [N] and decrease under the reverse scenario.

Response of photosynthesis

Photosynthesis typically increases with increased N input or [CO_2] as these can increase the amount of either the key enzyme or the substrate of the carboxylation reaction, respectively (Curtis 1996; Long et al. 2004). Published meta analyses have found on average c. 20–30% higher photosynthetic rates of C_3 plants grown under elevated compared to ambient [CO_2] (Long et al. 2004). However, the enhancement of photosynthesis following elevated [CO_2] may be lower than expected due to downregulation of photosynthesis as a consequence of high rate of C assimilation or increased growth rate that dilute the leaf [N] (Oechel et al. 1994; Lee et al. 2001).

Foliar diseases may affect photosynthetic capacity in several ways. Besides the obvious effects of reduced photosynthetic leaf area and drainage of plant assimilates and nutrients, fungal disease may disrupt electron transportation involved in the photosynthetic apparatus and decrease the amount of photosynthetic proteins or enzymes (Scholes 1992). Leaf diseases result in moderate to substantial reductions of photosynthetic rate (Hibberd et al. 1996a; de Jesus et al. 2001; Lopes and Berger 2001; Erickson et al. 2003; Robert et al. 2005), and the negative effect from the disease often extends beyond the visual area of leaf lesions (Bastiaans 1991; Lopes and Berger 2001; Erickson et al. 2003).

Because increased N supply and elevated [CO_2] have the potential to affect the performance of pathogens (Thompson and Drake 1994; Hibberd et al. 1996b; Strengbom et al. 2002; Mitchell et al. 2003b) as well as have direct effects on the general photosynthetic capacity of a plant (Curtis 1996; Ainsworth and Long 2005; Reich et al., unpublished), elevated [CO_2] and increased N supply, independently or in combination, could have complex effects on photosynthesis. To assess how increasing atmospheric [CO_2] and increased N input may influence foliar disease and related photosynthesis of the host plant, we collected data on disease severity and incidence and measured photosynthetic rates on diseased and asymptomatic leaves of *S. rigida* grown under ambient or elevated [CO_2] and N in a free-air CO_2 enrichment experiment in Minnesota, USA.

Materials and methods

Study site and experimental design

This study was conducted within the BioCON (Biodiversity, Carbon dioxide, and Nitrogen effects on ecosystem functioning, http://www.lter.umn.edu/biocon/) experimental setup located at Cedar Creek Natural History Area in east-central Minnesota, USA (45°N, 93°W). The soils at the site are sandy and plant growth is N limited (Tilman 1987). The climate is continental with cold winters (mean January temperature −11°C) and warm summers (mean July temperature 25°C). The mean annual precipitation is 660 mm $year^{-1}$.

The BioCON experimental setup was established on secondary successional grassland in 1997 (Reich et al.

2001). The experiment consists of six circular areas (rings) with a radius of 10 m. Within each ring, there are 61 2×2 m^2 plots that were planted with 12 g seed per m^{-2} in 1997. Three of the six rings are exposed to elevated [CO_2] (560 μmol mol^{-1}) by a free-air CO_2 enrichment system (FACE), with the three remaining rings exposed to ambient [CO_2] (368 μmol mol^{-1}). CO_2 is added during daytime throughout the growing season, from early April to early November. Within each ring, half of the plots are fertilized (in May, June, and July) with NH_4NO_3 at a rate of 4 g N m^{-2} $year^{-1}$. The treatments are arranged in a full factorial design with CO_2 as between plot factor and N as within plot factor. In the present study, we used a subset of plots (monocultures of *S. rigida*) within this experiment. For the *S. rigida* plots, each treatment is replicated twice (n=2, eight plots in total).

Disease incidence and severity

In mid-June 2003, we estimated the disease incidence by scoring leaves of *S. rigida* for leaf spot diseases in each study plot. The scoring was done by randomly choosing 50 leaves per plot and classifying them (visually) as either diseased or healthy. To avoid errors introduced by leaf age, we sampled only fully expanded leaves. We took a digital photo of all diseased leaves and these images were later used to assess disease severity (proportion leaf area with visual disease symptoms, i.e., including both the visual necrotrophic and biotrophic part of the lesions). We used the UTHSCSA Image Tool program (version 3.00) to manually digitalize the leaf area and the area with visual lesions. The majority of the lesions on diseased leaves were due to infection by *Cercospora* sp. On a few leaves, we also found a few conidia of *Septoria* sp., indicating that this pathogen was also present.

Gas exchange and relative photosynthetic rate

After scoring the plot level of disease, we marked and took digital images of a number of asymptomatic and diseased leaves in each plot. We tried to avoid sampling more than one leaf per plant. The visual leaf area diseased was calculated as described above. We used these leaves to measure the in situ rates of leaf net photosynthesis by using CIRAS-1 portable infrared gas exchange systems (PP Systems, Hitchin, UK) operated in open configuration with controlled temperature, CO_2 concentration, and vapor pressure. Each leaf was measured at three occasions between 16 and 21 June 2003. All measurements were performed between 0900 and 1500 hours local time. All measurements were taken at or near light saturated conditions on sunny days and under the [CO_2] regime that the plants were grown at (365±10 or 549±10 μmol mol^{-1}). Photosynthetic rates were calculated on a leaf area basis, as A, μmol m^{-2} s^{-1}. As the cuvette (area=2.5 cm^2) of the CIRAS was centered on a non-diseased area on each leaf, our measurement of photosynthetic rate represent the photosynthetic rate per leaf area without visible signs of disease, i.e., per asymptomatic leaf area (~healthy leaf area). The average net photosynthesis over the three measurements was used as an estimate of the photosynthetic rate for an individual leaf. We also estimated the proportional reduction in photosynthesis due to leaf disease (which we call relative photosynthetic rate), by comparing the rates of diseased and asymptomatic leaves per plot (rate of diseased leaf/rate of asymptomatic leaf).

Plant biomass, N content, and chemical analyses

In each plot in August 2002 and 2003, aboveground biomass was harvested by clipping a 10×100 cm^2 strip just above the soil surface, and belowground biomass was harvested from all plots using three 5-cm-diameter cores to a depth of 20 cm. The plant material was dried to constant weight at 40–45°C. The dried biomass from each plot was ground and analyzed for total nitrogen and carbon following standard methods on a 1,500 NA Carlo–Erba element analyzer (Elan Tech., N.J., USA).

Statistical analyses

To analyze for differences in disease severity and incidence between the treatments we used ANOVA with average plot disease severity and disease incidence (arcsin transformed) as dependent variables and level of CO_2 and N as factors. CO_2 was treated as between plot factor and N as within plot factor. Differences in biomass accumulation, N accumulation and N and C concentration were analyzed by ANOVA. To test for effects of the treatments on photosynthetic rate, we also used ANOVA with the absolute photosynthetic rate for each leaf measured as dependent variable and disease status (symptomatic or asymtomatic) of the leaf, levels CO_2 and N as factors. The effect on relative photosynthetic rate was tested with ANCOVA with level of CO_2 and N as factors with disease severity as covariate. All statistical analyses was performed with SPSS for Windows (release 11.01).

Results

S. rigida grown under elevated [CO_2] (ANOVA: $F_{1,2}$=594.43, P=0.002) and increased N supply

($F_{1,2}$=24.89, P=0.038) showed lower disease incidence (proportion diseased leaves) than plants grown under ambient conditions (Fig. 1). Disease incidence was on average more than twice as high under ambient as under elevated [CO_2], whereas under increased N supply the incidence was about 30% lower compared to ambient conditions (Fig. 1). We found no interaction between the two treatments ($F_{1,2}$=0.947, P=0.433), and the effects of CO_2 and N on disease incidence were similar at both levels of the other treatment (Fig. 1). Disease severity (proportion leaf area with lesions) was on average 67% lower under elevated [CO_2] compared to ambient conditions ($F_{1,2}$=14.33, P=0.063), while increased N supply had no effect on disease severity ($F_{1,2}$=0.031, P=0.877).

The N addition treatment had a marginally significant effect on tissue [N] (ANOVA: $F_{1,4}$=4.71, P=0.096), and elevated CO_2 resulted in significantly lower (by 13%) tissue [N] ($F_{1,4}$=16.04, P=0.016) (Fig. 2). The effect on [C] from the treatments was small (<7%), and we found no significant effect from either CO_2 ($F_{1,4}$=3.61, P=0.130) or N ($F_{1,4}$=2.25, P=0.208) treatments. Moreover, we found no significant interactions between N and CO_2 treatments either on [N] or [C] ($F_{1,4}$=2.07, P=0.224 and $F_{1,4}$=1.27, P=0.322, respectively). Treatment effects on leaf nutrient concentrations and photosynthetic rates were similar on area and mass bases, as there was no effect of treatments on leaf mass per area (data not shown).

The lack of N treatment effect on tissue [N] resulted from a large stimulation (≈70%) of both biomass and of total N in these plots due to N addition (Table 1). In essence, biomass production was very limited by N availability in the ambient N treatment, and increased dry matter production matched increased N uptake very closely, such that tissue [N] did not differ among N treatments. The increase in total plant N with added N was 3.5 g N m^{-2} $year^{-1}$ in 2003 (and 3.0 g N m^{-2} $year^{-1}$ in 2002), nearly matching the annual N addition rate of 4.0 g N m^{-2} $year^{-1}$.

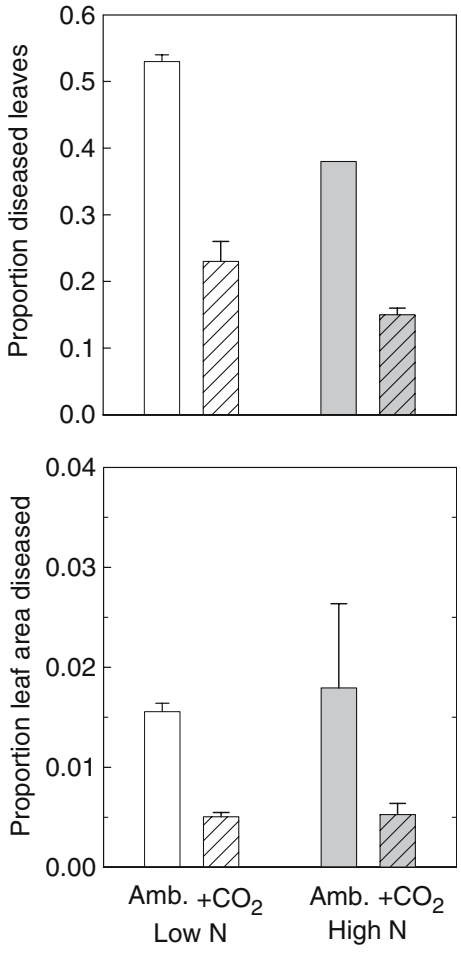

Fig. 1 Abundance of foliar disease on *S. rigida* showing the average proportion of diseased leaves (disease incidence) and the average proportion of leaf area diseased (disease severity). Plants were grown under ambient or elevated [CO_2] and N supply or a combination of both. The majority of the lesions on diseased leaves were due to infection by *Cercospora* sp. On a few leaves, we also found a few conidia of *Septoria* sp. *Error bars* represent ±SE

Overall, the absolute photosynthetic rate was lower on diseased leaves than on asymptomatic leaves (ANOVA: $F_{1,76}$=37.80, P<0.001). Since the measurements were

Table 1 Effect of N addition on biomass accumulation and plant N content and [N] in 2002 and 2003 in *Solidago* monocultures

Treatment	Year	Total biomass (g m^{-2})	Total N (g)	N concentration (mg N g^{-1})
Ambient N	2002	439.92±36.77	4.48±0.48	10.18±0.71
N fertilization[a]	2002	747.81±166.01	7.52±1.10	10.83±1.31
Ambient N	2003	517.23±63.13	5.27±0.74	10.14±0.35
N fertilization[a]	2003	880.23±158.84	8.75±0.62	10.59±1.22

In ANOVA analyses of CO_2, N, and year and their interactions, N treatment was the only significant (P<0.05) effect on biomass ($F_{1,8}$=10.18, P=0.013) and total N ($F_{1,8}$=19.29, P=0.002). Since there were no effects or interactions involving CO_2, data presented are averages pooled across CO_2 treatments±1 SE (n=4)

[a] The N fertilization treatment was 4 g N m^{-2} $year^{-1}$

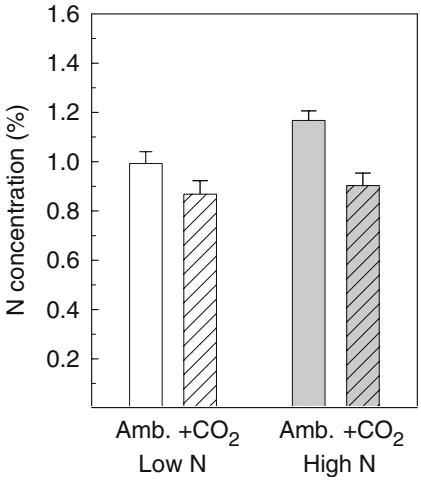

Fig. 2 Nitrogen concentration in 2003 in aboveground parts of *S. rigida* grown under ambient or elevated CO_2 and N conditions or a combination of both. *Error bars* represent ±SE

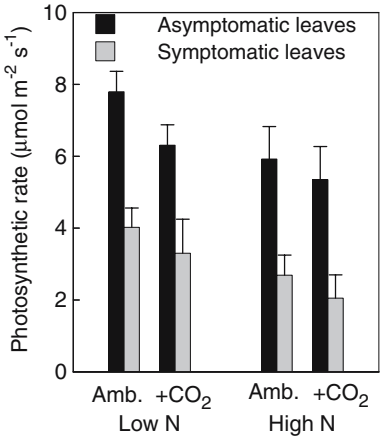

Fig. 3 Photosynthetic rates in diseased and asymtomatic leaves of *S. rigida* grown under ambient and elevated [CO_2] and N supply or a combination of both. All measurements were taken on asymptomatic leaf tissue, i.e., the values represent photosynthetic rates per asymptomatic area. *Error bars* represent ±SE

taken on asymptomatic areas of the leaves regardless of disease status, our data show that the effect of the foliar disease extends beyond the visual area of the lesions. This pattern was consistent across all treatments and asymptomatic leaf tissue on diseased leaves had on average 53% lower absolute photosynthetic rate than non-diseased leaves (Fig. 3). Moreover, the absolute photosynthetic rate was lower under elevated N conditions than under ambient N conditions for both diseased and healthy leaves ($F_{1,76}$=6.24, P=0.015) and tended to be lower under elevated [CO_2] ($F_{1,76}$=2.50, P=0.118; Fig. 3). There were no significant interactions between N and CO_2 treatments ($F_{1,76}$=0.21, P=0.646) or between disease and CO_2 and N treatments (N × disease: $F_{1,76}$=0.013, P=0.908; CO_2 × disease: $F_{1,76}$=0.11, P=0.747; N × CO_2 × disease: $F_{1,76}$=0.15, P=0.703).

When comparing the relative photosynthetic rate neither [CO_2] (ANCOVA: $F_{1,47}$=0.024, P=0.878) nor N input ($F_{1,47}$=1.10, P=0.299) had any effect (Fig. 4). This means that we found no support for the hypothesis that elevated [CO_2] or increased N input would enable plants to compensate for lost leaf tissue due to foliar diseases by higher photosynthetic rates in asymptomatic parts of the leaves.

Disease severity had a significant effect on the relative photosynthetic rate ($F_{1,47}$=5.68, P=0.021) and we found a significant negative relationship between relative photosynthetic rate and disease severity (Y=0.70–5.23X, df=51, R^2=0.092, P=0.028; Fig. 4). The negative relationship between relative photosynthetic rate and disease severity indicates that the degree of impairment increases with increasing level of disease, but as this relationship was weak (R^2=0.092) the degree of impairment of asymptomatic leaf tissue is not well correlated with disease severity, i.e., whether a leaf is diseased or not is more important for the photosynthetic rate than visually apparent disease severity.

Discussion

Our results show that both elevated [CO_2] and increased N input reduced foliar disease incidence, and therefore reduce the negative impact from disease on photosynthesis in *S. rigida*. Hence, we found no support for the hypothesis that elevated [CO_2] should favor fungal pathogens. Instead both disease incidence and severity were lower on plants grown under elevated [CO_2]. In addition, disease incidence, but not severity was also lower on N fertilized plants.

S. rigida grown under elevated [CO_2] had lower leaf [N] than plants grown under ambient [CO_2], and our results are in accordance with other studies that have found reduced pathogen performance following reduced [N] in plants grown under elevated [CO_2] (Thompson and Drake 1994). The results are, thus, also in accordance with studies that have found increased susceptibility following increased [N] of host plants (Huber and Watson 1974; Nordin et al. 1998; Strengbom et al. 2002) and may be seen as support for the N predisposition hypothesis.

Increased N input did not result in increased leaf [N], which may explain why the anticipated increase in disease did not occur. Still, it was unexpected that the disease incidence in N fertilized plots was lower than in ambient N plots. Decreased disease incidence following N fertilization has, however, been reported for several

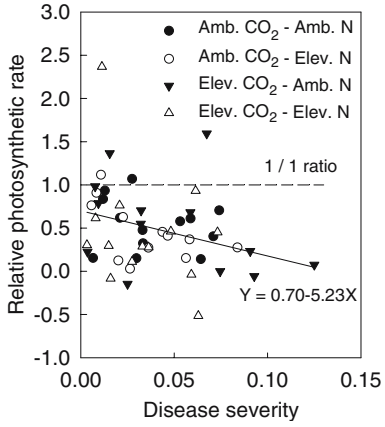

Fig. 4 Relative photosynthetic rate across all treatments in relation to disease severity. Relative photosynthetic rates were generated from the ratio between the average photosynthetic rate in asymptomatic leaves and the rate from diseased leaves under the different treatments. The *dotted line* describes the 1/1 ratio between asymptomatic and diseased leaves, i.e., no impairment of photosynthetic rate outside the visible area of the lesions and no compensatory effect in asymptomatic leaf tissue from elevated CO_2 or N conditions. The *solid line* Y=0.70 (±SE=0.11)−5.23(±2.32)X (df=51, R^2=0.092, P=0.028) describes the relationship across all treatments between relative photosynthetic rate and disease severity

fungal-crop systems (Huber and Watson 1974). Possibly increased N input may have changed the allocation pattern to various N-based compounds (e.g., amino acids, N-based secondary metabolites, etc.) and thereby altered plant susceptibility without changing the [N].

Effects on photosynthesis

The photosynthetic rate was lower under N fertilized conditions, which contradicts the general theory of plant response to increased N input (Curtis 1996). However, the consistently higher biomass accumulation and total N accumulation (+70%) in N fertilized plots suggests that plant growth at our site is strongly N limited and biomass accumulation is stimulated so much, and in essence so efficiently per unit N taken up, that the stoichiometry of C:N in these plants changes only marginally. Thus, it is not surprising that the photosynthetic rate was not increased by N addition at our site. Moreover, although leaf [N] did not change, leaf area index (LAI) increased by roughly 50% in these N fertilized plots (Reich et al., unpublished), and it is possible that *Solidago* leaves in such plots acclimated to this with a greater allocation of resources to light harvesting rather than CO_2 fixation, resulting in slightly reduced photosynthetic rate. Additionally, any mild soil water deficit that would reduce gas exchange rates would likely have a much larger effect in the high N treatment, given the almost double biomass of the plants. Although the negative response of photosynthesis to added N is unusual, *Solidago* photosynthesis was lower in added N treatment in 2 of 8 years (T. Lee and P. Reich, unpublished data) in limited annual sampling of all BioCON species.

Photosynthetic rate tended to be lower on both diseased and asymptomatic leaves grown under elevated [CO_2] and, although the reduction was not significant, it indicates that the enhancement effect on photosynthesis from elevated [CO_2] was very small or absent. From 1998 to 2005, elevated [CO_2] and ambient-grown *Solidago* plants had similar average photosynthetic rates (Lee and Reich, unpublished data), suggesting the results from the year of the current study were not unusual for this species. This contrasts with published meta analyses that have found on average c. 20–30% higher photosynthetic rates of C_3 plants grown under elevated [CO_2] (Long et al. 2004), but is consistent with the long-term weak responses for most species in the BioCON experiment (Lee et al. 2001; Lee and Reich, unpublished data).

Important to our goal of comparing direct and indirect effects on treatments on photosynthesis, we found that photosynthetic rates were substantially reduced by fungal disease and that both CO_2 and N treatments influenced the incidence of disease. Across CO_2 and N treatments, diseased leaves had only half the photosynthetic rate compared to apparently healthy leaves. Thus, we found an indirect effect from elevated [CO_2], i.e., lowering disease incidence, to be more important for photosynthesis than the direct effect from elevated [CO_2]. If our results are general, or even if elevated [CO_2] causes unpredictable but frequent effects on leaf disease that are sometimes positive and sometimes negative, it may be necessary to consider potential changes in susceptibility to foliar diseases to correctly estimate the effects on plant photosynthetic rates of elevated [CO_2].

Although both elevated [CO_2] and increased N input had direct effects on the susceptibility to disease, neither increased N supply nor elevated [CO_2] influenced the extent by which foliar disease reduced the photosynthetic rate in *S. rigida*. Hence, we found no support for the hypothesis that elevated CO_2 or N conditions would enable plants to compensate for lost leaf tissue due to foliar disease by increased photosynthetic rates in asymptomatic parts of the leaves. However, as elevated [CO_2] and increased N input did influence the photosynthetic capacity of plants by changing susceptibility to leaf spot diseases, plant diseases will likely contribute to complex multi-trophic interactive ways by which global change may influence ecosystems in the future.

Acknowledgments We would like to thank Dr. J.V. Groth for help with identification of the leaf diseases and two anonymous reviewers for valuable comments on an earlier draft of this paper. This study was financially supported by a post-doctoral fellowship from The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (to J.S.) and by grants from the US National Science Foundation (LTER: 0080382 Biocomplexity: 0322057) and Department of Energy Program for Ecological Research (Grant DE-FG02-96ER62291), and the University of Minnesota. The work presented in this paper conforms to the legal requirements of the country in which it was carried out, including those relating to conservation and welfare.

References

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. N Phytol 165:351–371

Bastiaans L (1991) Ratio between virtual and visual lesions size as a measure to describe reduction in leaf photosynthesis of rice due to leaf blast. Phytopathology 81:611–615

Cotrufo MF, Ineson P, Scott A (1998) Elevated CO_2 reduces the nitrogen concentration of plant tissues. Glob Change Biol 4:43–54

Curtis PS (1996) A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. Plant Cell Environ 19:127–137

de Jesus WC, do Vale FXR, Coelho RR, Hau B, Zambolim L, Costa LC, Bergamin A (2001) Effects of angular leaf spot and rust on yield loss of *Phaseolus vulgaris*. Phytopathology 91:1045–1053

Erickson JE, Stanosz GR, Kruger EL (2003) Photosynthetic consequences of Marssonia leaf spot differ between two poplar hybrids. N Phytol 161:577–583

Hibberd JM, Richardson P, Whitbread R, Farrar JF (1996a) Effects of leaf age, basal meristem and infection with powdery mildew on photosynthesis in barley grown in 700 μmol mol^{-1} CO_2. N Phytol 134:317–325

Hibberd JM, Whitbread R, Farrar JF (1996b) Effect of elevated concentrations of CO_2 on infection of barley *Erysiphe graminis*. Physiol Mol Plant P 48:37–53

Hoffland E, van Beusichem ML, Jeger MJ (1999) Nitrogen availability and susceptibility of tomato leaves to *Botrytis cinera*. Plant Soil 240:263–272

Hoffland E, Jeger MJ, van Beusichem ML (2000) Effect of nitrogen supply rate on disease resistance in tomato depends on the pathogen. Plant Soil 218:239–247

Houghton JT et al (2001) Climate change 2001. The scientific basis. Cambridge University Press, Cambridge

Huber DM, Watson RD (1974) Nitrogen form and plant disease. Annu Rev Phytopathol 12:139–155

Jarosz AM, Burdon JJ (1988) The effect of small-scale environmental changes on disease incidence and severity in a natural plant–pathogen interaction. Oecologia 75:278–281

Lee TD, Tjoelker MG, Ellsworth DS, Reich PB (2001) Leaf gas exchange responses of 13 prairie grassland species to elevated CO_2 and increased nitrogen supply. N Phytol 150:405–418

Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide: plants face the future. Annu Rev Plant Biol 55:591–628

Lopes DB, Berger RD (2001) The effects of rust and anthracnose on the photosynthetic competence of diseased bean leaves. Phytopathol 91:212–220

Manning WJ, von Tiedemann A (1995) Climate change: potential effects of increased atmopspheric carbon dioxide (CO_2), ozone (O_3), and ultraviolet-B (UV-B) radiation on plant diseases. Environ Pollut 88:219–245

Mitchell CE (2003a) Trophic control of grassland production and biomass by pathogens. Ecol Lett 6:147–155

Mitchell CE, Reich PB, Tilman D, Groth JV (2003b) Effects of elevated CO_2, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. Glob Change Biol 9:438–451

Nordin A, Näsholm T, Ericson L (1998) Effects of simulated N deposition on understorey vegetation of a boreal coniferous forest. Funct Ecol 12:691–699

Oechel WC et al (1994) Transient nature of CO_2 fertilization in arctic tundra. Nature 371:500–503

Paul ND (1990) Modification of the effects of plant pathogens by other components of natural ecosystems. In: Burdon JJ, Leather SR (eds) Pests, pathogens and plant communities. Blackwell, Oxford, pp 81–96

Reich PB et al (2001) Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. Nature 410:809–812

Robert C, Bancal MO, Ney B, Lannou C (2005) Wheat leaf photosynthesis loss due to leaf rust, with respect to lesion development and leaf nitrogen status. N Phytol 165:227–241

Schoeneweiss DF (1975) Predisposition, stress, and plant disease. Annu Rev Phytopathol 13:193–211

Scholes JD (1992) Photosynthesis, cellular and tissue aspects in diseased leaves. In: Ayers PG (ed) Pest and pathogens, plant responses to foliar attacks. BIOS Scientific, Oxford, UK, pp 85–106

Strengbom J, Nordin A, Näsholm T, Ericson L (2002) Parasitic fungus mediates change in nitrogen-exposed boreal forest vegetation. J Ecol 90:61–67

Thompson GB, Drake BG (1994) Insect and fungi on a C_3 sedge and a C_4 grass exposed to elevated atmospheric CO_2 concentrations in open-top chambers in the field. Plant Cell Environ 17:1161–1167

Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol Monogr 57:189–214

Vitousek PM et al (1997) Human alteration of the global nitrogen cycle, sources and consequences. Ecol Appl 7:737–750

Yin X (2002) Responses of leaf nitrogen concentration and specific leaf area to atmospheric CO_2 enrichment, a retrospective synthesis across 62 species. Glob Change Biol 8:631–642