Exploring influences of leaf-level physiology on plant community assembly in the Black Rock Forest

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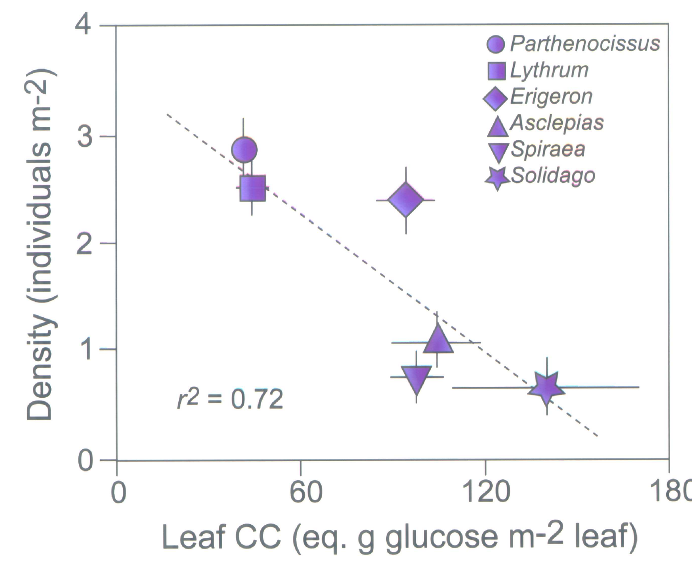
ABSTRACT

In three distinct Black Rock Forest communities, we designed projects to investigate the influence of leaf-level physiological properties and processes on the relative success of constituent plant species. We chose to focus our research on physiological properties related to energy acquisition, expenditure and use because energy is the most basic unit of comparison among organisms – spanning studies of molecules, individuals, communities, ecosystems and global dynamics. Because photosynthetic activity provides the energy essential for plant growth, and biomass production entails an energetic expense, it has been suggested that the most successful (i.e., the most abundant, the most productive, etc.) plant species within a given community would be those that maximize the physiological benefits of accrued costs to enhance their photosynthetic capacity. In the Black Rock Forest, we compared leaf-level energy acquisition, expenditure and use in three relatively successful species within their given communities with less successful co-existing species. These species included nonindigenous *Lythrum salicaria* (purple loosestrife) along pond banks, native *Acer rubrum* (red maple) in a deciduous forest, and nonindigenous *Berberis thunbergii* (Japanese barberry) in a forest understory community. We hypothesized that these relatively successful species would use energy more efficiently (i.e., acquire more energy via photosynthesis per unit of energy invested in photosynthetic biomass) than less successful co-existing species. All three studied species exhibited more efficient use of energy than their less successful neighbors in their respective communities, suggesting that this leaf-level physiological attribute could influence species' success within a community assemblage. Collectively, our research conducted in the Black Rock Forest presented a novel approach to understanding community assembly by considering physiological properties and processes related to both energy acquisition and expenditure *collectively* as mechanistic determinants of plant species' success at the community level.

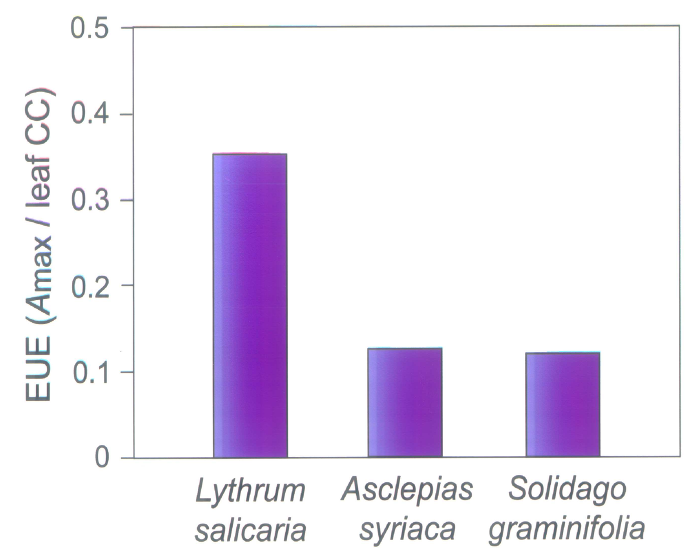
LYTHRUM SALICARIA
(purple loosestrife)

Introduced to the U.S. from Europe and Asia in the 1800s, *L. salicaria* has become common in many wetland and riparian areas. This invasive species has been associated with the displacement of native species and changes in ecosystem biogeochemistry. Along the banks of Upper Reservoir in the Black Rock Forest, we found that leaf *A* did not differ significantly in *L. salicaria* and less abundant native plant species.

However, leaf CC was significantly less in *L. salicaria* than many of its less abundant neighbors (**below**) enabling this invasive species to produce photosynthetic biomass with less energy than many of its neighbors.



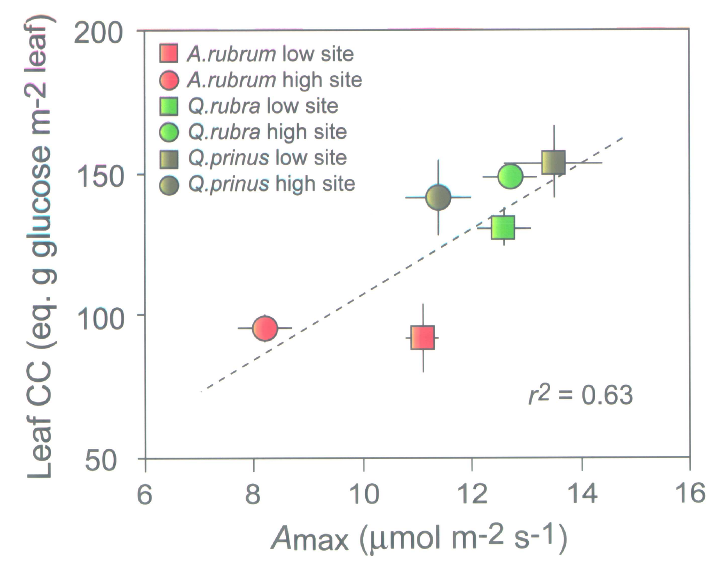
Consequently, we found that EUE was more than three times greater in *L. salicaria* than a selected group of its native neighbors (**below**) suggesting that this physiological variable could influence its invasive success.



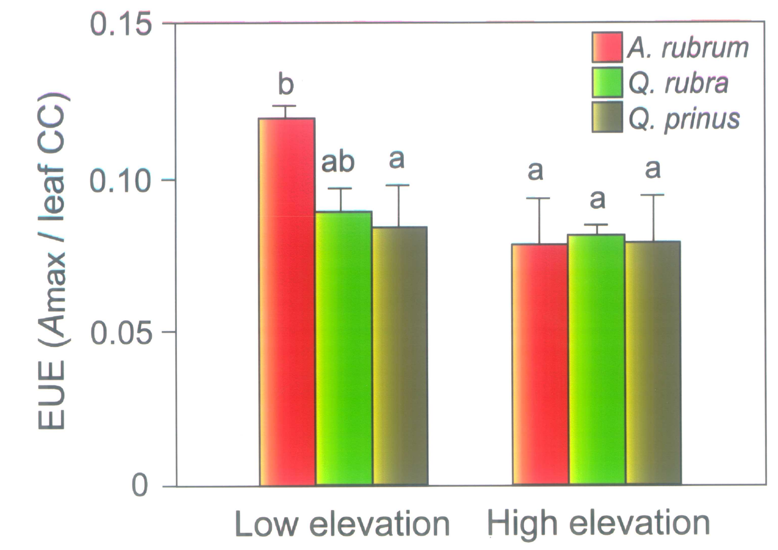
ACER RUBRUM
(red maple)

In many forests in eastern North America, *A. rubrum* has become increasingly dominant during the past century. As a consequence of this expansion, losses of dominant oak species (*Quercus* spp.) have been predicted in these communities. In the Black Rock Forest, the Cascade Brook Watershed contains co-existing *A. rubrum*, *Q. rubra* (red oak) and *Q. prinus* (chestnut oak). In agreement with previous research in other sites, we found that *A. rubrum* maintained lower photosynthetic rates than *Quercus* spp. in the watershed.

However, we found low photosynthetic rates in *A. rubra* were positively associated with low leaf CC compared to the co-existing *Quercus* spp (**below**).



As a result, EUE in *A. rubra* was higher than or comparable to that of *Quercus* spp. at both of our study sites (**below**). We suggest that this offset of its low photosynthetic rates could partially influence the reported success of *A. rubrum* in many forest communities.



METHODS

Measuring photosynthetic activity of invasive *B. thunbergii* in the Black Rock Forest with a Li-Cor 6400 portable gas-exchange system.

The relative success of *L. salicaria*, *A. rubrum* and *B. thunbergii* within their respective community types were assessed through field observations and/or reports in primary scientific literature. Individuals of these species and their less successful neighbors in Black Rock Forest communities were selected randomly for measurements of leaf-level physiological characteristics related to energy acquisition, expenditure and use:

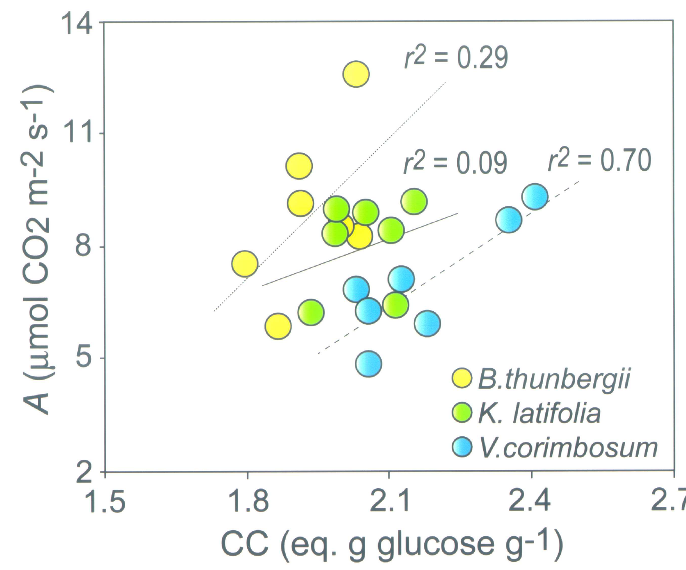
- Energy acquisition via leaf-level photosynthetic activity was assessed in all individuals selected for study by measuring instantaneous rates of carbon assimilation (*A*), and in select cases by estimating the maximum rate of carbon assimilation under optimal environmental conditions (A_{max}) using a Li-Cor 6400 portable gas-exchange system.
- Energy expenditure in photosynthetic biomass was determined for leaves selected for photosynthetic measurements by estimating biomass construction costs (CC) calorimetrically with the heat of combustion method described by Williams et al. (1987).
- Photosynthetic energy-use efficiency (EUE) was estimated by examining ratios of leaf-level energy acquisition (i.e., *A* or Amax) to energy expenditure (i.e., CC) in sampled individuals.

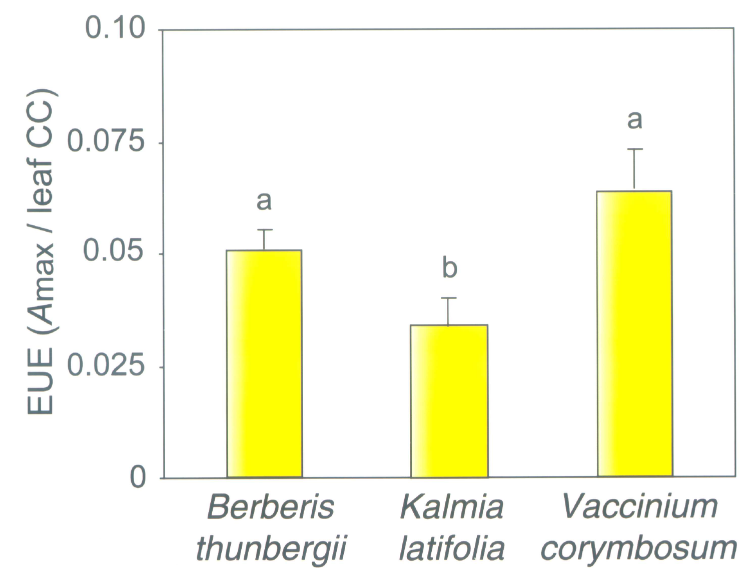
Leaf-level *A*, A_{max}, CC and EUE were compared across species using analysis of variance (ANOVA) statistical tests. When possible, physiological variables were compared directly to measurements of species' relative community-level success using linear regression analysis to determine the existence and strength of these associations.

BERBERIS THUNBERGII
(Japanese barberry)

Nonindigenous *B. thunbergii* has become increasingly invasive in the understories of many northeastern and midwestern U.S. forests. We compared this semi-evergreen species to co-existing shrubs in the Black Rock Forest understory representing different classes of leaf life-span – deciduous (*Vaccinium corymbosum*; highbush blueberry) and evergreen (*Kalmia latifolia*; mountain laurel). We found generally that leaf photosynthetic activity was greater and leaf CC was lower in *B. thunbergii* than either native shrub species (**right**).

Consequently, *B. thunbergii* exhibited greater EUE than native *K. latifolia*, while this factor did not differ significantly between *B. thunbergii* and *V. corymbosum* (**below right**) despite the longer leaf life-span of *B. thunbergii*.





When considered in the context of leaf longevity, our results suggest that relatively high energetic gains and low energetic costs could influence the performance of invasive *B. thunbergii* in forest understory communities.

RELATED PUBLICATIONS

Nagel JM, Griffin KL (2004) Can gas-exchange characteristics help explain the invasive success of *Lythrum salicaria*? *Biological Invasions* 6:101-111.

Nagel JM, Griffin KL, Schuster WSF, Tissue DT, Turnbull MH, Brown KJ, Whitehead D (2002) Energy investment in leaves of red maple and co-occurring oaks within a forested watershed. *Tree Physiology* 22:859-867.

Nagel JM, Griffin KL (2001) Construction cost and invasive potential: comparing *Lythrum salicaria* (Lythraceae) with co-occurring native species along pond banks. *American Journal of Botany* 88:2252-2258.