

Proposed Causes and Mechanisms for Variation in Photosynthesis of *Quercus rubra* Along an Urban to Rural Gradient

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Forests in the northeastern United States are currently sequestering atmospheric carbon dioxide released by fossil fuels. The effects of accelerating urbanization and global warming on plant carbon uptake will thus have important consequences for future atmospheric carbon dioxide concentrations and climate change. The urban environment of New York City (NYC) has been shown to produce increased plant growth and carbon sequestration in *Populus deltoides*. Here we investigate the effects of NYC's urban environment on native red oaks (*Quercus rubra* L.). We grew four-year-old oak seedlings at four sites along an urban to rural gradient from NYC to the Catskills for 1.5 years. We measured the short-term response of photosynthesis to [CO₂] in three seedlings at each site, as well as environmental parameters. Photosynthesis was highest in NYC, second highest in the Catskills, and lowest at the two intermediate sites. Comparison of photosynthesis data with environmental variables suggests that the combined effect of diurnal temperature range, [CO₂], and ozone account for most of the variation in photosynthesis and growth along the gradient. These results and interpretations differ from those of Gregg et al. (2003); we suggest that these differences are due to the species tested, and that *Quercus rubra* may provide a more accurate indicator of how urbanization and climate change will affect carbon cycling in forests in the eastern United States.

Introduction

Urbanization is accelerating across the globe (Pickett et al., 2001). It is important to know what effect cities have on the carbon cycling of plants, as plants are currently considered a major sink of CO₂ released from the burning of fossil fuels (Broecker and Peng, 1998). Urban centers generally have warmer temperatures, especially at night (Peterson, 1969), as well as elevated CO₂ concentrations (Idso et al., 2001), lower ozone relative to surrounding rural areas (Gregg et al., 2003), increased nutrient deposition (Lovett et al., 2000), and increased photochemical pollutants (Gatz, 1991; Freedman, 1995; Lovett et al., 2000).

Gregg et al. (2003) studied the effect of the urban environment on *Populus deltoides* (cottonwood), a native but non-dominant tree in the New York area,

grown along urban-rural transects in New York City, and found consistently higher biomass and growth in the urban-grown plants relative to their rural counterparts. Gregg et al. also conducted chamber experiments incorporating [CO₂] and diurnal temperature range (DTR), which failed to account for the variation in their results. They concluded that lower ozone at the urban sites was the cause for higher biomass and growth in their plants. Here, we investigate the effect of the urban environment on photosynthesis of *Quer-*

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cus rubra (red oak), a common tree native to the New York City area. We sought to untangle the mechanisms responsible for enhanced growth in urban air, and suspected that a native tree might respond differently than *P. deltoides*, and thus be more representative of the changes that Northeastern forests will experience under global climate change.

We measured photosynthesis on four-year-old *Q. rubra* seedlings at four sites along a transect from New York City to the Catskill mountains. We hypothesized that photosynthesis at the local CO_2 concentration would be highest in the urban-grown plants (hypothesis 1), and that this would be correlated with higher growth (hypothesis 2); however, we expected photosynthesis at a set $[\text{CO}_2]$ of 400ppm to be lowest in the urban-grown seedlings due to photosynthetic acclimation (hypothesis 3) (Delucia, 1985; Chen, 2005).

Materials and Methods

Q. rubra acorns were collected at Black Rock Forest, NY and planted together in a garden box in 2002. In the spring of 2005, the seedlings were dug up before any leaves developed, rinsed, weighed, measured for diameter and height, and repotted in soil from Black Rock Forest (BRF) (coordinates: 41.4219°N, 74.0298°W). Thirty seedlings were randomly selected to be relocated to each of the following sites: Swindler's Cove on Manhattan (urban site; coordinates: 40.7927°N, 73.9550°W), Lamont-Doherty Earth Observatory (LDEO) in Palisades, NY (suburban site; coordinates: 41.0053°N, 73.9078°W), and the Ashokan Reservoir (rural site; coordinates: 41.9249°N, 74.2475°W). Thirty seedlings were also left at BRF. At this time, approximately 12 additional seedlings were harvested to obtain biomass and diameter data, from which allometric equations could be derived to estimate the biomass of the remaining plants. The seedlings at Swindler's Cove were relocated to Central Park in the spring of 2006 before the leaves came out due to the possibly moderating effect of the river near Swindler's Cove.

All seedlings were potted in the same soil from BRF to remove the possible effects of urban soil on photosynthesis and growth. To control for precipitation, all plants were watered to saturation with a sprinkler or hose twice a week during the growing season, with the excep-

tion of the Central Park seedlings, which were rarely watered. All plants were grown in open fields with full sunlight.

Photosynthesis measurements were made September 22-24 and October 21-22 using an open-air gas exchange system (LI-6400, Li-cor, Lincoln, Nebraska). A/C_i curves (short term response of photosynthesis to $[\text{CO}_2]$) were measured on 3 plants at each site in September. Due to the high VPD measured at the Ashokan Reservoir relative to the other sites, it is very possible that the Li-cor was passing air through the desiccant tube at Ashokan, which could affect our measurements. To check for this effect, we took point measurements of photosynthesis at 400ppm $[\text{CO}_2]$ on seedlings along the transect in October (Figure 1). Although photosynthesis at LDEO is very different in October than in September, the consistency in photosynthesis measurements taken at Ashokan indicates that our September measurements were not significantly affected by high VPD.

Simple linear regressions were performed using Microsoft Excel. Multiple linear regressions were performed using R 2.4.0 (R Development Core Team). Results were considered significant if $p \leq 0.05$ and $R^2 > 0.4$. Mechanistic parameters of photosynthesis, such as A_{max} , J_{max} , V_{cmax} and photosynthesis at local $[\text{CO}_2]$ were calculated using Photosynthesis Assistant (Dundee Scientific, Dundee).

Results

Photosynthesis at 400ppm reference $[\text{CO}_2]$ was highest at Central Park, second highest at Ashokan, and lowest at BRF and LDEO, with no significant difference between the latter two sites (Figure 1).

Photosynthesis was recalculated for local ambient $[\text{CO}_2]$ using estimated $[\text{CO}_2]$ for each site. Ambient $[\text{CO}_2]$ was estimated to be 380ppm at Ashokan, BRF, and LDEO (Broecker, personal correspondence), and 450ppm at Central Park, based on $[\text{CO}_2]$ measurements taken for two days in Harlem by Wade McGillis (personal correspondence) and ^{14}C data from a tree in Central Park (Broecker, personal correspondence). In the recalculated data, the peak in photosynthesis in trees at Central Park is enhanced (Figure 2).

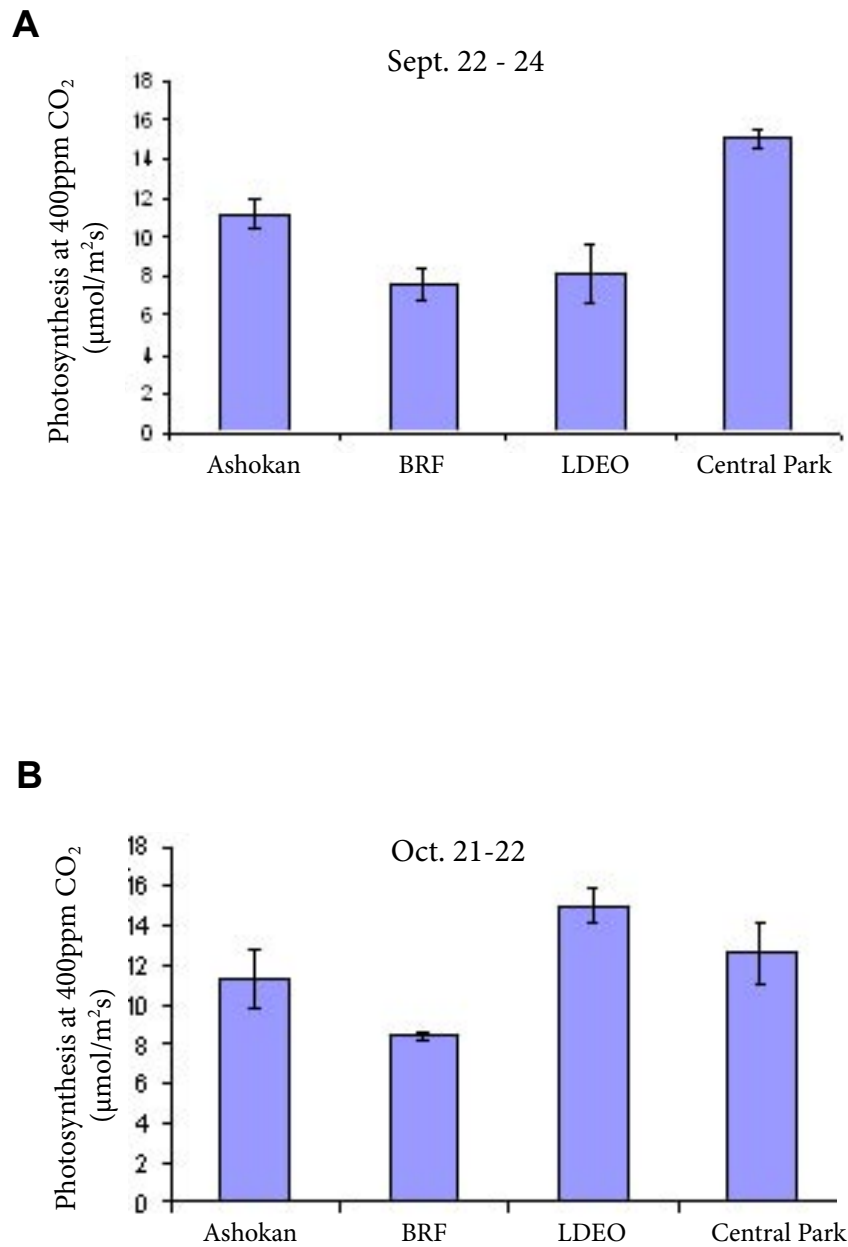


Figure 1. Photosynthesis measured at 400ppm reference CO₂.

Ashokan is the most rural site and Central Park the most urban site. (A) Sept 22-24, data taken from A/C_i curves. P-value = 0.0312. (B) Oct 21-22 point measurements at 400 ppm reference CO₂. Columns show means and error bars show standard error.

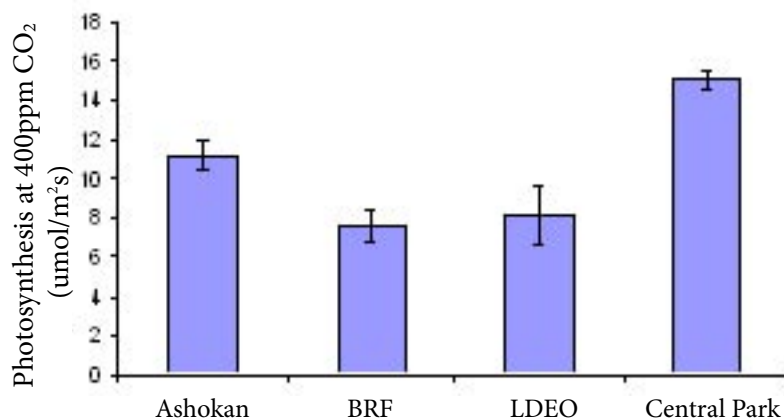


Figure 2. Photosynthesis at local [CO₂] estimated from A/C_i curves. Central Park [CO₂] estimated to be 450ppm. All other sites estimated to be 380ppm.

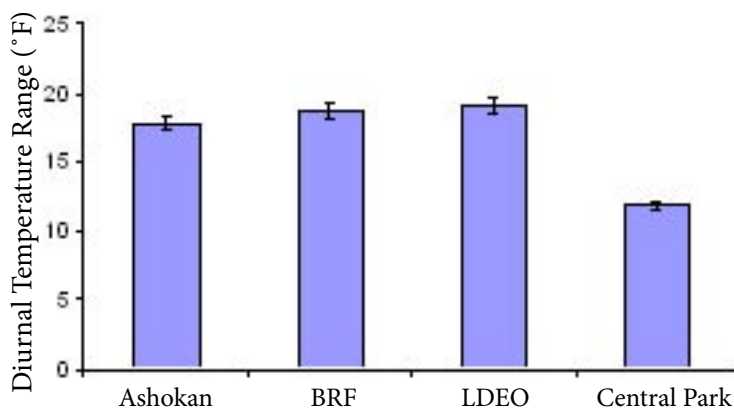


Figure 3. Diurnal temperature range, or difference between maximum and minimum temperatures in degrees Fahrenheit.

Values shown are averages for March 20th to Nov 10th, roughly the growing season. Data taken from Weather Underground. Ashokan data from Kingston, NY; BRF data from Cornwall, NY; LDEO data from Anton Court, Woodcliff Lake, NJ.

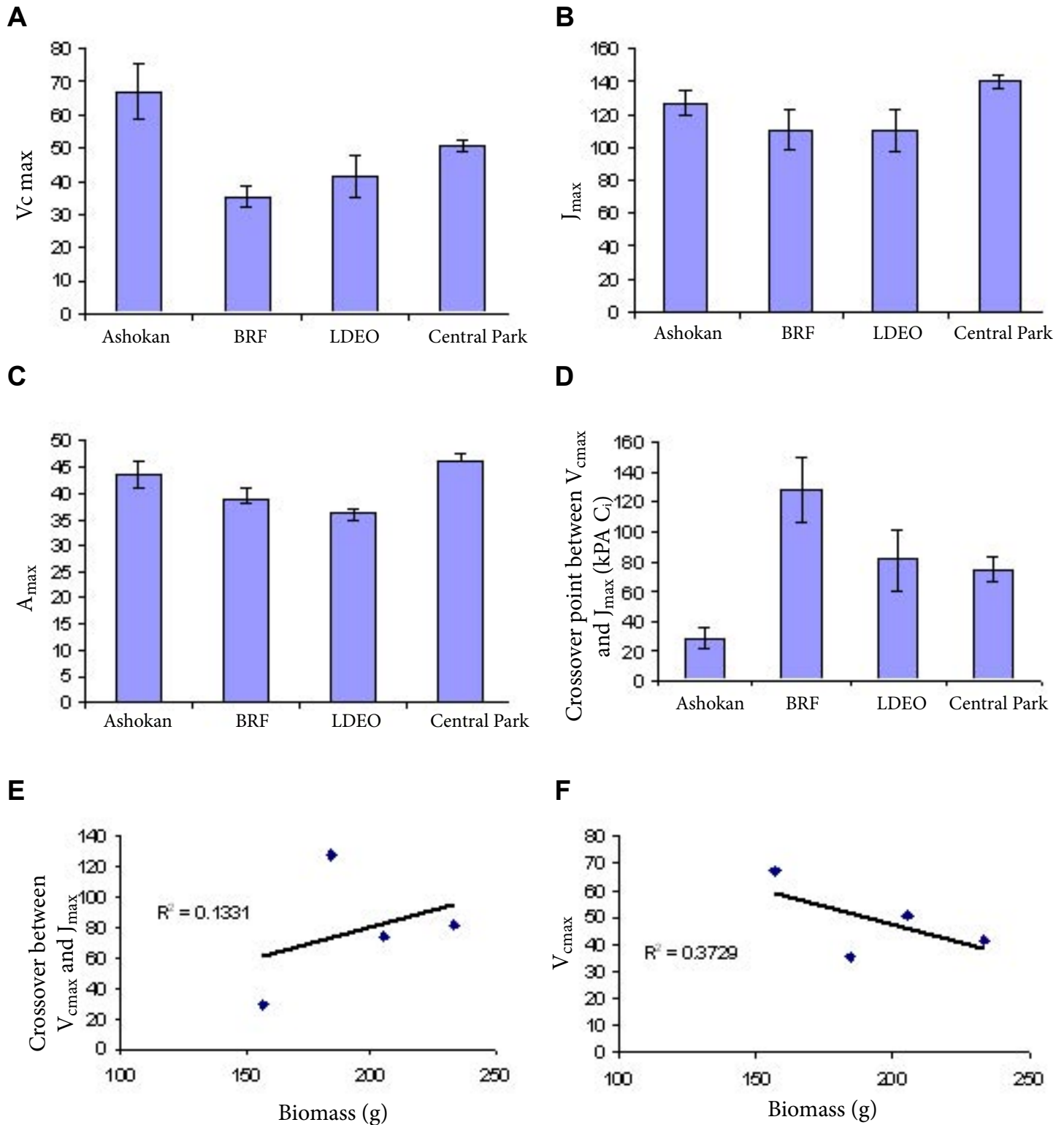


Figure 4. (A) V_{cmax} over the transect. (B) J_{max} over the transect. (C) A_{max} over the transect. (D) Value of C_i at which V_{cmax} and J_{max} intersect on A/C_i curves (kPa), which estimates the crossover from RuBisCO limitation to the limitation cause by RuBP regeneration. (E) Crossover between V_{cmax} and J_{max} plotted against total 2006 biomass, $R^2 = 0.133$. (F) V_{cmax} plotted against total 2006 biomass, $R^2 = 0.373$.



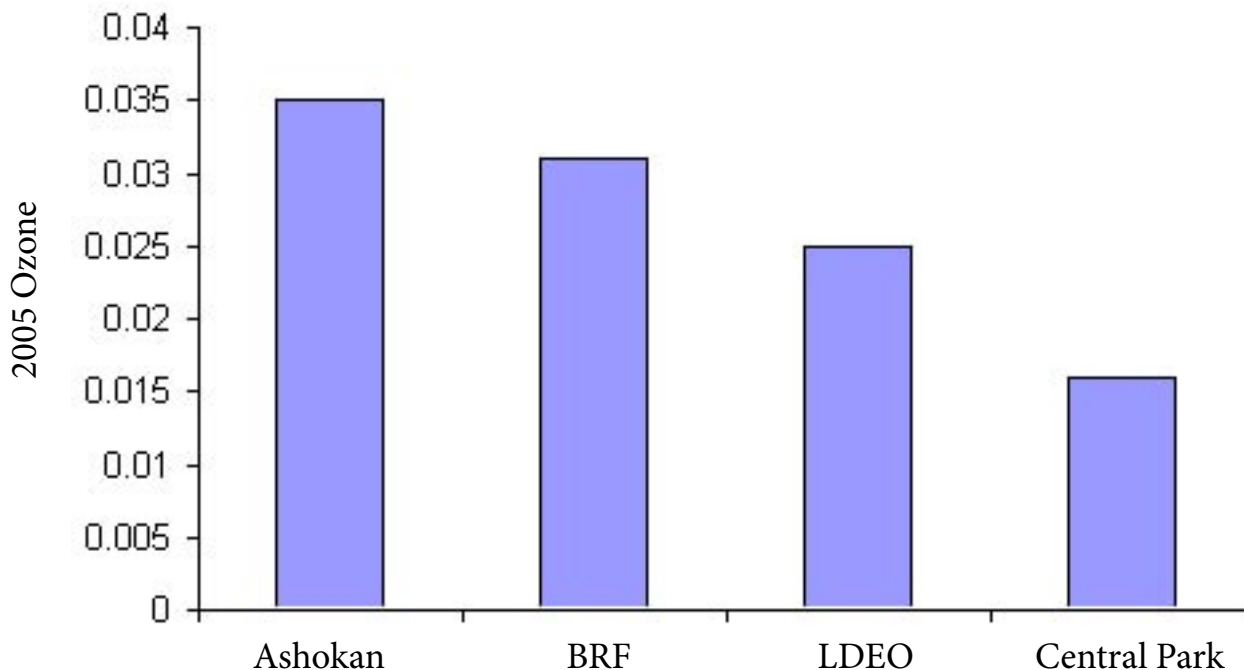


Figure 5. Ozone data from NY State Department of Environmental Conservation. Central Park data from IS-52; LDEO data from White Plains; BRF data from Valley Central; Ashokan data from Belleayre Mt.

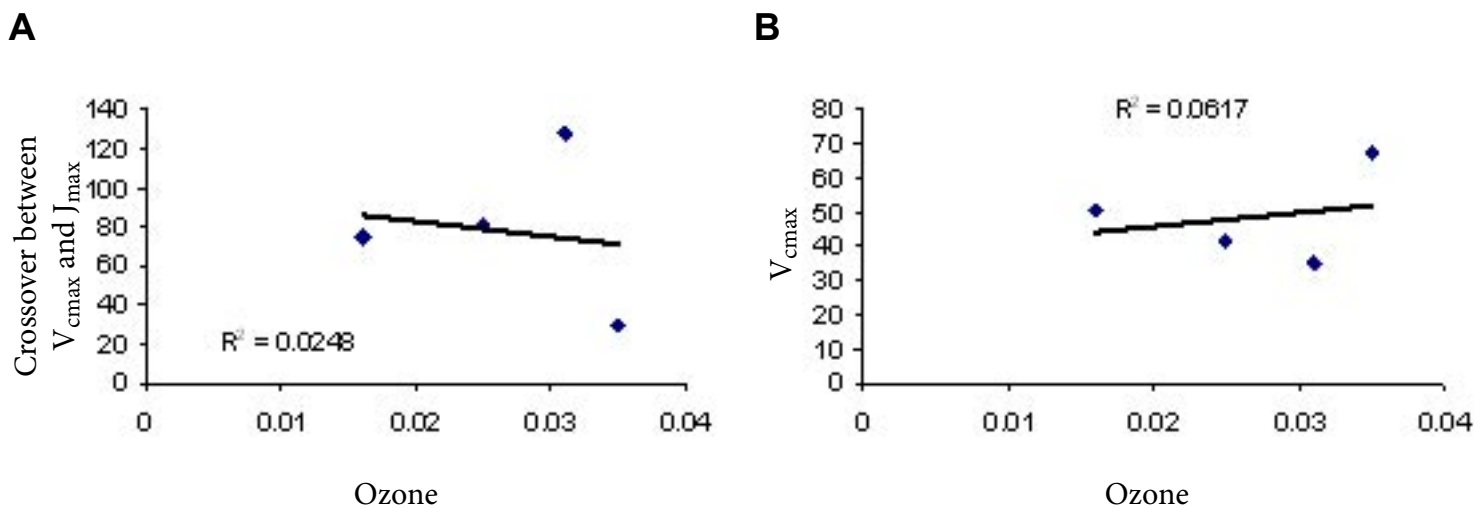


Figure 6. (A) Crossover between V_{cmax} and J_{max} plotted against ozone, $R^2 = 0.025$. (B) V_{cmax} plotted against ozone. Ozone data from 2005, $R^2 = 0.062$.

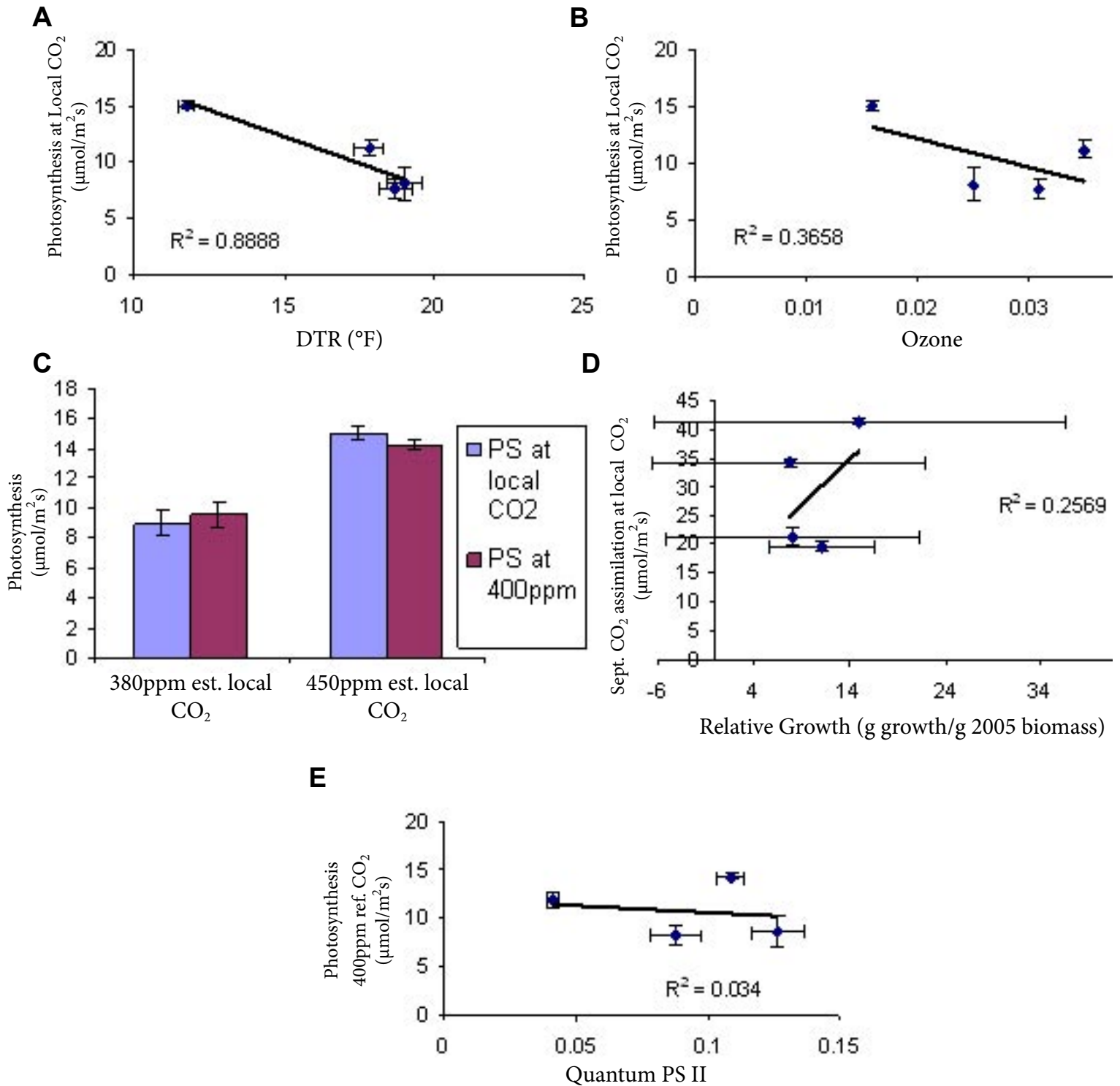


Figure 7. (A) Photosynthesis at local [CO₂] plotted against DTR, R² = 0.889. (B) Photosynthesis at local [CO₂] plotted against ozone, R² = 0.336. (C) Photosynthesis at local [CO₂] and Photosynthesis at 400ppm ref. [CO₂] plotted against local atmospheric [CO₂]. (D) Photosynthesis at local [CO₂] plotted against 2005-2006 growth relative to 2005 biomass, R² = 0.257. (E) Photosynthesis at local [CO₂] plotted against quantum PSII, a parameter of fluorescence, R² = 0.034.



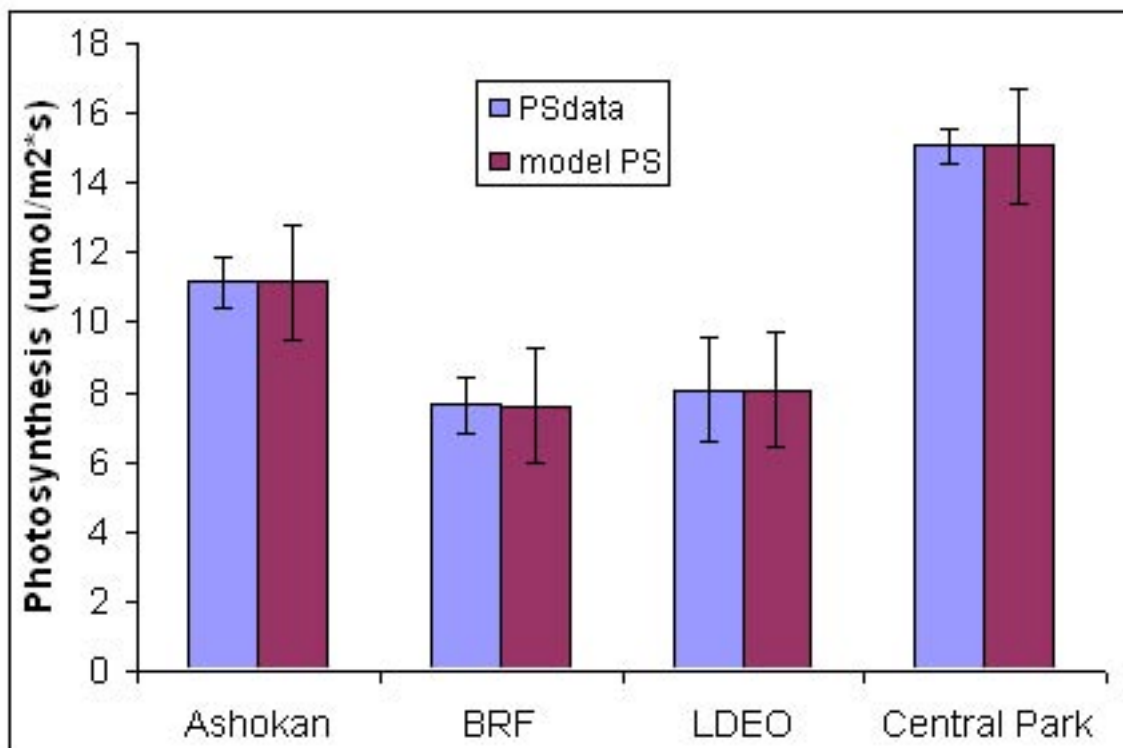


Figure 8. Actual photosynthesis data shown in blue; and photosynthesis predicted by our model in purple.

The diurnal temperature range (DTR) was significantly lower at Central Park than at the other sites (Figure 3). DTR data is averaged in °F from March 20th to November 10th, which is roughly the growing season (Weather Underground).

V_{cmax} was highest at Ashokan, with little difference between the other three sites (Figure 4A). J_{max} and A_{max} were both slightly higher at Central Park than at the other sites, but there was no significant difference in either of these parameters along the transect (Figure 4B,C). The crossover point between V_{cmax} and J_{max} , indicating RuBisCO limitation, was highest at BRF, intermediate at LDEO and Central Park, and lowest at Ashokan (Figure 4D). Ozone was highest at Ashokan and showed a negative linear trend towards Central Park (Figure 5) (New York State Dept. of Environmental Conservation).

All regressions reported are simple linear regressions. Ozone correlates with V_{cmax} , but not with the crossover between V_{cmax} and J_{max} (Figure 6). Photosynthesis at local $[\text{CO}_2]$ was significantly correlated

with DTR, and weakly correlated with ozone, $[\text{CO}_2]$, and growth. Photosynthesis at a set-point $[\text{CO}_2]$ of 400ppm was not correlated with quantum PSII (de Troy, unpublished data), a parameter of chlorophyll fluorescence which measures the potential of the light reactions of photosynthesis (Figure 7).

The combined effects of DTR, local $[\text{CO}_2]$, and ozone account for much of the variation in photosynthesis at local $[\text{CO}_2]$ (Figure 7). We ran a multiple linear regression on DTR, $[\text{CO}_2]$, and ozone against photosynthesis and used the resulting coefficients to create a model relating the combined effects of these 3 predictor variables on photosynthesis (eq. 1). None of the individual predictor variables were statistically significant; however, the model follows a very similar trend to actual photosynthesis data (Figure 8), with $R^2 = 0.8303$. The following equation describes our model, where PS = photosynthesis. The standard errors (S. E.) and p-values for each predictor are shown below.

Discussion

Photosynthesis at local $[\text{CO}_2]$ was highest in urban-grown plants, in agreement with hypothesis 1. However, photosynthesis at a set-point $[\text{CO}_2]$ was also highest in urban-grown plants, indicating that photosynthetic acclimation did not occur; thus, we reject hypothesis 3.

We were initially concerned that infrequent watering at Central Park may suppress photosynthesis in plants there. However, Bernacchi et al., (2006) found that the effect of elevated $[\text{CO}_2]$ on photosynthesis was greater under water stress. It would make sense that elevated $[\text{CO}_2]$ would mitigate for the detrimental effects of water stress on photosynthesis because leaf stomata would not have to open as much to obtain sufficient CO_2 , reducing transpiration. The elevated $[\text{CO}_2]$ in Central Park may explain why there does not appear to be a detrimental effect of water stress on photosynthesis.

In the mechanistic model used by Photosynthesis Assistant, V_{cmax} represents the potential of RuBisCO in photosynthesis, and J_{max} represents the potential of RuBP regeneration, which is related to electron transport. Thus, the crossover point between these two parameters should indicate the point at which RuBisCO is no longer limiting. V_{cmax} itself is inversely similar to the crossover point, confirming that RuBisCO potential is related to RuBisCO limitation. Both of these parameters show that the plants at Ashokan were the least limited by RuBisCO (Figure 4A,D). Because RuBisCO is largely composed of nitrogen, nitrogen deficiency is the most likely cause of RuBisCO limitation. The low RuBisCO limitation at Ashokan could possibly reflect the highest nitrogen availability. V_{cmax} is somewhat correlated with total 2006 plant biomass (Figure 4F). Since the size of the pots and amount of soil was equal for all plants at all sites, it is possible that the small size of the plants at Ashokan allowed them a higher ratio of soil nitrogen to biomass, while the large plants at Central Park were limited by the amount of available soil. However, the correlation between biomass and the crossover point of V_{cmax} and J_{max} is weak (Figure 4E), and no leaf nitrogen data is currently available; thus, this relationship is unclear and requires further investigation.

The negative relationship between ozone and photosynthesis suggests that ozone is having a detri-

mental effect on plant function. Ozone precursors are emitted in urban centers, but react with sunlight to form ozone in rural areas, resulting in higher rural concentrations of ozone (Hesstvedt, 1978; Isaksen, 1978). Ozone has been shown to cause a decrease in photosynthesis by denaturing RuBisCO (Inclan, 2005; Fares, 2006; Pell, 1997). However, there is no correlation between ozone and V_{cmax} or ozone and the crossover between V_{cmax} and J_{max} (Figure 5A,B). These results suggest that the effect of ozone on plant function is complicated.

There is no correlation between CO_2 assimilation (referred to as photosynthesis in this paper) and quantum PS II yield (Figure 7E). CO_2 assimilation measures the dark reactions of photosynthesis, while quantum PS II measures the light reactions of photosynthesis. These two processes are highly related; thus, the lack of correlation here is intriguing. Perhaps nitrogen availability is part of the explanation. However, it should be noted that CO_2 assimilation and quantum PS II were measured on different seedlings.

In contrast to the biomass results of Gregg (2003), photosynthesis in this study did not follow a clear trend with proximity to an urban center. The complexity of the data suggests multiple causes for the variation in photosynthesis. The correlation between photosynthesis predicted by our model (eq. 1) and actual data support the combination of $[\text{CO}_2]$, DTR, and ozone in explaining the variation in our results. As DTR has the lowest p-value as a predictor in the model, we suggest that it is the most influential factor in determining photosynthesis. An important strength of our model is that each of the predictors is a purely environmental variable; no physiological information about the plant is required to predict its photosynthesis.

The correlation between local CO_2 concentration (450ppm at Central Park and 380ppm at each of the other three sites) and photosynthesis at this concentration (Figure 7) indicates that the higher $[\text{CO}_2]$ in NYC is affecting photosynthesis. Gregg et al., (2003) concluded that $[\text{CO}_2]$ did not affect growth along her transects. However, *P. deltoides* is less sensitive to $[\text{CO}_2]$ than is *Q. rubra*. Doubling $[\text{CO}_2]$ (400ppm to 800ppm) resulted in a 96.15% relative increase in photosynthesis in the *Q. ru-*



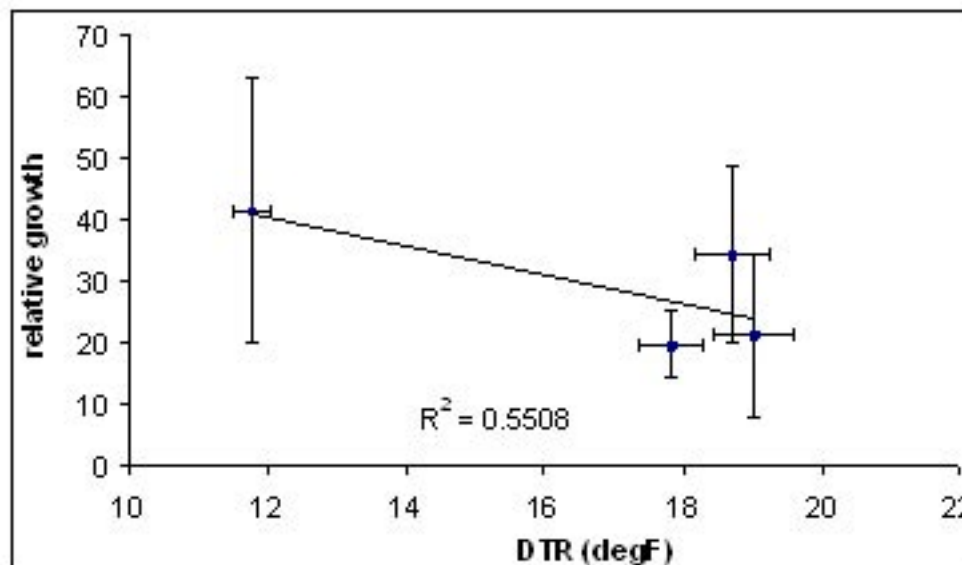


Figure 9. Relative growth (increase in biomass from 2005 to 2006 divided by 2005 biomass) plotted against DTR (degree Fahrenheit).

bra seedlings we measured at BRF, and an estimated 50.91% increase in photosynthesis in *P. deltooides* saplings (Turnbull et al., 2004).

DTR is also strongly correlated with photosynthesis at local $[CO_2]$. Elevated nocturnal temperature has been found to increase nighttime respiration in *P. deltooides*, resulting in a reduction in leaf carbohydrate concentration and enhanced photosynthetic capacity during the following day (Turnbull et al., 2002). This effect can be expected to vary with species; Larigauderie and Korner (1995) found that plant species vary widely in degree of acclimation to temperature change.

Here, we use an equation proposed by Atkin et al., (2006) to quantify the degree of acclimation in respiration (R) in both *P. deltooides* and *Q. rubra* (eq. 2), where LTR10 is the Long-Term Acclimation Ratio, or the proportional change in R of plants grown at one temperature compared with a temperature $10^\circ C$ lower, and Q_{10} is the similar short-term acclimation. No acclimation is defined to be $AcclimLTR_{10} = 0$ and full acclimation is $AcclimLTR_{10} = 1$.

$$AcclimLTR_{10} = 1 - ((LTR_{10} - 1)/(Q_{10} - 1))$$

(eq. 2)

Using data from Turnbull et al. (2004), we calculate the LTR10 of R in *P. deltooides* acclimating from $25^\circ C$ to

$15^\circ C$ to be 1.19; and, given a Q_{10} value of 1.78 (Turnbull et al., 2002), we calculate $AcclimLTR_{10} = 0.757$. Similarly, we use September upper canopy measurements by Xu and Griffin (2006) to calculate the LTR10 of R in *Q. rubra* from $20^\circ C$ to $10^\circ C$ to be 1.957. Xu and Griffin present an average Q_{10} of 2.09, leading to $AcclimLTR_{10} = 0.1225$. These calculations indicate that R in *Q. rubra* acclimates only slightly to temperature, while R in *P. deltooides* acclimates much more fully. Thus, we would expect R in *Q. rubra* to exhibit greater change than *P. deltooides* in response to a decrease in DTR, which should result in a relatively greater enhancement in photosynthesis the following day (Turnbull et al., 2002).

The $[CO_2]$ sensitivity and long term acclimation ratios of respiration in *Q. rubra* and *P. deltooides* do not necessarily explain the differences in observations reported in this study and in Gregg et al., (2003). Photosynthesis is correlated with relative growth in this study (Figure 7), but this is not always true (Chapin and Shaver 1996; Roden and Ball 1996). Increased respiration may be expected to suppress growth due to greater CO_2 efflux, but the data of Wolfe-Bellin et al., (2006) do not support this notion. In addition to increasing photosynthesis, heightened respiration may promote

growth by producing carbon skeletons and ATP. We can not test this effect directly due to a lack of respiration data along the transect; however, relative growth in our saplings correlates with DTR (Figure 9), indicating that elevated nocturnal temperatures have a positive effect on growth along our transect. Thus, it is possible that Gregg et al., (2003) did not find DTR and [CO₂] to be significant predictors for growth in *P. deltooides* because metabolism in *P. deltooides* is not as sensitive to these environmental parameters as is *Q. rubra*. The latter is a common species native to the New York area and may provide a more accurate test of how local forests will respond to increased urbanization.

Eastern United States forests have been shown to be important sinks for CO₂ released from fossil fuels. CO₂ concentrations are projected to continue to rise globally (IPCC, 2001) and DTR is projected to decrease globally (Easterling et al., 1997; Alward, Detling and Milchunas, 1999, IPCC, 2001; Dai, 2001). Our results suggest that both phenomena will produce an increase in growth in forests in the New York area via changes in metabolic activity. Further work, especially respiration measurements, is recommended to better understand the effects of urbanization on plant processes and how they relate to climate change.

Acknowledgements

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