Cost-effectiveness of leaf energy and resource investment of invasive *Berberis thunbergii* and co-occurring native shrubs

Jennifer Nagel Boyd, Cheng-Yuan Xu, and Kevin L. Griffin

Abstract: Photosynthetic energy gain and biomass energy and resource investment represent trade-offs between potential enhancements and limitations to plant productivity, respectively. We compared these characteristics in the exotic invasive *Berberis thunbergii* DC. with that of co-occurring natives *Kalmia latifolia* L. and *Vaccinium corymbosum* L. in a north-eastern United States forest. We hypothesized that invasion by *B. thunbergii* could be facilitated by a lower leaf construction cost (CC) and reduced leaf nitrogen content (*N*) relative to photosynthetic rate (*A*) and maximum photosynthetic capacity ($A_{\max}$), which would afford it greater energy-use efficiency (EUE) and nitrogen-use efficiency (NUE), and maximums of these variables (EUE_{max} and NUE_{max}), compared with native shrubs. Although *B. thunbergii* and *K. latifolia* exhibited similar peak-season *A* and $A_{\max}$, EUE, EUE_{max}, and NUE_{max} were greater in *B. thunbergii*, which exhibited lower leaf CC and density. In contrast, EUE, EUE_{max}, NUE, and NUE_{max} did not differ between *B. thunbergii* and *V. corymbosum* given their similar *A*, $A_{\max}$, and area-based leaf CC and leaf *N*. Considered with leaf phenology, our results suggest two distinct physiological mechanisms could influence *B. thunbergii* invasion. Specifically, deciduous *B. thunbergii* exhibited greater cost-effectiveness than evergreen *K. latifolia*, while a longer payback time for photosynthetic energy gain could offset instantaneous similarities in cost-effectiveness of earlier leafing *B. thunbergii* and deciduous *V. corymbosum*.

Résumé : Le gain en énergie produit par la photosynthèse et l'énergie de la biomasse ainsi que l'investissement en ressources sont respectivement le résultat de compromis entre les améliorations et les limites de la productivité végétale. Nous avons comparé ces caractéristiques chez une espèce exotique invasive, *Berberis thunbergii* DC., et deux espèces indigènes co-occurentes, *Kalmia latifolia* L. et *Vaccinium corymbosum* L. dans une forêt du nord-est des États-Unis. Nous avons formulé l'hypothèse que l'invasion de *B. thunbergii* pourrait être facilitée par un coût de construction des feuilles (CC) et une teneur en azote (*N*) plus faibles relativement au taux de photosynthèse (*A*) et à la capacité photosynthétique maximale ($A_{\max}$) qui se traduiraient par une plus grande efficacité d'utilisation de l'énergie (EUE) et de l'azote (EUN), ainsi que par des valeurs maximales plus élevées de ces variables (EUE_{max} et EUN_{max}) comparativement aux arbustes indigènes. Bien qu'en pleine saison les valeurs de *A* et $A_{\max}$ soient similaires chez *B. thunbergii* et *K. latifolia*, les valeurs de EUE, EUE_{max} et EUN_{max} sont plus élevées chez *B. thunbergii* dont le CC et la densité des feuilles sont plus faibles. Par contre, les valeurs de EUE, EUE_{max}, EUN et EUN_{max} chez *B. thunbergii* et *V. corymbosum* sont semblables étant donné qu'ils ont des valeurs de *A*, $A_{\max}$, ainsi qu'un CC et une teneur en *N* des feuilles par unité de surface similaires. En tenant compte de la phénologie des feuilles, nos résultats indiquent que deux mécanismes physiologiques distincts pourraient influencer l'invasion de *B. thunbergii*. En particulier, *B. thunbergii*, une espèce décidue, a un rapport coût-efficacité plus élevé que *K. latifolia*, une espèce sempervirente, tandis qu'une période de récupération plus longue pour le gain en énergie produit par la photosynthèse pourrait compenser les similarités instantanées des rapports coût-efficacité de *B. thunbergii* dont la feuillaison est plus hâtive et de *K. latifolia* qui est une espèce décidue.

[Traduit par la Rédaction]

Introduction

Invasive plant species can threaten biodiversity (Dukes and Mooney 1999; Chapin et al. 2000) and potentially impact ecosystem productivity and stability by altering environmental processes (Tilman 2000). While numerous studies have focused on understanding the performance of invasive species and their influence on co-occurring native species, the mechanisms that potentially influence the success of invasive species and the vulnerability of a community often are not well understood. Ultimately, however, identifying such mechanisms could provide valuable insight into the success of invasive plant species and their native competitors (Nagel and Griffin 2004). Physiological traits that enable invasive species to acquire substantial amounts

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J.N. Boyd,^{1,2} C.-Y. Xu,³ and K.L. Griffin. Lamont-Doherty Earth Observatory, Department of Earth and Environmental Sciences, Columbia University, 61 Route 9W, Palisades, NY 10964, USA.

¹Corresponding author (e-mail: jennifer-boyd@utc.edu).

²Present address: Department of Biological and Environmental Sciences, University of Tennessee at Chattanooga, 615 McCallie Avenue, Chattanooga, TN 37403, USA.

³Present address: CSIRO Entomology, 120 Meiers Road, Indooroopilly, QLD 4068, Australia.

of resources at low rates of biomass investment more so than co-occurring native species, in particular, could provide a mechanistic explanation of their success in many systems into which they have been introduced (Bazaaz 1986; Vitousek 1986; Baruch and Goldstein 1999; Funk and Vitousek 2007). In contrast, native species with a resource-use efficiency greater than that of introduced species could be superior competitors after overcoming recruitment suppression (Seabloom et al. 2003).

Berberis thunbergii DC. (Japanese barberry) is an exotic understory shrub that has become widespread in many deciduous forest communities in the northeastern United States (Ehrenfeld 1999). The occurrence of invasive *B. thunbergii* has been observed as both sparse populations of scattered individuals and dense thickets (Kourtev et al. 1998) in forested habitats ranging from low-lying wetlands to xeric ridgetops (Ehrenfeld 1999), suggesting an ability to adapt to a range of environmental conditions. Given its demonstrated proliferation, *B. thunbergii* has been classified as one of the most widely known exotic shrubs in the United States (Silander and Klepeis 1999). Invasions of *B. thunbergii* have been associated with suppressed growth of co-occurring native species (Silander and Klepeis 1999), as well as numerous other ecological impacts, including altered soil chemistry and microbial community structure and function (Kourtev et al. 2002). *Kalmia latifolia* L. (mountain laurel) and *Vaccinium corymbosum* L. (highbush blueberry) are common native shrubs of forest understory communities in the northeastern United States (Monk and Day 1985; Ehrenfeld 1999) and, thus, often co-occur with *B. thunbergii*. These three species are characterized by distinctly different leaf phenological characteristics. In the understory, deciduous *B. thunbergii* is one of the first woody plants to leaf out in the spring and retains its leaves after most of the tree canopy leaves have dropped in the autumn (Silander and Klepeis 1999). Although both are deciduous, *B. thunbergii* leafs out earlier in the growing season than *V. corymbosum*, with synchronous leaf loss in late fall. Leaf production by *B. thunbergii* also occurs earlier than a seasonal flush of new leaves by the evergreen *K. latifolia* (Xu et al. 2007a).

Early leafing in *B. thunbergii* combined with a relatively high photosynthetic capacity in early spring when light is more available in the forest understory than after canopy closure could provide *B. thunbergii* with a greater photosynthetic carbon subsidy than that available to *V. corymbosum* (Xu et al. 2007a). However, because *B. thunbergii* has a similar early-season carbon gain and a lower late-season carbon gain than that of *K. latifolia*, this suggests that the role of competitive carbon gain in influencing the invasive success of *B. thunbergii* in forest understories may be limited (Xu et al. 2007a). Additionally, the much greater annual carbon loss through investment in respiratory processes in *B. thunbergii* than in native shrubs suggests that higher respiratory costs per unit biomass could offset any benefits of a high photosynthetic capacity and an early photosynthetic energy gain in *B. thunbergii* (Xu et al. 2007b). Although earlier studies of *B. thunbergii* invasion have not explicitly studied energy and resource requirements for biomass production, it has been suggested that such requirements could be an important additional factor to consider for understanding the invasive success of *B. thunbergii* (Xu et al. 2007b).

Because leaf phenology affects the time available for a leaf to photosynthesize, which offsets its resource and energy investment (Mooney and Dunn 1970), we suggest that leaf phenology could be a significant additional consideration.

While comparing photosynthetic energy gains with respiratory losses represents one assessment of energetic efficiency, examining energy and resource investment in biomass provides another means by which to evaluate the cost-effectiveness of photosynthetic energy gain. We propose that the ratio of energy acquisition via gas-exchange processes to energy and resource investment in biomass could be a plausible physiological mechanism influencing the demonstrated invasiveness of *B. thunbergii* in forest understory communities. Although some biomass constituents require a relatively large energy and resource investment, others are relatively inexpensive to produce (Poorter and Villar 1997). For example, nitrogen is typically incorporated into energetically expensive compounds; however, nitrogen content (*N*) can influence the energetic return on its investment in biomass through its incorporation in photosynthetic machinery (Poorter and Villar 1997). Consequently, previous research has found leaf photosynthetic activity to be associated positively with the energetic cost of biomass (Sims and Percy 1991). Here, we examine instantaneous rates of leaf-level photosynthesis (*A*); maximum photosynthetic capacity ($A_{\max}$); biomass construction costs (*CC*); leaf biochemistry; photosynthetic energy-use efficiency (EUE; A/CC), nitrogen-use efficiency (NUE; A/N); and theoretical maximums of these measures of efficiency (EUE_{max} and NUE_{max}) in leaves of co-occurring *B. thunbergii*, *K. latifolia*, and *V. corymbosum* in a forest understory community. We premise that high photosynthetic energy acquisition or an extended growing season during which photosynthesis could occur could be offset by heavy energy and resource investment in biomass. Conversely, the benefits of possessing low energy and resource requirements for biomass could be offset by a low *A* or a shorter growing season during which photosynthesis could occur. Thus, comparing leaf energy gains with energy and resource investment provides a means by which to compare the cost-effectiveness of leaf biomass of *B. thunbergii* with that of co-occurring native shrubs.

Because previous research conducted near our study site reported that $A_{\max}$ throughout much of the growing season was greater in *K. latifolia* than in *B. thunbergii* (Xu et al. 2007a), consequently, we expected that neither peak-season instantaneous *A* nor $A_{\max}$ would explain the invasive success of *B. thunbergii* there. However, since photosynthetic activity provides the energy essential for plant growth, but biomass production entails an energetic expense (Mooney 1972), we hypothesized that low leaf *CC* and *N* could influence invasion by *B. thunbergii* by influencing the cost-effectiveness of its leaf biomass via EUE and NUE relative to native shrubs. We also predicted that peak-season potential maximums of energy-use efficiency (EUE_{max}; $A_{\max}/CC$) and nitrogen-use efficiency (NUE_{max}; $A_{\max}/N$) would be relatively greater in *B. thunbergii* than in co-occurring native shrubs. To examine the influence of both leaf phenological differences and temporal variations in leaf physiology on energy-use efficiency, we also investigated *CC*, EUE, and EUE_{max} throughout a growing season in the studied species.

Materials and methods

Study site

The Black Rock Forest is a 1500-ha scientific preserve established in 1927 (Tryon 1930). The forest is located adjacent to the intersection of the Hudson Highlands and the Hudson River Basin in Cornwall, New York, USA. Mean air temperature in the forest is strongly seasonal, ranging from -2.7°C in January to 23.4°C in July (Black Rock Forest field station database). Mean annual precipitation in the forest is 1190 mm. Forest soils are loams, with bedrock or glacial till parent material at depths ranging from 25 cm to 1 m (Olsson 1981). *Quercus rubra* L. (northern red oak), *Quercus prinus* L. (chestnut oak), and *Acer rubrum* L. (red maple) dominate the forest overstory. Species common in the forest understory include *B. thunbergii*, *K. latifolia*, and *V. corymbosum*, as well as the native species *Gaylussacia baccata* (Wangenh.) K. Koch (black huckleberry) and *Rhododendron periclymenoides* (Michx.) Shinners (pink azalea; W.S.F. Schuster, personal communication). Alec Meadow Reservoir is a man-made pond located centrally in the forest ($41^{\circ}24'\text{N}$; $74^{\circ}00'\text{W}$) and surrounded by oak woods. For this experiment, seven observably healthy individuals each of *B. thunbergii*, *K. latifolia*, and *V. corymbosum* were selected randomly in the forest understory around the northwest corner of Alec Meadow Reservoir for physiological measurements ($n = 7$). In 2004, Xu et al. (2007a) studied related leaf physiological variables of *B. thunbergii*, *K. latifolia*, and *V. corymbosum* individuals from this study site throughout the growing season.

Peak-season gas-exchange measurements

Leaf gas-exchange characteristics were measured on one fully expanded top canopy leaf from each selected individual using a portable gas-exchange system (LI-COR 6400, LI-COR, Lincoln, Nebraska, USA) equipped with a carbon dioxide (CO_2) control module during 8–11 July 2002 on warm, clear afternoons. Photosynthetic response to atmospheric CO_2 partial pressure (an A/C_i curve) was generated for each selected leaf by measuring the steady-state responses of photosynthesis to external CO_2 partial pressure (C_a) supplied in 10 steps from 0 to 100 Pa. At each C_a set-point, a photosynthetic measurement was made after gas exchange had equilibrated, which was determined when the coefficient of variation for the CO_2 partial pressure differential between the sample and reference analyzers was below 1%. During A/C_i measurements, leaf temperatures were kept at 25°C with thermoelectric coolers, and the water vapor pressure deficit was maintained between 1.0 and 1.5 kPa. A constant photon flux density of $1800\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was provided by blue–red light-emitting diodes mounted above the leaf cuvette.

Photosynthetic response curves were analyzed to calculate (i) the net photosynthetic rate at an external CO_2 partial pressure of 38 Pa and a photon flux density of $1800\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (A ; $\mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and (ii) the maximum rate of photosynthesis at saturating CO_2 partial pressure (A_{max} ; $\mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at an external CO_2 partial pressure of 38 Pa. The maximum carboxylation rate of ribulose biphosphate carboxylase oxygenase (V_{cmax} ; $\mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), the regeneration capacity of ribulose-1,5-

bisphosphate mediated by maximum electron transport rate (J_{max} ; $\mu\text{mol}\ \text{electrons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and the utilization of triose phosphate (TPU; $\mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), all of which are potentially limiting to photosynthesis, were also calculated from the A/C_i curves. These calculations were made using Photosynthesis Assistant (Dundee Scientific, Scotland, UK), a program that utilizes the biochemical model describing photosynthesis developed by Farquhar et al. (1980). This software was also used to model representative A/C_i curves for each species, using mean values of gas-exchange characteristics.

Leaf biochemistry, structure, and cost-effectiveness

Following in situ gas-exchange measurements, leaves used for measurements were harvested along with nearby leaves to yield enough material for subsequent analyses. Leaf material was processed through a portable area meter (Li-3000A, LI-COR) and then dried in a 60°C oven for 48 h and weighed to determine leaf mass per unit area (LMA; $\text{g}\cdot\text{m}^{-2}$) for each individual. Leaves were then ground into a fine powder with a ball mill (Cianflone Scientific Instruments, Pittsburgh, Pennsylvania, USA). Concentrations of organic carbon (C) and nitrogen (N) were determined for two 1–2 mg subsamples of dried leaf material with an elemental analyzer (Carlo Erba Na 1500, Milan, Italy) for each individual. These duplicate subsamples were averaged. We estimated the mineral concentration of each sample by multiplying the ash content by 0.67 (see Vertregt and Penning de Vries 1987). To determine ash content, a small pre-weighed subsample of material was burned in a 400°C muffle furnace for 8 h to obtain ash; the ash mass was then divided by the subsample dry mass.

Construction costs, expressed in equivalent grams of glucose per gram, were calculated according to the following biochemical equation (Vertregt and Penning de Vries 1987; Poorter 1994):

$$\text{CC} = (-1.041 + 5.007C)(1 - \text{Min}) + 5.235N_{\text{org}}$$

where C , Min , and N_{org} are the concentrations of carbon, minerals, and organic nitrogen, respectively. Although the equation includes only organic nitrogen, we substituted total N for this variable because NO_3 accumulation has been reported to be negligible in plants when leaf N is less than $29\ \text{mg}\cdot\text{g}^{-1}$ (Garnier and Freijssen 1994), a condition met by >95% of our samples.

For comparison with photosynthetic measurements, leaf N and CC were expressed per unit leaf area (N_{area} , CC_{area}) by multiplying their mass-based values by LMA for each sampled individual. Photosynthetic EUE ($\mu\text{mol}\ \text{CO}_2\cdot(\text{kg}\ \text{glucose})^{-1}\cdot\text{s}^{-1}$) and NUE ($\mu\text{mol}\ \text{CO}_2\cdot(\text{g}\ \text{nitrogen})^{-1}\cdot\text{s}^{-1}$) of sampled leaves were calculated as mean leaf A/CC and A/N , respectively. Theoretical EUE_{max} ($\mu\text{mol}\ \text{CO}_2\cdot(\text{kg}\ \text{glucose})^{-1}\cdot\text{s}^{-1}$) and NUE_{max} ($\mu\text{mol}\ \text{CO}_2\cdot(\text{g}\ \text{nitrogen})^{-1}\cdot\text{s}^{-1}$) were calculated similarly with A_{max} values.

Temporal variations in leaf energetic properties

To examine the influence of both leaf phenological differences and temporal variations in leaf energy investment on EUE, we estimated leaf EUE and EUE_{max} of *B. thunbergii*, *K. latifolia*, and *V. corymbosum* in our study site throughout the 2004 growing season from measurements of photosyn-

Table 1. Summary of one-way ANOVA results between groups for all measured leaf photosynthetic, structural, and biochemical variables, where species was considered the fixed independent variable.

Variable*	Sum of squares	df	Mean square	F	P
A ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	2.384	2	1.192	0.296	0.747
A _{max} ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	42.841	2	21.420	2.659	≤0.1
V _{cmax} ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	33.738	2	17.869	0.538	0.593
J _{max} ($\mu\text{mol electrons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	1019.432	2	509.716	2.634	≤0.1
TPU ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	83.147	2	41.574	4.780	≤0.05
CC (eq. g glucose g ⁻¹)	0.284	2	0.142	116.320	≤0.01
CC _{area} (eq. g glucose m ⁻²)	44951.178	2	22475.589	29.087	≤0.01
LMA (g·m ⁻²)	16419.115	2	8209.557	24.639	≤0.01
C (%)	114.843	2	57.422	128.597	≤0.01
N (%)	0.629	2	0.314	9.346	≤0.01
C/N	417.470	2	208.735	17.105	≤0.01
EUE ($\mu\text{mol CO}_2\cdot(\text{kg glucose})^{-1}\cdot\text{s}^{-1}$)	5425.085	2	2712.542	7.078	≤0.01
EUE _{max} ($\mu\text{mol CO}_2\cdot(\text{kg glucose})^{-1}\cdot\text{s}^{-1}$)	47090.930	2	23545.465	19.616	≤0.01
NUE ($\mu\text{mol CO}_2\cdot(\text{g nitrogen})^{-1}\cdot\text{s}^{-1}$)	9.714	2	4.857	1.614	0.227
NUE _{max} ($\mu\text{mol CO}_2\cdot(\text{g nitrogen})^{-1}\cdot\text{s}^{-1}$)	138.056	2	69.028	5.959	≤0.01

*A, mean rate of leaf net photosynthesis at an external CO₂ partial pressure of 38 Pa and photon flux density of 1800 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; A_{max}, maximum rate of photosynthesis at saturating external CO₂ partial pressure and photon flux density of 1800 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; V_{cmax}, maximum carboxylation rate of ribulose biphosphate carboxylase oxygenase; J_{max}, ribulose-1,5-biphosphate regeneration capacity mediated by maximum electron transport rate; TPU, triose phosphate utilization rate; CC, construction cost; CC_{area}, area-based construction cost; LMA, leaf mass per unit area; EUE, energy-use efficiency; EUE_{max}, maximum energy-use efficiency; NUE, nitrogen-use efficiency; NUE_{max}, maximum nitrogen-use efficiency.

thesis and leaf biochemistry made by Xu et al. (2007a). In that study, the researchers measured leaf photosynthetic rate of two upper canopy leaves of three individuals of each of these species at the study site during five measurement periods in 2004: 6–8 May, 12–13 June, 23–25 August, 24–25 September, and 16–17 November. In May, these measurements included only *B. thunbergii* and *K. latifolia* individuals because fully mature leaves were not yet present on *V. corymbosum*. In November, when both *B. thunbergii* and *V. corymbosum* were dormant, only leaves of *K. latifolia* were measured. For each point in time, the photosynthetic response to internal leaf CO₂ partial pressure was assessed for each selected leaf with a portable gas-exchange system (LI-COR 6400) equipped with a CO₂ control module on warm, clear afternoons. In situ leaf A was calculated from this response for each leaf during each measurement date, as described by Xu et al. (2007a). Following photosynthesis measurements, leaves were harvested, oven-dried, ground, and analyzed for carbon and nitrogen content with an elemental analyzer (2400 series II, Perkin-Elmer, Boston, Massachusetts, USA; see Xu et al. 2007a). To investigate temporal changes in energy- and resource-use efficiency throughout a growing season, we estimated leaf CC for these leaves with the biochemical equation previously described. The mean mineral concentration of each species from our 2002 measurements was used as an estimate of mineral concentration because mineral content was not measured in 2004 and its contribution to overall CC is minimal. Both EUE and EUE_{max} were then calculated from A and CC estimates, as previously described.

Statistical analyses

Measurements of each dependent variable were averaged for each species. One-way analysis of variance (ANOVA) was performed to test for the effect of species on all variables measured in peak season 2002. A repeated measures

ANOVA design was used to test for the effect of species on EUE and NUE across the 2004 growing season (SPSS for Windows, Rel. 7.5.1, 1996, SPSS, Inc., Chicago, Illinois, USA). Mean differences were considered significant if *P* was ≤0.05, unless otherwise noted. Species were compared to determine if the means of the dependent variable were significant with least significant difference post hoc analysis (Sokal and Rohlf 1981) following the verification of equal sample variances with Levene's test. Means of gas-exchange variables were used to model representative peak-season A/C_i curves for each species using the model developed by Farquhar et al. (1980).

Results

Leaf carbon acquisition

In general, interspecific differences in peak-season instantaneous measures of leaf photosynthetic activity were limited. Neither mean leaf A or A_{max} varied significantly among the studied species (Table 1). Species did not significantly affect instantaneous peak-season V_{cmax} or J_{max}; however, there was a significant species effect on TPU (Table 1). Mean TPU was 68.8% greater in *B. thunbergii* than in *K. latifolia* (*P* = 0.038), although TPU did not differ between *B. thunbergii* and *V. corymbosum* (Table 2). Representative curves modeled using mean gas-exchange characteristics illustrate minimal interspecific differences in photosynthetic response to external CO₂ partial pressure. Invasive *B. thunbergii* exhibited the greatest modeled photosynthetic response to increasing external CO₂ partial pressure, while the responses for the two native species were similar (Fig. 1).

Peak-season biomass investment and cost-effectiveness

All measured leaf structural and biochemical traits exhibited significant species effects (Table 1). Peak-season leaf

Table 2. Instantaneous peak-season leaf-level photosynthetic variables of invasive (*Berberis thunbergii*) and co-occurring native (*Kalmia latifolia*, *Vaccinium corymbosum*) understory forest shrubs with distinct leaf phenological characteristics.

Variable*	<i>B. thunbergii</i>	<i>K. latifolia</i>	<i>V. corymbosum</i>
A ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	9.3 $\pm$ 0.9a	9.9 $\pm$ 0.5a	9.1 $\pm$ 0.8a
A _{max} ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	21.1 $\pm$ 1.2a	17.6 $\pm$ 0.7a	19.4 $\pm$ 1.3a
V _{cmax} ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	35.9 $\pm$ 2.2a	33.8 $\pm$ 1.6a	32.7 $\pm$ 2.7a
J _{max} ($\mu\text{mol electrons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	109.9 $\pm$ 6.2a	93.4 $\pm$ 3.9a	97.7 $\pm$ 9.0a
TPU ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	11.8 $\pm$ 1.5b	7.0 $\pm$ 0.4a	9.2 $\pm$ 1.1ab

Note: Values presented are species means $\pm$ 1 standard error. Within a row, values followed by different letters are statistically different at the $P \leq 0.05$ level of significance.

*A, mean rate of leaf net photosynthesis at an external CO₂ partial pressure of 38 Pa and photon flux density of 1800 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; A_{max}, maximum rate of photosynthesis at saturating external CO₂ partial pressure and photon flux density of 1800 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; V_{cmax}, maximum carboxylation rate of ribulose biphosphate carboxylase oxygenase; J_{max}, ribulose-1,5-bisphosphate regeneration capacity mediated by maximum electron transport rate; TPU, triose phosphate utilization rate.

CC was 15.2% less in *B. thunbergii* than in either *K. latifolia* or *V. corymbosum* ($P < 0.001$ for both comparisons; Table 3). Because of the influence of LMA, which was 57.8% and 85.6% greater in leaves of *K. latifolia* than in *B. thunbergii* and *V. corymbosum*, respectively ($P < 0.001$ for both comparisons; Table 3), leaf CC_{area} differed among species. Mean leaf CC_{area} of *B. thunbergii* was 46.3% less than that of native *K. latifolia* ($P < 0.001$); however, this variable did not differ significantly between *B. thunbergii* and *V. corymbosum* (Table 3).

Peak-season leaf biochemical variables were significantly affected by species (Table 1). Mean leaf C of *B. thunbergii* was 9.6% less than that of *K. latifolia* and 9% less than that of *V. corymbosum* ($P < 0.001$ for both comparisons); however, leaf C did not differ significantly between the native species (Table 3). Invasive *B. thunbergii* exhibited 21.4% greater mean leaf N than native *K. latifolia* ($P = 0.002$), although this variable did not differ significantly between *B. thunbergii* and *V. corymbosum* (Table 3). Conversely, *K. latifolia* exhibited significantly greater leaf C/N than *B. thunbergii* (35.8%; $P < 0.001$); however, leaf C/N did not differ significantly among the *B. thunbergii* and *V. corymbosum* (Table 3).

There were significant species effects on most instantaneous peak-season measures of energy- and resource-use efficiency (Table 1). Mean EUE was 69.2% greater in exotic *B. thunbergii* than in native *K. latifolia* ($P = 0.003$), but EUE did not differ significantly between *B. thunbergii* and *V. corymbosum* (Fig. 2a). In contrast to EUE, instantaneous NUE was not affected by species (Table 1; Fig. 2b). Conversely, both EUE_{max} and NUE_{max} were affected significantly by species (Table 1) and appeared to exhibit similar interspecific differences. *Berberis thunbergii* was characterized by a 119.8% greater EUE_{max} ($P < 0.001$) and 51.5% greater NUE_{max} than that of *K. latifolia* ($P = 0.01$); however, neither of these variables differed significantly between deciduous *B. thunbergii* and *V. corymbosum* (Figs. 2c and 2d).

Seasonal trends in biomass investment and cost-effectiveness

Leaf energy investment in biomass (CC) and its use efficiency (EUE) differed significantly between species and across the growing season in 2004 (Fig. 3). Mean leaf CC, which exhibited significant within-subjects and between-

Fig. 1. Representative curves depicting leaf photosynthetic response to intracellular carbon dioxide (CO₂) partial pressure at a photon flux density of 1800 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (A/C_i) as modeled from mean values of gas-exchange characteristics measured for invasive *Berberis thunbergii* (○) and co-occurring natives *Kalmia latifolia* (□) and *Vaccinium corymbosum* (▼) in a forest understory during early to mid-July 2002. A/C_i curves were generated using the model developed by Farquhar et al. (1980).

subjects main and interactive effects of month and species ($P < 0.001$ for all effects), were similar in range to peak-season 2002 measurements for each species throughout its period of mature leaf presence. Throughout the growing season, leaf CC was consistently lower in *B. thunbergii* than in native *K. latifolia* or *V. corymbosum* (Fig. 3a). Similar to leaf CC, both EUE and EUE_{max} exhibited significant within-subjects and between-subjects main and interactive effects of month and species ($P < 0.001$ for all effects for both variables). Overall, the ranges of EUE for all the studied species were lower throughout the 2004 growing season than during peak-season 2002; however, interspecific comparisons of EUE were similar to those made from our peak-season 2002 measurements. Mean EUE was similar in *B. thunbergii* and *V. corymbosum* throughout the time in which both species had mature leaves in 2004, whereas *K. latifolia* exhibited lower EUE throughout the 2004 growing season (Fig. 3b). Mean leaf EUE_{max} estimates for the 2004 growing season were also generally lower than our

Table 3. Leaf biochemical and structural variables of invasive (*Berberis thunbergii*) and co-occurring native (*Kalmia latifolia*, *Vaccinium corymbosum*) understory forest shrubs with distinct leaf phenological characteristics.

Variable*	<i>B. thunbergii</i>	<i>K. latifolia</i>	<i>V. corymbosum</i>
CC (eq. g glucose·g ⁻¹)	1.28±0.02a	1.51±0.01b	1.51±0.02b
CC _{area} (eq. g glucose·m ⁻²)	106.8±4.1a	198.7±9.7b	106.9±13.5a
LMA (g·m ⁻²)	83.2±2.6a	131.3±6.6b	70.6±8.7a
C (%)	45.4±0.2a	50.2±0.1b	49.9±0.3b
N (%)	1.7±0.1b	1.4±0.1a	1.8±0.1b
C/N	26.8±1.1a	36.4±1.5b	28.6±1.0a

Note: Values presented are species means ± 1 standard error. Within a row, values followed by different letters are statistically different at the $P \leq 0.05$ level of significance.

*CC, leaf construction cost, expressed per unit dry mass and per unit surface area; LMA, leaf mass per unit area; C, percent leaf carbon concentration; N, percent leaf nitrogen concentration; C/N, ratio of leaf carbon to nitrogen.

Fig. 2. (a–d) Mean photosynthetic energy-use efficiency (EUE), nitrogen-use efficiency (NUE), maximum potential energy-use efficiency (EUE_{max}), maximum potential nitrogen-use efficiency (NUE_{max}) of leaves of invasive *Berberis thunbergii* and co-occurring natives *Kalmia latifolia* and *Vaccinium corymbosum* in a forest understory during early to mid-July 2002. Error bars represent 1 standard error of the mean. Different letters above bars indicate values that are statistically different at $P \leq 0.05$.

peak-season 2002 estimates. However, unlike EUE, interspecific comparisons of EUE_{max} differed from our peak-season 2002 comparisons, with *B. thunbergii* exhibiting greater EUE_{max} than both *K. latifolia* and *V. corymbosum* across measurement intervals (Fig. 3c).

Discussion

Photosynthetic measurements provide a basic assessment

of the energy supply of a plant, while CC reflects the energy demand of a plant for biomass production. Considered collectively, these measures could provide insightful evaluation of plant growth and proliferation. Overall, our findings provide partial support for our hypothesis that the demonstrated invasive success of *B. thunbergii* in forest understory communities can be influenced by greater cost-effectiveness of its energy gain and investment in leaf biomass via EUE, as

Fig. 3. (a) Mean leaf construction cost (CC), (b) photosynthetic energy-use efficiency (EUE), and (c) maximum potential energy-use efficiency (EUE_{max}) of leaves of invasive *Berberis thunbergii* (○) and co-occurring natives *Kalmia latifolia* (□) and *Vaccinium corymbosum* (▼) in a forest understory throughout the 2004 growing season. Error bars represent 1 standard error of the mean.

demonstrated both during peak season and through time, which could afford it a competitive advantage over native shrubs. Specifically, we suggest that greater EUE of *B. thunbergii* could enhance its competitive success over co-occurring native *K. latifolia* to some extent in our study sites (Figs. 2a and 3b). Furthermore, the significantly greater EUE_{max} of *B. thunbergii* compared with that of *K. latifolia* suggests that an enhanced capacity to maximize energy return per unit of energy invested in leaf biomass could influence invasion of *B. thunbergii* in forest understories where *K. latifolia* occurs if resources that promote photosynthesis become more plentiful, such as light and CO₂ (Figs. 2c and 3c). However, various demonstrated advantages of evergreen leaves, such as having a potentially longer time period for photosynthetic carbon gain each year and greater drought endurance (Givnish 2002), could offset such advantages,

which could be enhanced further by seasonal or long-term reductions in water availability. In contrast, the lack of a significant difference in EUE and EUE_{max} between *B. thunbergii* and native *V. corymbosum* indicates that cost-effectiveness (both actual and potential) during the peak season and through time cannot mechanistically explain the demonstrated invasive success of *B. thunbergii* in communities where *V. corymbosum* co-occurs (Figs. 2a, 2c, and 3b). Instead, we propose that having a longer payback time for photosynthetic energy return on biomass investment relative to later-leafing *V. corymbosum* could influence invasion of *B. thunbergii* in forest understories co-inhabited by *V. corymbosum*.

Interspecific differences in EUE and EUE_{max} among the studied species could only be partly explained by differences in leaf-level photosynthesis, which demonstrated the contextual importance of leaf biomass CC in these species. In particular, although leaves of *B. thunbergii* were characterized by greater EUE than those of *K. latifolia*, leaf *A* and *A*_{max} did not differ significantly between these species (Table 2). This finding demonstrates that peak-season photosynthetic activity alone, despite its fundamental role in the acquisition of energy required for growth, does not appear to influence the invasive success of *B. thunbergii* in the studied community. Photosynthetic activity is influenced by the biochemical reactions that regulate gas-exchange processes (Wullschlegel 1993). Here, the lack of interspecific differences in *A* and *A*_{max} appeared to be influenced, in particular, by interspecific similarities in the processes that regulate gas-exchange at increasing concentrations of CO₂ (Table 2, Fig. 1). Only TPU varied among species; the greater TPU exhibited by *B. thunbergii* compared with *K. latifolia* suggests that photosynthetic responses to very high concentrations of CO₂ are less limited by TPU in *B. thunbergii* than in *K. latifolia* (Table 2).

Since leaves are the primary location of photosynthetic energy gain, leaf CC can be particularly influential to the cost-effectiveness of energy investment. In particular, a relatively low leaf CC could enhance the efficiency with which energy is converted into leaf biomass; whereas a high leaf CC would require greater energy investment in leaf biomass production. Here, the lower mass-based leaf CC of *B. thunbergii* compared with that of both of the studied native species suggests that *B. thunbergii* could construct relatively more leaf material per unit of available energy, which could in turn influence its photosynthetic energy gain on an organismal level (Table 3). Furthermore, the lower leaf CC expressed per unit leaf surface area (CC_{area}) of *B. thunbergii* compared with *K. latifolia* suggests that *B. thunbergii* individuals could increase their leaf surface area with less energetic cost than could *K. latifolia* individuals, which could be competitively advantageous for *B. thunbergii*. Specifically, because leaf CC_{area} provides information about processes influenced by leaf surface area, such as light interception or gas diffusion to the plant surface (Griffin 1994), a reduced CC_{area} indicates that the efficiency of these processes could be enhanced in *B. thunbergii* in comparison with *K. latifolia*. Furthermore, interspecific differences in CC_{area} between *B. thunbergii* and *K. latifolia* reflect both differences in CC and in leaf thickness and (or) cellular density as evidenced by LMA between those species

(Table 3). Plants with relatively high LMA typically contain relatively more energetically expensive lignin and cell wall components than those with lower LMA (Groeneveld et al. 1998), which could be reflected by the greater CC of *K. latifolia* than *B. thunbergii* in our study. Overall, we suggest that the invasive success of *B. thunbergii* in communities with *K. latifolia* could be influenced by differences in their CC, CC_{area} , and LMA, which could afford *B. thunbergii* a higher capacity for light interception and photosynthetic energy assimilation, with limited energetic expense. However, similarities in CC_{area} and LMA do not provide an explanation for the demonstrated invasion of *B. thunbergii* in communities with *V. corymbosum*.

Nitrogen is generally contained in relatively expensive biochemical compounds, such as proteins and amino acids (Penning de Vries et al. 1974; Williams et al. 1987), and therefore typically exhibits a positive correlation with leaf CC (Griffin et al. 1993, 1996). Consequently, leaf *N* is an inherent component of the determination of leaf CC (see eq. 1). Although leaf *C* also influences CC (see eq. 1), the magnitude of such influence can be affected significantly by the incorporation of carbon into relatively expensive secondary compounds versus inexpensive storage carbohydrates (Griffin 1994). Here, *B. thunbergii* exhibited a combination of a greater leaf *N* than *K. latifolia* and a lower leaf *C* and CC than both *K. latifolia* and *V. corymbosum* (Table 3). These results indicate that both *K. latifolia* and *V. corymbosum* may invest increased carbon in relatively expensive structural compounds, such as cellulose and lignin (Herms and Mattson 1992), than does *B. thunbergii*. In terms of cost-effectiveness of leaf biomass investment, we suggest this carbon investment could offset the greater leaf *N* of *B. thunbergii* than *K. latifolia* as well as the lack of difference in leaf *N* of *B. thunbergii* and *V. corymbosum* in our study site. We propose that this unique combination of carbon and nitrogen attributes relatively to co-occurring native shrubs could facilitate the invasion of *B. thunbergii* in our study site and similar understory environments.

Although we found partial support for our hypothesis — that EUE would influence the invasive success of *B. thunbergii* in forest understory communities — our prediction that the cost-effectiveness of resource investment in leaf biomass via NUE also would be influential was not supported (Fig. 2b). Despite *K. latifolia*'s reduced leaf *N* but similar *A* compared with both *B. thunbergii* and *V. corymbosum*, *K. latifolia*'s NUE may have been negatively influenced by its thicker and (or) denser leaf biomass, since increased nitrogen would be required to produce a given unit of leaf surface area. In contrast, we suggest that leaf NUE_{max} , like EUE_{max} , potentially could influence the invasive success of *B. thunbergii* in the studied community to some extent. Specifically, the greater NUE_{max} of *B. thunbergii* compared with that of native *K. latifolia* (Fig. 2d) indicates that *B. thunbergii* could have an advantage over *K. latifolia* under conditions in which photosynthesis is maximized (such a high light or atmospheric CO_2). Additionally, the greater EUE of *B. thunbergii* than *K. latifolia*, without a concurrent variation in NUE among these species, supports our previous suggestion that *K. latifolia* may be influenced negatively by the investment of its carbon into more expensive biochemical compounds

compared with *B. thunbergii*. In contrast to *B. thunbergii* – *K. latifolia* comparisons of NUE_{max} , *B. thunbergii* and *V. corymbosum* exhibit similar peak-season NUE_{max} , which indicates that this variable does not provide a viable mechanistic explanation for the invasive success of *B. thunbergii* in communities where it co-occurs with *V. corymbosum*.

The distinct leaf phenological characteristics of our studied species require consideration of the potential implications of instantaneous measures of peak-season cost-effectiveness of leaf biomass on energetic gains and costs throughout a growing season. Differences in EUE between the deciduous and evergreen species in our study agreed with those of previous research examining relationships between CC and photosynthetic rates of plant species in warm climates, which found that increased EUE was associated typically with decreased leaf life-span (Sobrado 1991; Eamus and Prichard 1998; Eamus et al. 1999). Collectively, these results indicate that a relatively long pay-back time for photosynthetic energy gain could be characteristic of leaves with a relatively high energy investment in biomass. Although *K. latifolia* has longer-lived leaves, we suggest that the greater EUE, EUE_{max} , and NUE_{max} of *B. thunbergii* compared with evergreen *K. latifolia* during peak-season could offset any benefits of a longer leaf life-span on the seasonal cost-effectiveness of leaf biomass in *K. latifolia*. In contrast, we suggest that the longer-lived deciduous leaves of *B. thunbergii* compared with *V. corymbosum* could offset the similar peak-season cost-effectiveness of their leaf energy investment when integrated across leaf life-span.

In general, peak-season cost-effectiveness could influence plant performance by allowing more advantageous resource use when environmental conditions, such as temperature, are most optimal for photosynthetic activity. However, seasonal trends in leaf energy investment in biomass and its cost-effectiveness provide a more complete picture of the potential influence of these variables on plant performance. In particular, intraspecific differences in CC, EUE, and EUE_{max} assessed at various intervals throughout a growing season illustrate the potential combined importance of leaf-level biochemistry, physiology, and phenology to the relative performance of various species in a community. When compared across species, invasive *B. thunbergii* exhibited lower CC than either of the studied native species throughout a growing season, suggesting this species maintains its lower energetic cost of leaf biomass production over time (Fig. 3a). We suggest that the greater EUE exhibited by *B. thunbergii* than *K. latifolia* throughout the growing season could influence the invasion of *B. thunbergii* in the forest understory. Furthermore, although the cost-effectiveness of biomass production in both *B. thunbergii* and native *V. corymbosum* was similar throughout their concurrent periods of leaf presence, both *B. thunbergii*'s earlier leaf emergence over *V. corymbosum*'s and its much greater early-season EUE than late-season EUE could also influence its invasive success (Fig. 3b). Finally, the comparatively greater EUE_{max} of *B. thunbergii* than either *K. latifolia* or *V. corymbosum* exhibited throughout a growing season indicates that a greater potential for energy return on leaf biomass investment could promote *B. thunbergii* invasion in forest understories if and when light and CO_2 increase

(Fig. 3c). Although EUE_{max} did not similarly vary between *B. thunbergii* and *V. corymbosum* during peak-season 2002 (Fig. 2c), possibly due to interseasonal differences in leaf physiology of those species, even similar values of instantaneous EUE_{max} could provide *B. thunbergii* with a competitive advantage over *V. corymbosum* when considered across their respective periods of leaf presence.

Overall, our results indicate that two distinct mechanisms could influence the invasive success of *B. thunbergii* in forest understory communities where *K. latifolia* and *V. corymbosum* are common. Specifically, we suggest that a combination of relatively high peak-season and across-season cost-effectiveness of leaf energy investment in comparison to evergreen species and a longer payback time for photosynthetic energy return on biomass investment relative to later-leafing deciduous species could collectively influence the demonstrated invasive success of *B. thunbergii* in these communities. These traits add to those determined by Xu et al. (2007a, 2007b) to be potential mechanisms of *B. thunbergii* invasion, including a spring carbon subsidy and effective acclimation to seasonal changes in light availability, despite the relatively high annual carbon loss via leaf respiration. Considered collectively, these findings illustrate that possessing a combination of physiological characteristics influential to energetic gains and cost could be potentially important for enhancing the invasive success of plant species within diverse communities. Because gas-exchange processes and the chemical composition of biomass can be influenced by abiotic factors, we propose that examining the influence of various environmental factors on the cost-effectiveness of leaf investment in invasive species and their native competitors could provide information useful for understanding how these species may respond to future environmental changes.

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