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Combined effects of elevated CO_2 and natural climatic variation on leaf spot diseases of redbud and sweetgum trees

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Climatic variation had a greater impact than elevated CO_2 on Cercospora *diseases, especially since leaf photosynthetic efficiency increased under elevated CO_2.*

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ABSTRACT

Atmospheric CO_2 concentrations are predicted to double within the next century and alter climate regimes, yet the extent that these changes will affect plant diseases remains unclear. In this study conducted over five years, we assessed how elevated CO_2 and interannual climatic variability affect *Cercospora* leaf spot diseases of two deciduous trees. Climatic data varied considerably between the five years and altered disease expression. Disease incidence and severity for both species were greater in years with above average rainfall. In years with above average temperatures, disease incidence for *Liquidambar styraciflua* was decreased significantly. When significant changes did occur, disease incidence and severity always increased under elevated CO_2. Chlorophyll fluorescence imaging of leaves revealed that any visible increase in disease severity induced by elevated CO_2 was mitigated by higher photosynthetic efficiency in the remaining undamaged leaf tissue and in a halo surrounding lesions.

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1. Introduction

Anthropogenic emissions are drastically increasing the concentration of atmospheric CO_2 and levels are expected to double sometime in the coming decades (IPCC, 2007). Elevated CO_2 directly alters plant physiology, growth and yield (reviewed in Ainsworth et al., 2002; Drake et al., 1997; Saxe et al., 1998). Elevated CO_2 can also modify plant–pathogen interactions primarily through changes in host plants, but far fewer studies addressed these effects especially under field conditions with natural pathogen loads and ambient abiotic variability (Chakraborty et al., 2000a, 2008; Coakley et al., 1999; Manning and Tiedemann, 1995; Runion, 2003). Given that pathogens persistently reduce plant productivity in forested, agricultural and natural ecosystems worldwide (Pimentel et al., 2000), more work is needed to elucidate how plant disease will respond to the interacting factors of future climatic conditions. Understanding such relationships is vital to making predictions about overall plant and ecosystem health and for managing plants in a range of systems in the future.

Expression of plant disease for any given pathosystem requires a susceptible host, a prevalent/virulent pathogen, and favorable environmental conditions (Scholthof, 2007). Changes in environmental conditions are known to exacerbate plant disease symptoms (e.g. Boyer, 1995; McElrone et al., 2001) and are implicated in 44% of new disease emergence (Anderson et al., 2004). The rapidly increasing atmospheric [CO_2] is not only expected to modify plant–pathogen interactions (Chakraborty et al., 2000a, 2008; Garrett et al., 2006; Manning and Tiedemann, 1995), but also contribute considerably to the predicted changes in the Earth's climate over the coming decades (IPCC, 2001, 2007). According to model predictions, many regions will experience higher temperatures and

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altered precipitation patterns. Because of the importance of abiotic environmental conditions to disease expression, there is a need to evaluate disease responses to atmospheric change concurrently with the effects of altered temperature and precipitation.

In the current study, we assessed how elevated CO_2 affects *Cercospora* leaf spot diseases of *Liquidambar styraciflua* (sweetgum) and *Cercis canadensis* (redbud) saplings. Species of the genus *Cercospora* also affect numerous economically important plant species around the world including grapes, cereals, soybeans, peanuts, orchids, coffee, alfalfa and potatoes (Sinclair et al., 1987). This study was conducted at the Duke Forest Free-Air CO_2 Enrichment (FACE) experiment, and we examined disease incidence and severity for both pathosystems over a five-year period that encompassed a range of natural climatic variability. This longer term dataset allowed us to examine not only the effects of elevated CO_2 but also the interacting effects of interannual changes in temperature and precipitation.

2. Materials and methods

2.1. Field site description

The Duke FACE (Free-Air CO_2 Enrichment) experiment is located in the Blackwood Division of the Duke Forest, Orange County, NC (35°97′N 79°09′W). The site contains a loblolly pine (*Pinus taeda*) plantation established in 1983. Since then, other plant species have been allowed to establish within the plantation. The most abundant understory tree species include sweetgum (*L. styraciflua*), redbud (*C. canadensis*), red maple (*Acer rubrum*), winged elm (*Ulmus alata*), and hickory (*Carya* spp.). Additional site details are available in DeLucia et al. (1999).

Within the Duke FACE site, six 30 m-diameter circular plots (rings) were established in 1996. Each ring is equipped with thirty-two vertical pipes that extend from the forest floor through the canopy and deliver either elevated CO_2 or ambient air. Three experimental rings are fumigated with CO_2 to raise the atmospheric CO_2 concentration 200 μL L^{-1} above ambient (elevated rings, ~586 μL L^{-1} and 577 μL L^{-1} at 0.25 and 1.0 m height, respectively; Knepp et al., 2005). Three additional rings are supplied with ambient air only (~385 μL L^{-1}) and serve as controls to accommodate any effects of air movement on the vegetation (ambient rings). Climate data were collected at the Duke FACE site using relative humidity/air temperature sensors and rain gauges as in Schäfer et al. (2003). The data were provided by R. Oren. The compiled data were used to calculate cumulative precipitation and cumulative degree-days greater than 15 °C in each of the growing seasons.

2.2. Host plants and fungal pathogens

Both *L. styraciflua* (sweetgum) and *C. canadensis* (eastern redbud) are deciduous trees that grow abundantly throughout the eastern US, and are known to tolerate a variety of soils and habitats. Sweetgum is commonly found in bottomlands and can occupy the forest canopy or understory while redbud habitats commonly include the forest understory, riparian zones, open rocky woods and abandoned farmlands (Gleason and Cronquist, 1991; USDA-Natural Resources Conservation Service-Plant Guide: http://plants.usda.gov). Both species are also cultivated and used extensively in landscaped settings.

Cercospora is a large genus of ascomycete fungi, and numerous species cause disease on a variety of host plants. Most diseases caused by *Cercospora* are characterized by chlorotic to necrotic localized lesions, and occur in all temperate habitats with particular abundance in warm, humid regions such as the southeastern US (Sinclair et al., 1987). Visual surveys confirmed that sweetgum and redbud are commonly infected by *Cercospora* leaf spots throughout the Duke FACE site and the surrounding forest. The Plant Disease Clinic at North Carolina State University confirmed our initial surveys using leaf tissue samples tissue for each species, and identified the *Cercospora* species for each host. The *Cercospora* species infecting redbud and sweetgum at the Duke FACE site were identified as *Cercospora liquidambaris* Cooke & Ellis and *Cercospora cercidicola* Ellis (syn. *Passalora cercidicola*), respectively. Both pathogens are co-extensive throughout the hosts' range and occur frequently throughout the eastern and southeastern US (Wolf, 1940). Lesions of both infections typically range from 2 to 10 mm diameter and are angular to nearly round. Lesions caused by *C. liquidambaris* are dark-brown with a purplish black border and a diffuse purplish halo. The pathogen sporulates on both surfaces of the lesions, producing conidia on dark-brown stromata (Sinclair et al., 1987). *C. cercidicola* lesions are rusty-brown to dark-brown with a definite and raised border. These spots become grayish above but remain rusty-brown on the lower surface, and the tissue surrounding the lesions develops a chlorotic halo (Wolf, 1940). Conidophores are produced on both leaf surfaces and emerge through the stomata. The conidia continue to be formed throughout the entire summer whenever moisture conditions are favorable.

2.3. Disease incidence and severity assessment: digital image analysis

In all years of the study, we surveyed disease incidence and severity on even-aged sweetgum and redbud saplings planted in herbivore exclosures within the Duke FACE rings. Eight month old tree saplings were grown from seed and transplanted into eight 1.44 m^2 exclosures inside the canopy of each experimental ring in October 1998. The saplings were grown from locally collected and genetically diverse seeds of each species, were germinated in a greenhouse prior to transplanting, and were planted at 30 cm intervals in a random order (see details in Mohan, 2002).

Throughout the study, *L. styraciflua* and *C. canadensis* saplings were surveyed for disease incidence (% leaves infected) and severity (% leaf area infected and lesion area). A digital camera was used to capture images of leaves while still attached to the plants. Leaves were photographed over a contrasting paper background that contained a fine resolution scale needed for size calibration during image analysis. In each year, fully expanded leaves of both species were randomly selected from numerous saplings in multiple exclosures within each ring (between 174 and 336 leaves were sampled/analyzed for each species in each year). In some years, an unequal number of leaves were sampled in each ring due to differences in sapling survival rate among rings. In the laboratory, incidence was determined through visual inspection of the leaves. To determine disease severity (% leaf area infected, individual lesion size) leaf and lesion areas were measured for each leaf using *ASSESS: Image analysis software for plant disease quantification* (American Phytopathological Society, St. Paul, MN, USA). Percent severity was calculated as (lesion area/leaf area) × 100. Individual lesion sizes within a leaf were determined using the total lesion area and the number of lesions. Disease parameters measured on all leaves within a given ring were averaged into a single replicate ($n = 3$ rings per atmospheric treatment).

2.4. Chlorophyll fluorescence imaging

To determine how photosynthetic capacity surrounding pathogen damage was affected by CO_2 exposure, the spatial pattern of photosystem II operating efficiency (Φ_{PSII}) was quantified on *C. canadensis* leaves still attached to plants with an imaging

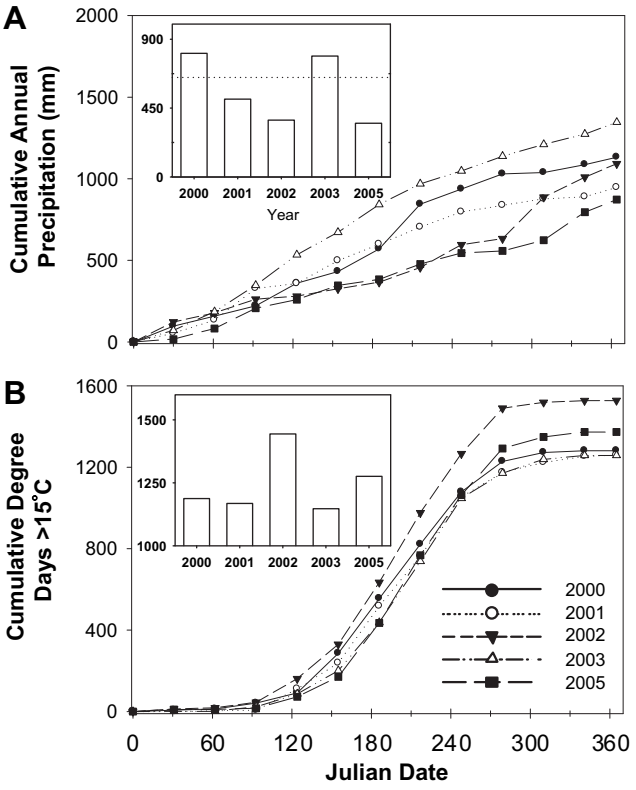

Fig. 1. Weather data collected at the Duke FACE site in Chapel Hill, NC, USA from 2000 to 2003 and 2005. Precipitation (top panel) and cumulative degree-days >15 °C (bottom panel) summed across each growing season is represented by the line and scatter plot in each panel, while the growing season (i.e. when the deciduous tree species are leaved) sum for each parameter is represented by the inset bar graph in each panel. The dashed line on the precipitation inset panel represents the mean growing season precipitation (~650 mm). The cumulative degree-day >15 °C was used as a proxy for representative seasonal temperature.