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PHYSIOLOGICAL ADJUSTMENTS OF LEAF RESPIRATION TO ATMOSPHERIC WARMING IN *BETULA ALLEGHANIENSIS* AND *QUERCUS RUBRA*

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ABSTRACT

Global air temperatures are predicted to rise 1° to 4.5° Celsius by the year 2100. This climatic change is expected to have a great effect on the succession and migration of temperate deciduous forest species. Most physiologically based models of forest response to climatic change focus on the ecosystems as a whole instead of on individual tree species, assuming that the effects of warming on respiration are generally the same for each species, and that processes can not adjust to a changing climate. Experimental data suggest that physiological adjustments are possible, but there is a lack of data in deciduous species. In order to correctly model the effects of climate change on temperate species, species-specific respiration acclimation (adjustment) to rising temperatures is being determined in this experiment. Two temperate deciduous tree species *Betula alleghaniensis* (BA) and *Quercus rubra* (QR) were grown over a span of four years in open-top chambers and subjected to two different temperature treatments; ambient and ambient plus 4° Celsius (E4). Between 0530 hours and 1100 hours, respiration was measured over a range of leaf temperatures on several comparable, fully expanded leaves in each treatment. Circular punches were taken from the leaves and dried at 60°C to determine leaf mass per area (LMA). Respiration rates at a common temperature decreased by 15-18% in both species, and the entire respiration versus temperature curve shifted by at least 4°C, indicating a large degree of physiological acclimation. Foliar mass per area decreased with increasing growth temperature for both species. It can be concluded that there is a relationship between leaf respiration and foliar mass as it relates to respiratory acclimation, and that these two species had similar patterns of adjustment to warming.

INTRODUCTION

Global air temperatures are expected to rise 1° to 4°C by the year 2100 as a result of increasing concentrations of greenhouse gases [4]. Such a change in air temperatures can have a tremendous effect on the succession and migration of temperate deciduous forest species. Most models of forest response to climatic change focus on the ecosystems as a whole instead of each individual tree species, assuming that the effects of warming on respiration are generally the same for each species, and that physiological responses can not adjust to a changing climate [2]. Although it is predicted that forest species will not be able to adjust to the increasing temperatures [5],

experimental data suggests that physiological adjustments can and do occur. Plant respiratory adaptations have been documented and reported, particularly in evergreen species, but little information is available for temperate deciduous species [2]. In order to correctly model the effects of warming on respiration, growth, and survival in temperate species, their ability to acclimate must be assessed and included in model predictions [6].

The objective of this study was to investigate the potential respiratory acclimation of two temperate deciduous trees with different geographic and climatic distributions. A broadly distributed temperate species, *Quercus rubra* (northern red oak, mean annual temperatures from 5°-16°C over its natural range) was grown

with *Betula alleghaniensis* (yellow birch), which typically grows in somewhat cooler climates (mean annual temperatures from 5°-7°C) [1,8]. Respiratory responses to increased growth temperatures and differences in foliar mass per area for each species were determined. It is hypothesized that leaf respiration will decrease with an increase in growth temperatures, thus moderating the impacts of warming on respiratory CO₂ losses. Likewise, it is hypothesized that foliar mass per area will decrease with an increase in growth temperatures, as respiration is often correlated with mass and nitrogen (N) content [7,9].

MATERIALS AND METHODS

Plant Material and Growth Conditions

Bare root seedlings were planted directly in the ground in open-top chambers (OTCs) at the Global Change Field Research Site on the Oak Ridge National Environment Research Park in the spring of 2002. Seedlings were maintained in naturally varying rainfall, day length, and sunlight. Additional watering was provided in the summer of 2002 to ensure seedling establishment. The trees were grown in three blocks and subjected to two temperature treatments: ambient and ambient + 4°C (E4). Each block contained one ambient treatment and one E4 treatment chamber. Chamber temperatures were maintained by a combination of evaporative coolers through spring, summer, and fall months and electrical resistance heaters throughout all months.

Plants of *Quercus rubra* and *Betula alleghaniensis* were purchased as one year old bare root seedlings from commercial nurseries. The seedlings were grown with two other temperate species, *Liquidambar styraciflua* and *Populus grandidentata*, within the chamber. The trees were positioned so that all trees would potentially receive the same amount of rain and sunlight. *Q. rubra* and *B. alleghaniensis* grew in the southeast and southwest quadrant respectively.

Gas Exchange and Leaf Properties

Two comparable, fully expanded leaves were chosen from two trees of each species in each chamber and marked with flagging tape for easy recognition in the dark. Between 0530 hours and 1100 hours, respiration was measured using a LI-6400 portable photosynthesis system (LI-COR INC. Lincoln, NE) on marked leaves in a darkened 2cm by 3cm cuvette over a range of leaf temperatures. Starting block temperature was, on average, 6°C below ambient outside air temperature. Block temperatures were increased by 2.5°C to cover a span of 14°C from the starting block temperature. Five measurements were taken at each block temperature using an auto program with a minimum wait time of 0.6 minutes, a maximum wait time of 4 minutes, and a maximum coefficient of variance of 0.3%. CO₂ concentration for the measurements was set at 450 ppm based on nighttime CO₂ concentrations at the site, and flow rate at 400 μmol s⁻¹.

Average respiration and leaf temperature were calculated for each block temperature and used to determine the temperature responses of each leaf. Exponential respiration curves were linearized by taking log₁₀ of the respiration rate in order to calculate slope and

intercept values for each leaf and generate an average equation for each treatment.

After respiration measurements were completed, leaf chlorophyll content was estimated using a Minolta SPAD 502, taking the average of four readings per leaf. Arbitrary SPAD units are strongly correlated with area based chlorophyll content (chlorophyll mg cm⁻² = 0.885 x SPAD - 3.5614 for these species, data not shown) and are used to estimate leaf N in agricultural applications. Several 6.38 mm diameter punches were taken from each measured leaf. The punches were dried at 60°C for 2-4 days. Once dry, the punches were weighed using a digital top loading balance to determine leaf mass per area (LMA). The remainder of the leaf was freeze-dried for later biochemical analyses.

RESULTS

Respiration rates increased exponentially with temperature in each treatment (Fig. 1), but respiration rates in the E4 treatment

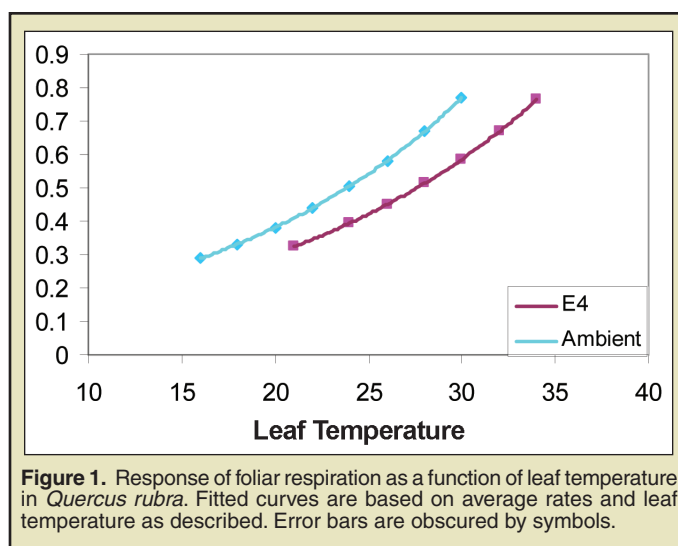


Figure 1. Response of foliar respiration as a function of leaf temperature in *Quercus rubra*. Fitted curves are based on average rates and leaf temperature as described. Error bars are obscured by symbols.

were shifted to the right by 4°C relative to the ambient treatment. Respiration rates in *Q. rubra*, measured at a common temperature (25°C), decreased by as much as 0.1 μmol m⁻²s⁻¹ from the ambient treatment to the E4 treatment as represented in Figure 2. The mean

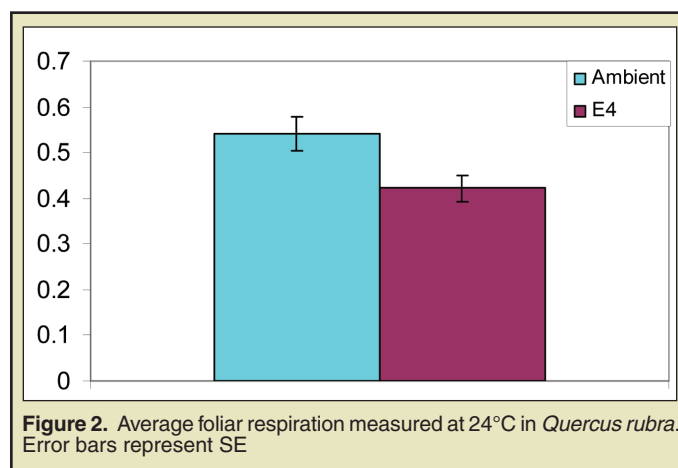
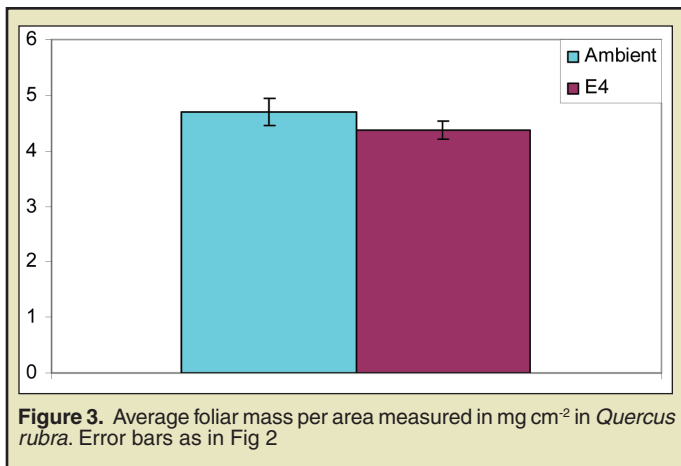


Figure 2. Average foliar respiration measured at 24°C in *Quercus rubra*. Error bars represent SE

respiration rate for the ambient treatment at 25°C was $0.51 \mu\text{mol m}^{-2}\text{s}^{-1} \pm 0.037$. The mean respiration rate for the E4 treatment was $0.42 \mu\text{mol m}^{-2}\text{s}^{-1} \pm 0.028$. Figure 3 shows a decrease of 0.326 mg cm^{-2} in foliar LMA between treatments. The LMA for the ambient



treatment was found to be $4.70 \text{ mg cm}^{-2} \pm 0.255$, and the LMA for the E4 treatment was $4.37 \text{ mg cm}^{-2} \pm 0.173$. Mean leaf chlorophyll content of *Q. rubra* leaves was 33.27 ± 2.32 for the ambient treatment and 33.08 ± 2.06 for the E4 treatment, in SPAD units. However, there was no significant difference ($P=0.7$) in the average leaf chlorophyll content between treatments.

Respiration rates increased exponentially with temperature in each treatment (Fig. 4), but respiration rates in the E4 treatment

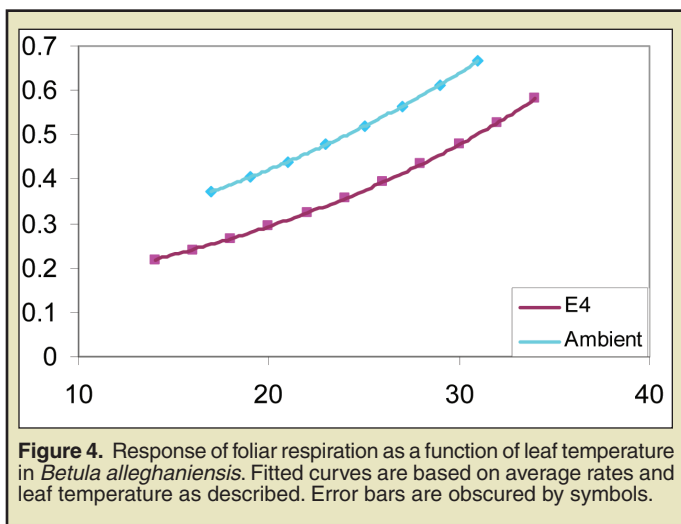


Figure 4. Response of foliar respiration as a function of leaf temperature in *Betula alleghaniensis*. Fitted curves are based on average rates and leaf temperature as described. Error bars are obscured by symbols.

were shifted to the right by 6°C relative to the ambient treatment. Similar to *Q. rubra*, respiration rates in *B. alleghaniensis* measured at 22°C decreased by as much as $0.1 \mu\text{mol m}^{-2}\text{s}^{-1}$ from the ambient treatment to the E4 treatment, as represented in Figure 5. The mean respiration rate for the ambient treatment was $0.46 \mu\text{mol m}^{-2}\text{s}^{-1} \pm 0.026$. The mean respiration rate for the E4 treatment was lower; $0.39 \mu\text{mol m}^{-2}\text{s}^{-1} \pm 0.054$. Foliar LMA decreased by 0.618 mg cm^{-2} in the E4 treatment (Fig. 6). The LMA for the ambient treatment was $5.49 \text{ mg cm}^{-2} \pm 0.230$, and the LMA for the E4 treatment was

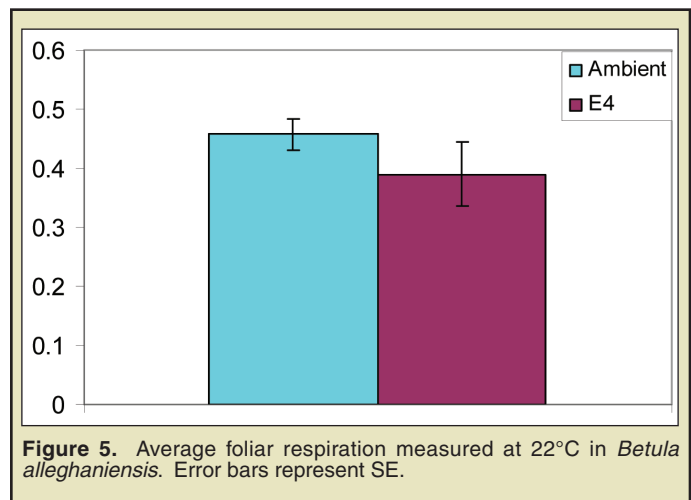


Figure 5. Average foliar respiration measured at 22°C in *Betula alleghaniensis*. Error bars represent SE.

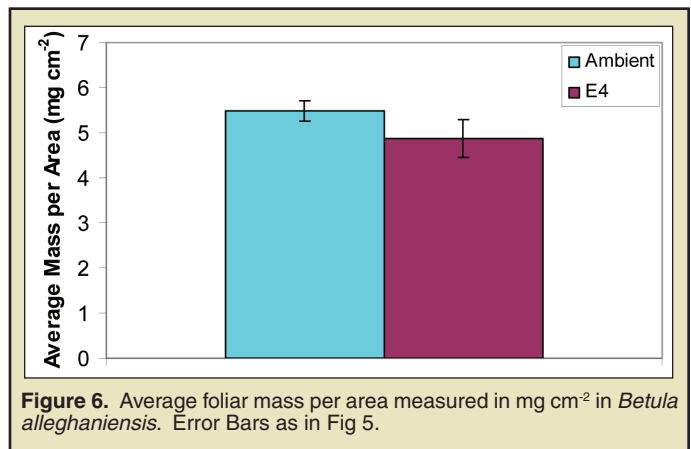


Figure 6. Average foliar mass per area measured in mg cm^{-2} in *Betula alleghaniensis*. Error Bars as in Fig 5.

$4.87 \text{ mg cm}^{-2} \pm 0.420$. Leaf chlorophyll for *B. alleghaniensis* was 31.6 ± 2.439 for the ambient treatment and 33.6 ± 5.019 for the E4 treatment. However, there was no significant difference ($P=0.48$) in the average leaf chlorophyll content between treatments.

DISCUSSION AND CONCLUSIONS

In *Q. rubra*, respiration at 24° was 17.6% lower in E4 leaves than in ambient leaves ($P=0.026$) on an area basis, in $\mu\text{mol m}^{-2}\text{s}^{-1}$, suggesting that models based on ambient leaf responses would overestimate respiratory losses. LMA in E4 leaves was only 6.9% lower than in ambient, but not significantly different (ns, $P=0.32$). Chlorophyll content was 0.6% higher in E4 than in ambient, but also not significantly different (ns, $P=0.95$). Thus, changes in LMA and N, if N correlates with chlorophyll content, do not account for the decrease in respiration in *Q. rubra*.

Similarly, in *B. alleghaniensis*, respiration at 22°C was 15.2% lower in E4 leaves than in ambient leaves ($P<0.01$) on an area basis, $\mu\text{mol m}^{-2}\text{s}^{-1}$. LMA in E4 leaves was 11.2% lower than ambient, but not significantly different (ns, $P=0.22$). Chlorophyll content was 6.22% lower in ambient than in the E4, but also not significantly different (ns, $P=0.48$). Thus changes in LMA and N, again if N correlates with chlorophyll content, do not account for the decrease in respiration in *B. alleghaniensis*. The mechanisms behind

respiratory acclimation in both species remain to be determined and may be related to substrate (carbohydrate) availability.

Q. rubra and *B. alleghaniensis* both showed complete acclimation of leaf respiration to increased growth temperatures. This is shown by the decrease in respiration rates, measured at a common temperature, with warmer growing temperatures, and by the right shift of the respiration curves of both species. A shift of 4°C when growing temperatures are 4° different represents a complete homeostatic adjustment. Both species maintained a constant respiration rate that is lower than would be predicted from a respiration curve developed in ambient-grown seedlings. There was no significant correlation between respiration and chlorophyll content, so if leaf nitrogen content is correlated with chlorophyll content, then nitrogen content will not explain the differences in respiration rates and thus can not be used to model acclimation to warming. Leaf N and carbohydrates will be measured later to directly test correlations with respiration. Current forest models predict accelerated carbon losses and negative carbon balance associated with increased respiration as temperatures rise. These data suggest no such acceleration in carbon losses as plants acclimate to warming. The complete acclimation observed here implies a need for models to incorporate physiologically based research in order to correctly portray ecosystem function in a changing environment and to interpret which changes could ultimately influence species survival [3,7].

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