Sugar Maple Canopy Photosynthetic Responses to the Environment

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ABSTRACT Leaf photosynthetic responses to light and carbon dioxide (CO_2) supply were measured in sugar maple trees located near the Proctor Maple Research Center VMC tower. Leaf photosynthetic responses to environmental factors were determined by analysis of measurements of photosynthetic responses to short-term, experimental manipulations of leaf environmental conditions. Photosynthetic responses to light and to CO_2 supply inside of the leaf were determined for leaves at different canopy positions and in stands characterized by differences in soil fertility. There was a strong dependence of many physiological parameters on leaf nitrogen (N) status. A computer model based on the physiology and biochemistry of photosynthesis (called PHOTO-N) and using standard meteorological variables as inputs was produced to simulate leaf and canopy photosynthesis over time periods of days to weeks. The computer model can be used to examine possible changes in photosynthesis related to climate change and gaseous pollutants (elevated ozone or CO_2). While still only a research tool, it is envisaged that in the future stand productivity models may be useful in integrated assessment of potential environmental impacts on sugar maple forests in Vermont and elsewhere in the northeastern U.S.

INTRODUCTION

There is a critical need to develop methods to address issues of forest canopy productivity and the role of environmental conditions in regulating forest productivity. Recent observations of insect damage to sugar maple and reports of crown dieback or growth declines in northern hardwood forests (cf. Allen et al. 1992, Wilmot et al. 1995) have raised concern over the continued productivity of sugar maple forests.

The objective of my work on sugar maple physiology over the past few years has been to quantify key leaf photosynthetic responses of sugar maple that play an important role in regulating forest productivity. Another goal has been to formalize this understanding of sugar maple forest processes in a computer model designed to aggregate leaf responses to predict sugar maple forest canopy responses to the current environment and to anticipated changes in the environment.

METHODS

Sugar maple leaf photosynthesis was measured on intact leaves in the crowns of mature trees using a portable infra-red gas analyzer and photosynthesis system. Light was supplied to the measurement leaf by means of a metal halide projector lamp, and light levels were increased from darkness by removing progressive layers of shade cloth and neutral density filters shading the leaf. Under high light conditions, CO_2 supply to the leaf was changed by adding variable amounts of CO_2 from an external CO_2 source to the gas stream over a leaf. Care was taken to ensure that the leaf remained undamaged during measurements and that other environmental conditions in the leaf chamber such as air temperature and humidity were near optimal. Additional measurements of photosynthesis were made on leaves from trees in several Vermont sugarbushes that varied in soil acidity and nutrient conditions (see Ellsworth and Liu 1994).

Canopy structure was measured by a remote optical technique that uses fisheye sensor measurements of diffuse light within the forest canopy. Measurements were made at multiple levels within the forest to quantify the vertical distribution of leaf area in the sugar maple stand. Individual leaves measured for photosynthesis were harvested from multiple heights in the forest stand for analyses of leaf morphology and leaf nitrogen concentration.

RESULTS TO DATE

The vertical structure of the sugar maple forest near the PMRC tower is shown in Figure 1. The majority of the leaves in the stand are located between 10-13m height in the 17m tall forest stand. Canopy structure was remarkably similar between 1992 and 1993.

Figures 2 and 3 illustrate the typical response of leaf photosynthesis to light (Fig. 2) and leaf internal CO_2 (Fig. 3) in sugar maple. The curves in Figures 2 and 3 are from statistical fits to the data shown in the Figures. The photosynthetic light response curves showed lower saturation values for leaves in more shaded locations such as at 10-12m height. Leaf photosynthesis under high light and current ambient CO_2 conditions was closely related to total leaf nitrogen (N) content, as has been found previously for sugar maple (Ellsworth and Liu 1994). The initial slope of the CO_2 response curve, which is an indication of the biochemical capacity of the leaf to fix CO_2

in photosynthesis, was also closely correlated with leaf N content. I used the relationships between key physiological parameters such as leaf carboxylation capacity and leaf N to parameterize a computer model (PHOTO-N) based on leaf physiology and the biochemistry of photosynthesis that can simulate theoretical rates of leaf and canopy photosynthesis over time periods of days to weeks. Preliminary results from an early version of the model are shown in Figure 4. The data show a series of days in August 1993 the simulations were done using VMC meterological data. Days 2 and 3 were partly cloudy and show greater temporal variation in predicted photosynthesis than on Day 1, which was a clear sunny day. Photosynthesis is much lower for leaves at 8m than at 13.5m, largely due to the influence of shade in the forest. These results highlight the paramount importance of light in regulating photosynthesis in sugar maple.

FUTURE PLANS

I am developing a version of the model that predicts the impacts of chronic, low-level ozone exposure on leaf and canopy photosynthesis such as would be experienced in some years in Vermont. The model is parameterized using relationships between cumulative ozone dose and reductions in photosynthesis based on a field exposure of a mature sugar maple canopy to elevated ozone (Tjoelker et al. 1995). It is anticipated that the photosynthesis model will be revised to use more detailed assessments of spatial variation in stand leaf area and leaf characteristics. Analyses of model sensitivity to inputs and of model robustness are under way. A validation dataset is being assembled to test the model predictions. The model can be modified to use remotely sensed information on stand structure, leaf chemistry, and leaf area index for landscape units dominated by sugar maple so that complex spatial and ecological relationships between forest structure and canopy photosynthesis can be examined.

CONTEXT

Because data were collected from stands on a number of different soils, the measurements are likely to be applicable to sugar maple on spodic and other similar soils. Ellsworth and Liu (1994) showed that the physiological relationships examined in relation to leaf N compare favorably to those published for sugar maple in other regions within its natural range. The model was devised using fundamental physiological relationships to enable it to be parameterized for sugar maple growing throughout the northeastern U.S.

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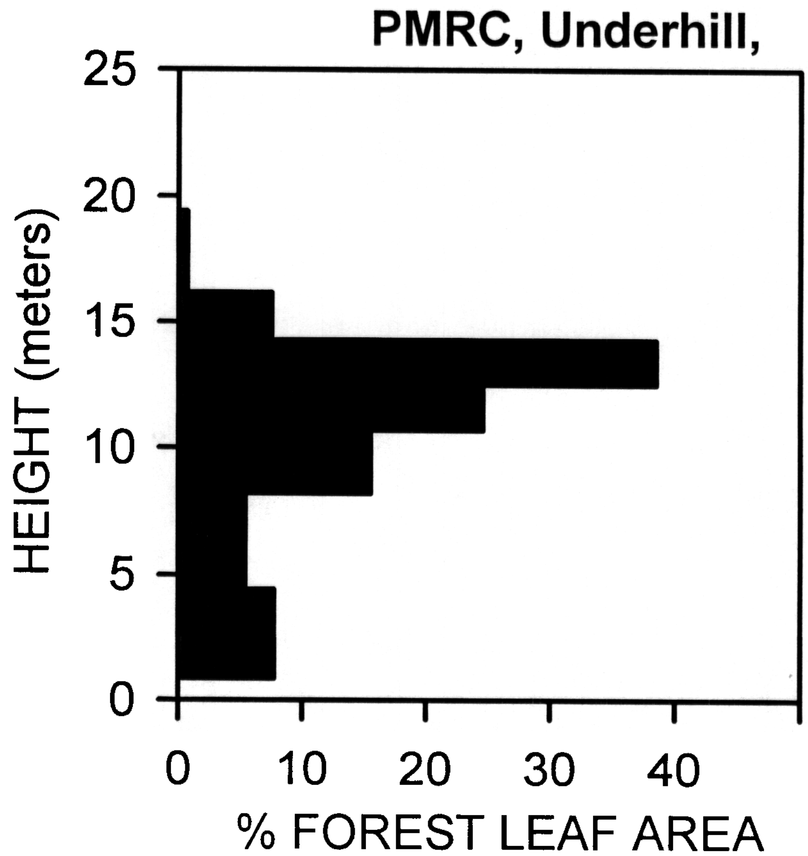

Figure 1. Structure of the forest in proximity of the Proctor Maple Research Center (PMRC) tower in July 1993. Each bar indicates the fraction of stand leaf area at a given level in the canopy.

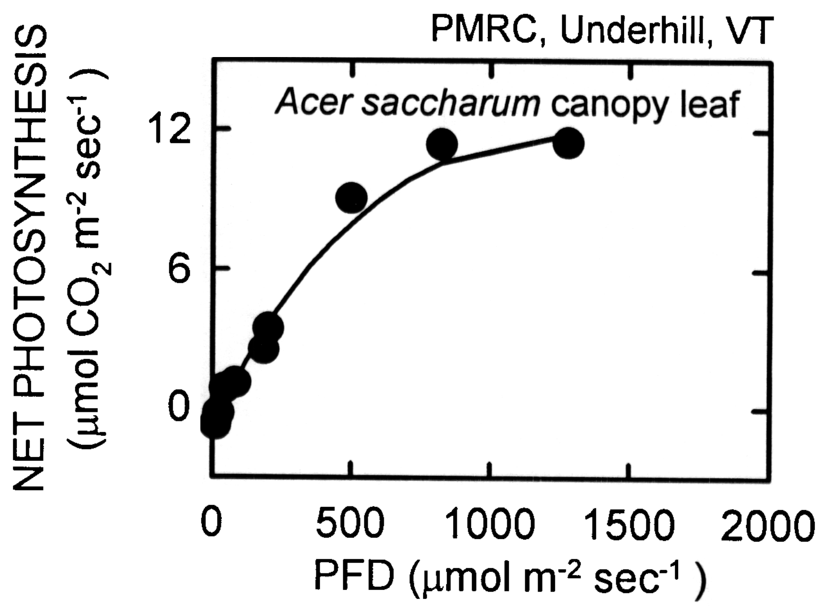

Figure 2. A typical photosynthetic light response curve for an intact leaf located at 16m in the canopy near the PMRC tower. PFD (photon flux density) is the flux density of light incident on the leaf.

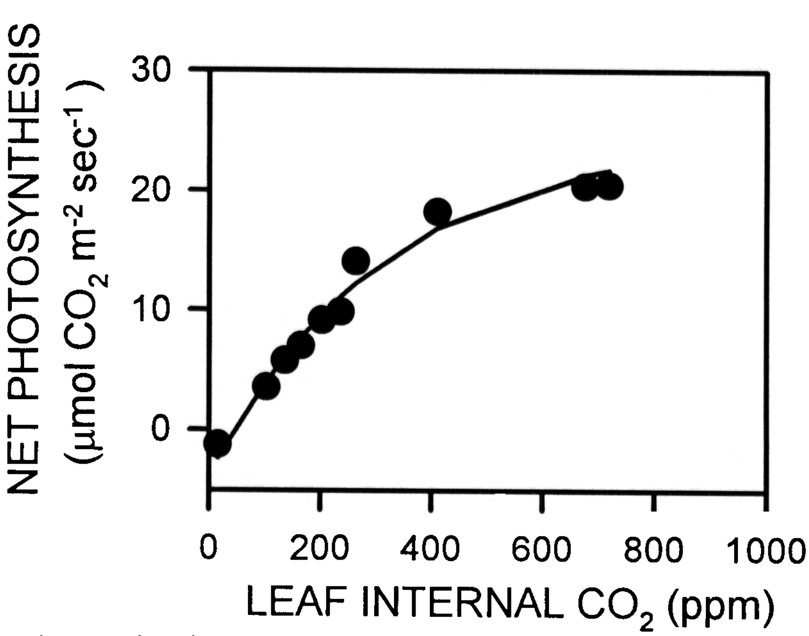

Figure 3. Dependence of leaf photosynthesis on the CO_2 supply to leaf internal air spaces. Measurements were made on an intact leaf of sugar maple at 16m height near the PMRC tower according to techniques in Ellsworth and Liu (1994).

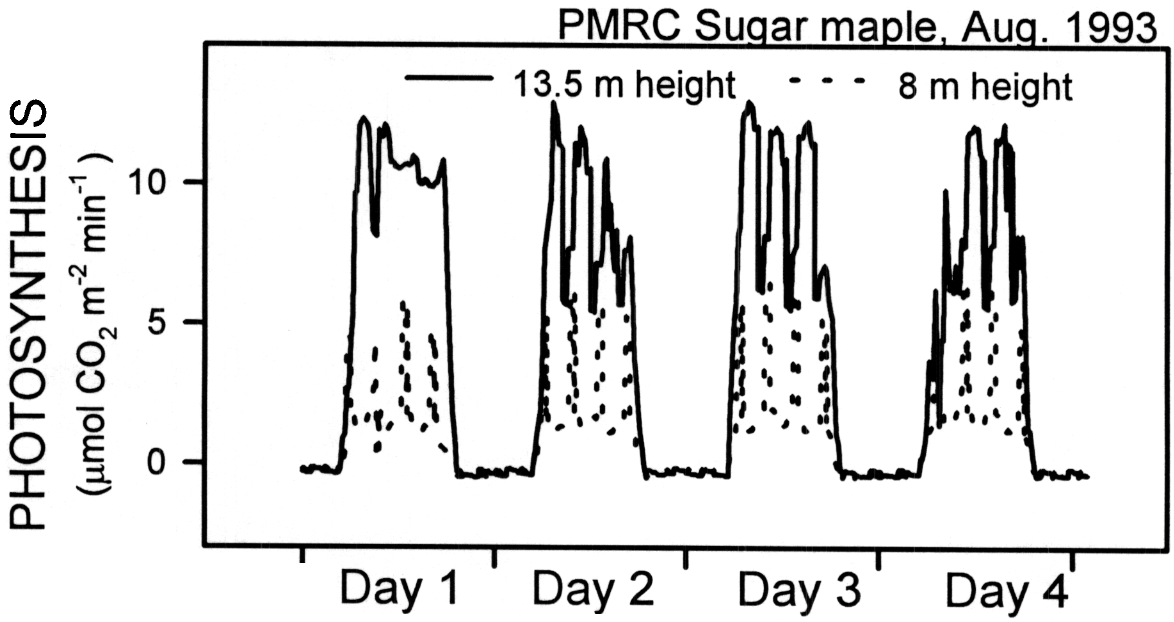

Figure 4. Time course of predicted photosynthesis for a representative leaf at two different canopy positions (13.5m height and 8m height). Data were generated by the photosynthesis model PHOTO-N using leaf and stand characteristics from data collected near the PMRC tower and using meteorological inputs from VMC monitoring.