

Invasive *Buddleja davidii* allocates more nitrogen to its photosynthetic machinery than five native woody species

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Abstract The general-purpose genotype hypothesis and the hypothesis of the evolution of invasiveness predict that invasive species are characterized by particular traits that confer invasiveness. However, these traits are still not well-defined. In this study, ecophysiological traits of eight populations of the invasive shrub *Buddleja davidii* from a wide range of European locations and five co-occurring native woody species in Germany were compared in a common garden experiment. We hypothesized that the invader has higher resource capture ability and utilization efficiency than the natives. No differences were detected among the eight populations of *B. davidii* in any of the traits evaluated, indicating that the invader did not evolve during range expansion, thus providing support to the general-purpose genotype hypothesis. The invader showed significantly higher maximum electron transport rate, maximum carboxylation rate, carboxylation efficiency, light-saturated photosynthetic rate (P_{\max}) and photosynthetic nitrogen utilization efficiency (PNUE) than the five natives. Leaf nitrogen content was not significantly different between the invader and the natives, but the invader allocated more nitrogen to the photosynthetic machinery than the natives. The increased nitrogen content in the photosynthetic

machinery resulted in a higher resource capture ability and utilization efficiency in the invader. At the same intercellular CO_2 concentration, P_{\max} was significantly higher in the invader than in the natives, again confirming the importance of the higher nitrogen allocation to photosynthesis. The invader reduced metabolic cost by increasing the ratio of P_{\max} to dark respiration rate (R_d), but it did not reduce carbon cost by increasing the specific leaf area and decreasing leaf construction cost. The higher nitrogen allocation to the photosynthetic machinery, P_{\max} , PNUE and P_{\max}/R_d may facilitate *B. davidii* invasion, although studies involving a wide range of invasive species are needed to understand the generality of this pattern and to fully assess the ecological advantages afforded by these features.

Keywords Capture ability · Comparison · Construction cost · Utilization efficiency · Water

List of symbols

C_B	ratio of leaf chlorophyll to leaf nitrogen in light-harvesting components in mmol g^{-1}
C_C	leaf chlorophyll concentration in mmol g^{-1}
C_i	intercellular CO_2 concentration in $\mu\text{mol mol}^{-1}$
CC	leaf construction cost in g dm^{-2}
CE	carboxylation efficiency
G_s	stomatal conductance in $\text{mol m}^{-2} \text{s}^{-1}$
J_{\max}	maximum electron transport rate in $\mu\text{mol m}^{-2} \text{s}^{-1}$
J_{mc}	the potential rate of photosynthetic electron transport per unit cytochrome <i>f</i> in $\mu\text{mol } \mu\text{mol}^{-1} \text{s}^{-1}$
K_c	the Michaelis–Menten constant of Rubisco for carboxylation in $\mu\text{mol mol}^{-1}$
K_o	the Michaelis–Menten constant of Rubisco for oxidation in mmol mol^{-1}

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N_A	total leaf nitrogen content in g m^{-2}
N_M	mass-based leaf nitrogen content in g g^{-1}
N_P	nitrogen content in photosynthetic machinery in g m^{-2}
O	intercellular oxygen concentration in mmol mol^{-1}
P_B	fraction of leaf nitrogen allocated to bioenergetics in g g^{-1}
P_C	fraction of leaf nitrogen allocated to carboxylation in g g^{-1}
P_L	fraction of leaf nitrogen allocated to light-harvesting components in g g^{-1}
P_{\max}	light-saturated photosynthetic rate in $\mu\text{mol m}^{-2} \text{s}^{-1}$
$P_{\max-M}$	mass-based light-saturated photosynthetic rate in $\mu\text{mol g}^{-1} \text{s}^{-1}$
P_{\max}'	light- and CO_2 -saturated photosynthetic rate in $\mu\text{mol m}^{-2} \text{s}^{-1}$
P_n	net photosynthetic rate in $\mu\text{mol m}^{-2} \text{s}^{-1}$
P_T	fraction of leaf nitrogen allocated to all components of photosynthetic machinery in g g^{-1}
PNUE	photosynthetic nitrogen utilization efficiency (P_{\max}/N_A) in $\mu\text{mol g}^{-1} \text{s}^{-1}$
PPFD	photosynthetic photon flux density in $\mu\text{mol m}^{-2} \text{s}^{-1}$
R_d	dark respiration rate in $\mu\text{mol m}^{-2} \text{s}^{-1}$
RE	respiration efficiency (P_{\max}/R_d)
SLA	specific leaf area in $\text{cm}^2 \text{mg}^{-1}$
V_{cmax}	maximum carboxylation rate in $\mu\text{mol m}^{-2} \text{s}^{-1}$
V_{cr}	specific activity of Rubisco in $\mu\text{mol g}^{-1} \text{s}^{-1}$
WUE	water utilization efficiency (P_{\max}/G_s) in $\mu\text{mol mol}^{-1}$
Γ^*	CO_2 compensation point in $\mu\text{mol mol}^{-1}$

Introduction

Biological invasion is a serious environmental problem and is becoming more and more severe as the scale of international trade and global change increases (Lodge 1993; Chapin et al. 2000). Invasive species have an impact on biodiversity, species composition, structure and function of invaded ecosystems (Lodge 1993; Vitousek et al. 1997; D'Antonio and Kark 2002), and may cause huge economic losses (Normile 2004). However, the mechanisms that underlie invasiveness are still not well explained (McDowell 2002). It is very important to identify the factors that influence invasions by alien plant species because it could improve our ability to predict and control potentially invasive species.

Vitousek (1986) proposed that successful invasive species must either use limiting resources more efficiently than native species or use them at times when they are

unavailable to the latter, if life history traits and susceptibility to herbivory are similar between native and invasive species. Pattison et al. (1998) found that invasive species have higher growth rates and P_{\max} values than native species, and hypothesized that successful invasive species have ecophysiological traits that can increase resource capture ability and utilization efficiency. However, only a few studies have been conducted to test these hypotheses, and the results from such studies are inconsistent. For example, P_{\max} and SLA are higher for invasive species than for native species (Pattison et al. 1998; Baruch and Goldstein 1999; Durand and Goldstein 2001), whereas similar or lower P_{\max} and SLA are also reported for invasive species (Harrington et al. 1989; Pattison et al. 1998; Smith and Knapp 2001; McDowell 2002; Ewe and Sternberg 2003).

Invasive species are suggested to accumulate more carbon and light energy and to increase growth or reproduction by increasing P_{\max} (Baruch and Goldstein 1999; Durand and Goldstein 2001). Similarly, invasive species may benefit from decreasing costs of resource capture. It has been reported that invasive species have a higher SLA and a lower leaf CC than native species (Baruch and Goldstein 1999; Durand and Goldstein 2001; Nagel and Griffin 2001; Smith and Knapp 2001). Invasive species can also reduce carbon cost by increasing RE (Pattison et al. 1998; McDowell 2002). Nitrogen and water are often the limiting resources for plants in natural ecosystems. Invasive species can use them efficiently, leading to a competitive advantage over native species (Pattison et al. 1998; Baruch and Goldstein 1999; Durand and Goldstein 2001; McDowell 2002; Ewe and Sternberg 2003).

Niinemets et al. (2003) found that the high PNUE of an invasive species was due to its high P_{\max} rather than to its low leaf-nitrogen content. Nitrogen allocation to the photosynthetic machinery is an important influence on PNUE. As the nitrogen allocated to photosynthesis is increased, PNUE will increase. In addition, the differences between invasive and native species in WUE and in the relationship between PNUE and WUE are not clear (Delucia and Schlesinger 1991; McDowell 2002; Hill et al. 2006).

Traits facilitating invasion by alien species may evolve in the introduced range (Blossey and Nötzold 1995; Bosdorf et al. 2005); this factor has received little attention in ecophysiology so far (but see Niinemets et al. 2003). In addition, local genetic adaptation to the different environments encountered during range expansion may take place in invasive species (McKay et al. 2001; Sexton et al. 2002; Lambrinos 2004). Alternatively, invasive species may consist of general-purpose genotypes that are able to colonize different environments (Baker 1965; Parker et al. 2003). DeWalt et al. (2004) compared traits between introduced and native populations of an invasive shrub, and

found that ecophysiological traits can evolve rapidly in the introduced range. However, both the hypothesis of the evolution of invasiveness and the general-purpose genotype hypothesis suggest that successful invaders are characterized by particular traits, including the ability to optimize resource allocation.

Buddleja davidii Franchet (Loganiaceae), native to China, was first introduced to Britain as an ornamental plant in the 1890s (Binggeli 1998). It can tolerate a wide range of climates and soil types, but prefers dry open disturbed sites such as bomb pits, mining towns, roadsides, abandoned areas, pastures, scree slopes, open woodlands and forestry plantations (Binggeli 1998). The plant can quickly form dense monocultures, displacing native species (Humphries and Guarino 1987). *B. davidii* has become naturalized as an invasive deciduous shrub in Europe, New Zealand, Australia and the United States (Binggeli 1998). However, few works investigating the causes of its invasiveness have been conducted. In this study, the ecophysiological characteristics of eight European populations of *B. davidii* and five woody species native to Europe were contrasted. The main aims of this study were (1) to test the hypothesis that *B. davidii* has a higher resource capture ability (P_{\max}) and utilization efficiency (PNUE, WUE and RE) than the native species; (2) to detect the differences among the invader and the five native species in leaf nitrogen allocation and their ecological significance; (3) to explore the ecophysiological differences among the eight populations of *B. davidii*, shedding light on evolution hypothesis and the general-purpose genotype hypothesis.

Materials and methods

Study site and plant materials

This study was carried out in Halle (51°29'N, 11°58'E, 110 masl), Germany. The mean annual temperature there is 8.8 °C and the mean annual precipitation is 480 mm.

The seeds of *B. davidii* were collected from eight populations distributed over a wide range of environmental zones in Europe (Table 1). About ten seed families were collected from each population in 2004. The seeds were germinated in a greenhouse in March 2005. In May 2005, when the seedlings were approximately 10 cm high, 80 similar-sized seedlings (two seedlings per seed family, five seed families per population) were transplanted to five plots at an open site in the Botanical Garden of the Martin-Luther University in Halle. Each plot contained one seed family from each population. The seedlings were spaced 50 cm apart and were positioned randomly. No water and fertilizer were added to the plots during the experiment after the seedlings had recovered from transplantation.

For our comparative study, we choose five woody species native to Europe that can grow in the same habitats as *B. davidii* and are, thus, among its main competitors. The shrubs *Berberis vulgaris* L. (Berberidaceae), *Cornus sanguinea* L. (Cornaceae) and *Sambucus nigra* L. (Caprifoliaceae), and the shrub or small tree *Crataegus monogyna* Jacq. (Rosaceae) can co-occur with *B. davidii* in nitrophilous ruderal communities, in dry scrub or on river banks (Schmitz 1991; Schubert et al. 2001). The native pioneer tree *Betula pendula* Roth (Betulaceae) can be outperformed by *B. davidii* on nitrogen-poor sites as well as under conditions of water stress (Humphries et al. 1982; Humphries and Guarino 1987). Individuals of *B. vulgaris*, *C. sanguinea* and *S. nigra* were chosen in an open area in the Botanical Garden, within a distance of 5–15 m from the plots of *B. davidii*. Individuals of *B. pendula* and *C. monogyna* were chosen at an open site in the yard of the Helmholtz Centre for Environmental Research, at a distance of about 2,000 m from the Garden. Individuals of the native species were approximately the same size and grew in habitats similar to the site of the *B. davidii* plants studied.

Measurements

In September 2005, measurements were taken on fully expanded leaves (the third leaf from the tip) in five individuals per population (one per seed family) of *B. davidii* and in four individuals per native species. The same leaf was used if possible for measurements of photosynthesis, SLA and the contents of chlorophyll, carbon and nitrogen. In this way, differences among leaves of the same plant could be avoided when the relationships among the variables were analyzed.

Under a PPFD of 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, P_n was measured at 400, 350, 300, 260, 220, 180, 140, 110, 80, 50 $\mu\text{mol mol}^{-1} \text{CO}_2$ in the reference chamber with a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA). The relative humidity of the air in the leaf chamber was held constant at 40% by the equipment, and the leaf temperature at 25 °C. P_n , G_s and C_i were recorded when the sample leaf was balanced for 200 s under each CO_2 step. Afterwards, P'_{\max} was detected after 500 s under 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD and 1,500 $\mu\text{mol mol}^{-1} \text{CO}_2$. Prior to the measurement, each sample leaf was illuminated with 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD provided by the LED light source of the equipment for 3–15 min to achieve fully photosynthetic induction. No photoinhibition occurred during the measurements.

The P_n - C_i curve was fitted using the linear equation ($P_n = k C_i + i$) within 50–200 $\mu\text{mol mol}^{-1} C_i$, where k was the CE, $-i/k$ was equal to Γ^* in the absence of mitochondrial respiration (Laisk 1977), which was very low under

Table 1 Background information on the eight studied populations of *Buddleja davidii*

Site	Country	Latitude	Longitude	Environmental zone ^a
Manchester	Britain	53°28'40"N	2°14'44"W	Atlantic north
Eastleigh	Britain	50°58'0"N	1°21'2"W	Atlantic central
St Malo	France	48°36'44"N	2°3'9"W	Atlantic central
Leioa	Spain	43°19'40"N	2°59'13"W	Lusitanian
Meran	Italy	44°31'0"N	8°17'51"E	Alpine south
Halle	Germany	51°29'4"N	11°58'5"E	Continental
Tettwang	Germany	47°38'1"N	9°35'5"E	Continental
Geneva	Switzerland	46°12'30"N	6°8'34"E	Continental

^a Environmental zones of Europe are based on Metzger et al. (2005)

illumination. V_{cmax} and R_d were calculated according to Farquhar and Sharkey (1982) as follows:

$$V_{cmax} = \{k \times [C_i + K_c \times (1 + O/K_o)]^2 / [\Gamma^* + K_c \times (1 + O/K_o)]\} \quad (1)$$

$$R_d = \{V_{cmax} \times (C_i - \Gamma^*) / [C_i + K_c \times (1 + O/K_c)] - (k \times C_i + i)\} \quad (2)$$

where K_c and K_o were $404.9 \mu\text{mol mol}^{-1}$ and $278.4 \text{ mmol mol}^{-1}$ at 25°C , respectively (Bernacchi et al. 2001), and O was $210 \text{ mmol mol}^{-1}$. J_{max} was calculated according to Loustau et al. (1999) as:

$$J_{max} = \{[4 \times (P'_{max} + R_d) \times (C_i + 2 \times \Gamma^*)] / (C_i - \Gamma^*)\} \quad (3)$$

A disc with a definite area was taken from each sample leaf, oven-dried at 60°C for 48 h, weighed with an analytic balance, and finely ground. To determine leaf nitrogen and carbon concentrations, the leaf powder was subjected to high temperature combustion with subsequent gas analysis by means of an Element Analyser Vario EL (Elementar Analysensysteme GmbH, Hanau, Germany). SLA was calculated as the ratio of leaf area to leaf mass. CC was calculated according to Vertregt and Penning de Vries (1987).

The absolute chlorophyll content of the native species was determined chemically according to Lichtenthaler and Wellburn (1983). The relative chlorophyll content of *B. davidii* was measured with a Chlorophyll Meter (SPAD-502, Minolta Co. Ltd., Osaka, Japan). Twenty readings were recorded on different parts of each sample leaf to avoid the influence of leaf heterogeneity on the readings. The absolute chlorophyll content of the sample leaf was calculated from the mean of 20 readings of the meter using a regression equation (chlorophyll content in $\text{g m}^{-2} = -0.1750 + 0.0108 \times \text{meter reading}$, $n = 12$, $r = 0.9752$). To establish the equation, relative and absolute chlorophyll contents were measured in 12 leaves of *B. davidii* with a chlorophyll meter and a chemical method, respectively.

P_C , P_B and P_L were calculated according to Niinemets and Tenhunen (1997) as:

$$P_C = V_{cmax} / (6.25 \times V_{cr} \times N_A) \quad (4)$$

$$P_B = J_{max} / (8.06 \times J_{mc} \times N_A) \quad (5)$$

$$P_L = C_C / (N_M \times C_B) \quad (6)$$

Where V_{cr} and J_{mc} were $20.78 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ Rubisco s}^{-1}$ and $155.65 \mu\text{mol electrons } \mu\text{mol}^{-1} \text{ cyt f s}^{-1}$ at 25°C , respectively, C_B was 2.15 mmol g^{-1} (Niinemets et al. 1998), 6.25 (g Rubisco g^{-1} nitrogen in Rubisco) was the conversion coefficient between nitrogen content and protein content in Rubisco, and 8.06 ($\mu\text{mol cyt f g}^{-1}$ nitrogen in bioenergetics) was the conversion coefficient between cyt f and nitrogen in bioenergetics.

P_T was calculated as the sum of P_C , P_B and P_L , and N_P as the product of N_A and P_T .

Statistical analyses

The differences among the eight populations of *B. davidii* and the differences between *B. davidii* and the five native species were analyzed with one-way ANOVA, and a post hoc test (Duncan test) was conducted if the differences were significant. A one-way ANCOVA was used to detect differences between *B. davidii* and the pooled native species in the relationships between different variables. All of the analyses were carried out using SPSS 10.0 (SPSS Inc., Chicago, IL, USA).

Results

There were no significant differences between the values of any of the variables measured in this study among the eight populations of *B. davidii* according to the results from a one-way ANOVA. The F - and P -values for the variables ranged from 0.189 and 0.985 (for P_B) to 1.946 and 0.096 (for chlorophyll concentration) (data not shown). Therefore, the populations were not differentiated when the

differences between *B. davidii* and the five native species were evaluated. The differences between the six studied species were significant in all variables except N_A and Γ^* , in which the differences were not significant (Table 2).

As P_T , P_C and P_B increased, PNUE increased linearly for *B. davidii* and for the five native species pooled together, and was significantly higher for the former than for the latter at the same value of P_T , P_C or P_B (Fig. 1). In addition, P_T , P_C and P_B were significantly higher in *B. davidii* than in the native species (Table 2). These results led to significantly higher PNUE for *B. davidii* than for the native species. For *B. davidii*, PNUE increased significantly with P_L , but the positive relationship disappeared when the outliers were removed from the analysis (Fig. 1). For the natives, PNUE showed decreasing trends with P_L .

V_{cmax} , CE and J_{max} increased linearly with increasing PNUE, P_T and N_P , and were evidently higher for *B. davidii* than for the natives (Fig. 2). However, the differences between the invader and the natives disappeared according to

the results of a one-way ANCOVA with PNUE, P_T and N_P as a covariate, respectively; all the data were distributed around the same line in each plot, indicating that the higher V_{cmax} , CE and J_{max} of the invader were due to its higher PNUE, P_T and N_P . The higher N_P of the invader was due to its higher P_T , P_C and P_B because N_A was not significantly different between the invader and the natives (Table 2). As N_A increased, V_{cmax} , CE and J_{max} also increased linearly (Fig. 2).

P_{max} increased significantly with V_{cmax} , CE, J_{max} (Fig. 3), P_T , N_P and N_A (Fig. 4), and was significantly higher for *B. davidii* than for the natives at the same value of V_{cmax} , CE, J_{max} , P_T , N_P or N_A , contributing to the higher P_{max} in the invader. However, the higher V_{cmax} , CE, J_{max} , P_T and N_P were more important for the higher P_{max} in *B. davidii* than the different P_{max} responses between the invader and the natives. The invader and the natives showed a similar increase in P_{max} with PNUE (Fig. 4). At the same value of N_A , *B. davidii* exhibited higher P_{max} , V_{cmax} , CE

Table 2 The results from one-way ANOVA with species ($n = 6$) used as the independent variable

Species variable	<i>Buddleja davidii</i>	<i>Berberis vulgaris</i>	<i>Cornus sanguinea</i>	<i>Sambucus nigra</i>	<i>Betula pendula</i>	<i>Crataegus monogyna</i>	F-values among species
P_C	0.60 ± 0.01a	0.22 ± 0.03d	0.40 ± 0.07b	0.35 ± 0.06bc	0.42 ± 0.02b	0.26 ± 0.01cd	23.46***
P_B	0.095 ± 0.012a	0.055 ± 0.003c	0.066 ± 0.004bc	0.061 ± 0.001bc	0.070 ± 0.002b	0.057 ± 0.003bc	29.32***
P_L	0.036 ± 0.004cd	0.049 ± 0.011b	0.056 ± 0.004a	0.032 ± 0.003d	0.036 ± 0.003cd	0.039 ± 0.007c	17.31***
P_T	0.73 ± 0.12a	0.32 ± 0.02c	0.52 ± 0.08b	0.44 ± 0.06bc	0.53 ± 0.02b	0.35 ± 0.01c	24.82***
PNUE	17.02 ± 2.35a	5.31 ± 0.66c	8.09 ± 1.19c	7.13 ± 0.90c	11.89 ± 1.33b	7.89 ± 0.67c	54.74***
N_P	1.20 ± 0.31a	0.51 ± 0.04c	0.90 ± 0.08ab	0.71 ± 0.14bc	0.90 ± 0.07ab	0.64 ± 0.06bc	9.10***
N_A	1.63 ± 0.32	1.60 ± 0.08	1.75 ± 0.25	1.60 ± 0.17	1.72 ± 0.13	1.82 ± 0.16	0.52
P_{max}	27.53 ± 5.57a	8.53 ± 1.24c	14.13 ± 2.58bc	11.40 ± 2.14c	20.48 ± 3.13b	14.40 ± 2.15bc	23.60***
P_{max-M}	0.42 ± 0.10a	0.07 ± .01c	0.21 ± .02b	0.20 ± 0.04b	0.33 ± 0.06a	0.12 ± 0.03bc	23.90***
V_{cmax}	128.0 ± 35.9a	45.0 ± 6.6c	89.5 ± 11.0ab	73.0 ± 16.1bc	93.5 ± 8.0ab	60.3 ± 5.7bc	9.91***
CE	0.20 ± 0.06a	0.07 ± 0.01c	0.14 ± 0.02ab	0.12 ± 0.03bc	0.15 ± 0.01ab	0.10 ± 0.01bc	9.71***
J_{max}	193.6 ± 40.2a	110.3 ± 10.3b	144.9 ± 15.4b	122.9 ± 14.8b	151.6 ± 12.3a	130.1 ± 16.7b	8.92***
G_s	0.40 ± 0.12a	0.08 ± 0.02c	0.14 ± 0.05bc	0.10 ± 0.03c	0.26 ± 0.07b	0.16 ± 0.04bc	16.61***
R_d	1.64 ± 0.56a	0.67 ± 0.08b	1.10 ± 0.53ab	0.83 ± 0.18b	1.65 ± 0.47a	1.20 ± 0.29ab	4.75***
WUE	73.6 ± 17.9c	107.6 ± 13.5a	103.5 ± 18.2ab	116.2 ± 13.7a	82.4 ± 13.9bc	95.7 ± 20.2abc	8.35***
CC	0.81 ± 0.15b	1.61 ± 0.09a	0.78 ± 0.12b	0.69 ± 0.04b	0.86 ± 0.05b	1.50 ± 0.37a	32.46***
SLA	0.15 ± 0.03a	0.08 ± 0.01b	0.15 ± 0.02a	0.17 ± 0.01a	0.16 ± 0.01a	0.08 ± 0.02b	11.85***
C_i	196.5 ± 22.3a	170.0 ± 19.0ab	155.8 ± 26.9b	152.8 ± 20.6b	202.3 ± 19.0a	193.8 ± 31.6a	5.46***

Species mean values ± SD are given ($n = 40$ for *Buddleja davidii*; $n = 4$ for each native species)

Different letters in the same row indicate significant differences among species (Duncan test)

P_C the fraction of leaf nitrogen allocated to carboxylation in $g\ g^{-1}$, P_B the fraction of leaf nitrogen allocated to bioenergetics in $g\ g^{-1}$, P_L the fraction of leaf nitrogen allocated to light-harvesting components in $g\ g^{-1}$, P_T the fraction of leaf nitrogen allocated to all components of the photosynthetic machinery in $g\ g^{-1}$, PNUE photosynthetic nitrogen utilization efficiency in $\mu mol\ g^{-1}\ s^{-1}$, N_P nitrogen content in the photosynthetic machinery in $g\ m^{-2}$, N_A total leaf nitrogen content in $g\ m^{-2}$, P_{max} light-saturated photosynthetic rate in $\mu mol\ m^{-2}\ s^{-1}$, P_{max-M} mass-based light-saturated photosynthetic rate in $\mu mol\ g^{-1}\ s^{-1}$, V_{cmax} maximum carboxylation rate in $\mu mol\ m^{-2}\ s^{-1}$, CE carboxylation efficiency, J_{max} maximum electron transport rate in $\mu mol\ m^{-2}\ s^{-1}$, G_s stomatal conductance in $mol\ m^{-2}\ s^{-1}$, R_d dark respiration rate in $\mu mol\ m^{-2}\ s^{-1}$, WUE water utilization efficiency in $\mu mol\ mol^{-1}$, CC leaf construction cost in $g\ dm^{-2}$, SLA specific leaf area in $cm^2\ mg^{-1}$, C_i intercellular CO_2 concentration in $\mu mol\ mol^{-1}$

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

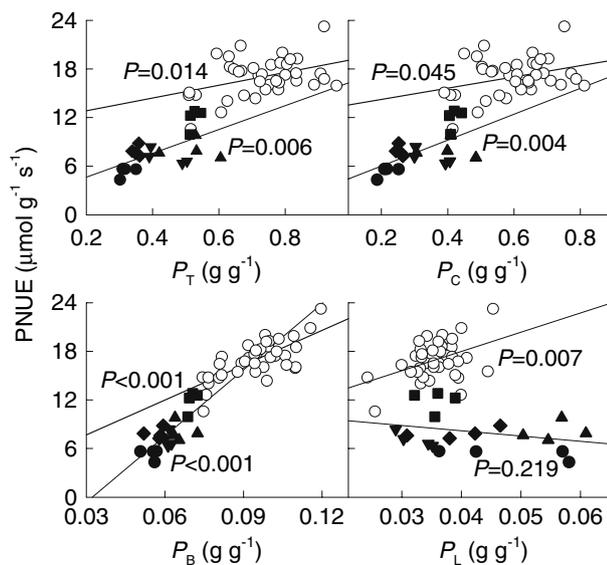


Fig. 1 Photosynthetic nitrogen utilization efficiency (PNUE) as a function of the fraction of leaf nitrogen allocated to all components of the photosynthetic machinery (P_T), to carboxylation (P_C), to bioenergetics (P_B) and light-harvesting components (P_L), respectively, for *Buddleja davidii* (open circles, $n = 40$) and for the five native species (*Berberis vulgaris*, closed circles; *Cornus sanguinea*, triangles pointing up; *Sambucus nigra*, triangles pointing down; *Betula pendula*, squares; *Crataegus monogyna*, diamonds; $n = 4$ for each native species). The lines fitted for the invasive and native species are significantly different in each plot ($P < 0.001$) according to the result of one-way ANCOVA with origin (invasive vs. native species) as independent variable, and the variable indicated by the abscissa as covariate

and J_{\max} than the natives (Fig. 2, 4), which was related to its higher nitrogen allocation to the photosynthetic machinery, and therefore to its higher N_P and higher PNUE.

G_s is another factor that affects photosynthesis by influencing C_i . P_{\max} increased significantly with increasing G_s and C_i (Fig. 5). The invader was significantly higher than all five native species in G_s , but not in C_i , in which it was only higher than *C. sanguinea* and *S. nigra* (Table 2). The difference in the orders of G_s and C_i among the six species was related to the fact that C_i is determined by both stomata and photosynthesis. *B. davidii* showed a higher P_{\max} than the native species at the same value of C_i (Fig. 5). The results showed that the ability to use intercellular CO_2 (related to N_P) was more important to the invader if it was to realize a higher P_{\max} than the ability to absorb CO_2 (related to G_s), indicating that the difference between invasive and native species in nitrogen allocation was the more important factor in the difference in P_{\max} than the difference in G_s . This conclusion was at least partially supported by the fact that the invader was not significantly lower in WUE than *B. pendula* and *C. monogyna*, although its G_s was significantly higher (Table 2).

As R_d increased, P_{\max} increased linearly and was significantly higher at the same value of R_d in *B. davidii* than in natives (Fig. 6), indicating that the invader had a higher RE and lower carbon cost than the natives.

As SLA increased, $P_{\max-M}$ increased, whereas CC decreased (Fig. 7). At the same value of SLA, the invader exhibited higher $P_{\max-M}$ but lower CC (in low SLA range) than the natives. Compared to *B. vulgaris* and *C. monogyna*, *B. davidii* was significantly higher in SLA but lower in CC. However, the differences in SLA and CC were not significant between *B. davidii* and the other three native species (Table 2).

Discussion

Compared to the native species, *B. davidii* was significantly higher in PNUE (Table 2), which is consistent with the results of other authors (Baruch and Goldstein 1999; Durand and Goldstein 2001; McDowell 2002; Ewe and Sternberg 2003). The high PNUE of invasive species is usually attributed to their low nitrogen content (McDowell 2002) and high photosynthesis (Niinemets et al. 2003). However, it was the higher allocation of leaf nitrogen to the photosynthetic machinery that explains the higher PNUE and not a low leaf-nitrogen content, which was not the case for *B. davidii* (Table 2). The invader invested more leaf nitrogen to the photosynthetic machinery than the five native species, leading to higher N_P and therefore to higher $V_{c\max}$, CE, J_{\max} , P_{\max} and PNUE (Figs. 1, 2, 3, 4). The higher G_s was not important in explaining the higher P_{\max} in the invader because it did not lead to consistently higher C_i (Fig. 5). At the same value of C_i , P_{\max} was significantly higher in the invader than in the natives, again confirming the importance of the higher nitrogen allocation to photosynthesis in the invader. These results may shed important light on functional differences among co-occurring species.

Resource utilization efficiency greatly affects growth, survival and distribution of plants in changing environments (Bazzaz 1996; Chen et al. 2005). Nitrogen and water are two of the most important resources for plants. Increasing nitrogen- and water-utilization efficiencies will facilitate invasion by alien species, especially in dry and infertile environments. However, there is an intrinsic trade-off between WUE and PNUE (Delucia and Schlesinger 1991). A decrease in G_s tends to increase WUE but decrease C_i , thus leading to a decrease in PNUE. This trade-off was also detected for *B. davidii* in this study. The increased P_{\max} due to the increased nitrogen allocation to photosynthesis could not completely compensate for the negative effect of the increased G_s on WUE. In contrast, Durand and Goldstein (2001), McDowell (2002) and Ewe and Sternberg (2003) reported that some invasive species

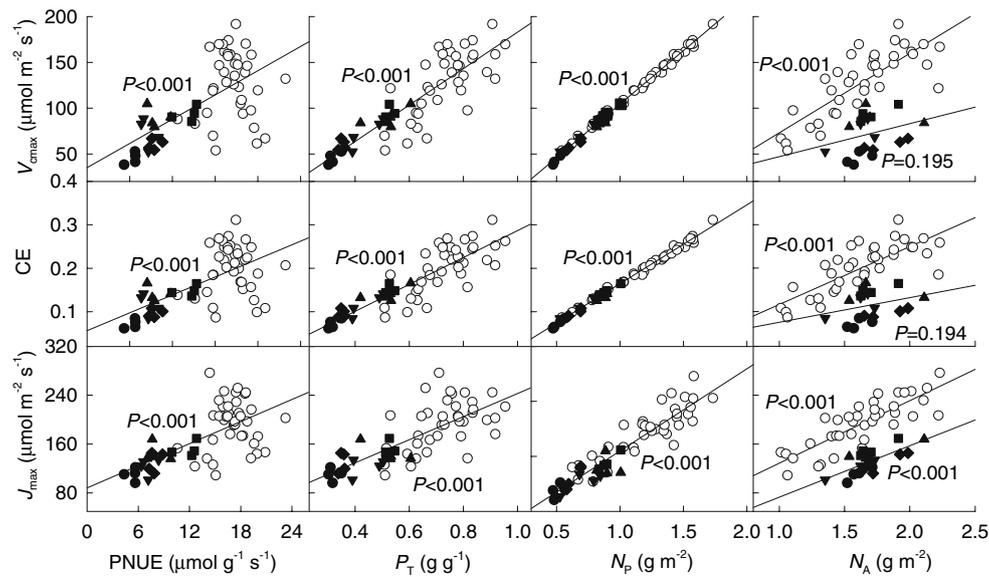


Fig. 2 Maximum carboxylation rate (V_{max}), carboxylation efficiency (CE) and maximum electron transport rate (J_{max}) as a function of photosynthetic nitrogen utilization efficiency (PNUE), the fraction of leaf nitrogen allocated to the photosynthetic machinery (P_T), nitrogen content in the photosynthetic machinery (N_p) and total leaf nitrogen content (N_A) for *Buddleja davidii* and the five native species,

respectively. According to the results of one-way ANCOVA, the lines fitted for the invasive and native species are significantly different ($P < 0.001$) in the three plots of the last column, but not in others, in which only one fitted line for the pooled data of the six species was given. Species symbols and replicates as in Fig. 1

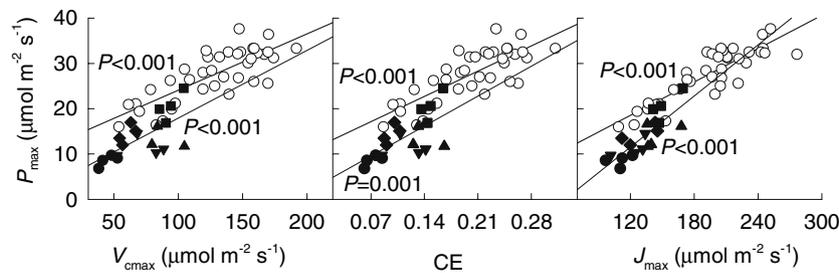


Fig. 3 Maximum photosynthetic rate (P_{max}) as a function of maximum carboxylation rate (V_{max}), carboxylation efficiency (CE) and maximum electron transport rate (J_{max}) for *Buddleja davidii* and the five native species, respectively. The lines fitted for the invasive

and native species are significantly different in each plot ($P < 0.001$) according to the results of one-way ANCOVA. Species symbols and replicates as in Fig. 1

could break the trade-off, showing both higher WUE and higher PNUE than native species. Water availability was not likely to be a limiting factor for *B. davidii* in the late summer of 2005 at our study site due to the sufficient level of precipitation. Therefore, the invader with higher G_s will benefit from the higher P_{max} and PNUE at the expense of the decreased WUE under sufficient water conditions. Water conservation may not be advantageous to a species when competitors consume the otherwise conserved soil water (Hill et al. 2006).

The high R_d in *B. davidii* did not reduce its RE. At the same value of R_d , P_{max} was higher in the invader than in the native species (Fig. 6). This result is consistent with those of Pattison et al. (1998) and McDowell (2002).

However, the invader did not reduce carbon costs by increasing SLA and reducing CC compared to the native species. The invader was higher in SLA while only lower in CC than two of the five native species (Table 2). This contrasted with the statistically significant trend toward invasive species having higher SLA and lower CC than native species (Daehler 2003), but was consistent with the results in some studies (Harrington et al. 1989; Pattison et al. 1998; Nagel and Griffin 2001; Smith and Knapp 2001; McDowell 2002). Invasive species may also benefit from low SLA, as a leaf with low SLA may have a longer longevity and a higher level of photosynthesis (Fig. 7; Reich et al. 1997; Feng et al. 2007). Farnsworth and Meyerson (2003) found that the invasive species

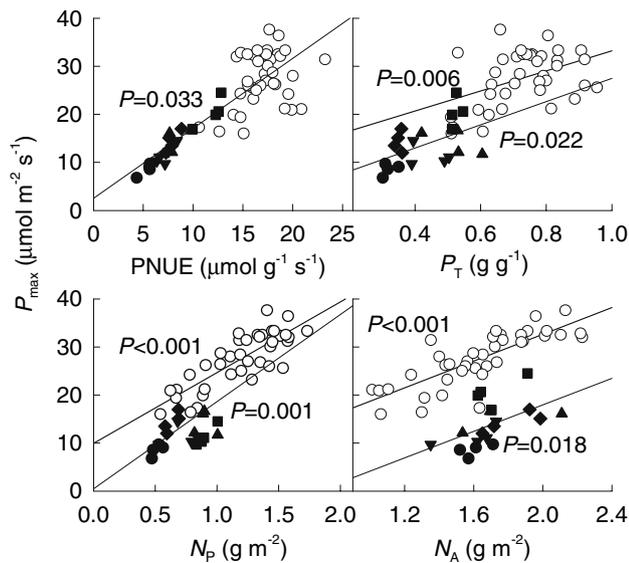


Fig. 4 Light-saturated photosynthetic rate (P_{\max}) as a function of photosynthetic nitrogen utilization efficiency (PNUE), the fraction of leaf nitrogen allocated to the photosynthetic machinery (P_T), nitrogen content in the photosynthetic machinery (N_P) and total leaf nitrogen content (N_A) for *Buddleja davidii* and the five native species, respectively. According to the results of one-way ANCOVA, the lines fitted for the invasive and native species are not significantly different ($P < 0.001$) in the top left plot, in which only one fitted line for the pooled data of the six species was given. Species symbols and replicates as in Fig. 1

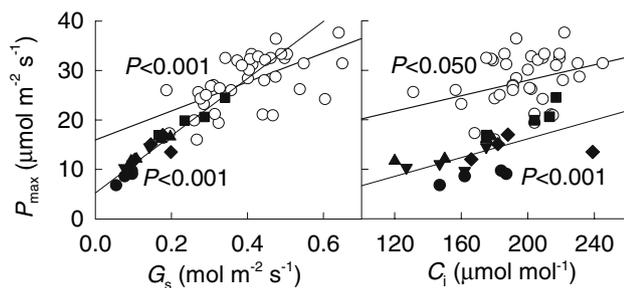


Fig. 5 Light-saturated photosynthetic rate (P_{\max}) as a function of stomatal conductance (G_s) and intercellular CO_2 concentration (C_i) for *Buddleja davidii* and the five native species, respectively. The lines fitted for the invasive and native species are significantly different in each plot ($P < 0.001$) according to the results of one-way ANCOVA. Species symbols and replicates as in Fig. 1

Phragmites australis and *Typha angustifolia* grown in freshwater marshes showed lower SLA and lower leaf turnover rate compared to a less invasive species. Forming leaves with a long lifespan can increase annual carbon gain per unit leaf mass, facilitating invasions of alien species (Harrington et al. 1989; Farnsworth and Meyerson 2003).

Traits evaluated in this study were not significantly different among the eight populations of *B. davidii*, indicating that there is not genetic change (local adaptation) in

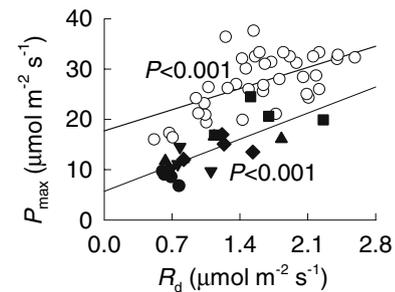


Fig. 6 Light-saturated photosynthetic rate (P_{\max}) as a function of dark respiration rate (R_d) for *Buddleja davidii* and the five native species, respectively. The lines fitted for the invasive and native species are significantly different ($P < 0.001$) according to the results of one-way ANCOVA. Species symbols and replicates as in Fig. 1

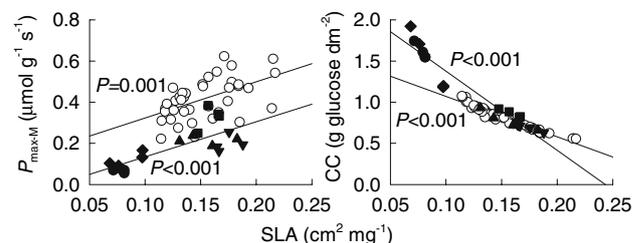


Fig. 7 Mass-based light-saturated photosynthetic rate ($P_{\max-M}$) and leaf construction cost (CC) as a function of specific leaf area (SLA) for *Buddleja davidii* and the five native species, respectively. The lines fitted for the invasive and native species are significantly different in each plot ($P < 0.001$) according to the results of one-way ANCOVA. Species symbols and replicates as in Fig. 1

the invader during its range expansion. This result indicates that the invader may realize its success across a wide range of different environments through phenotypic plasticity (Sexton et al. 2002; Parker et al. 2003), supporting the general-purpose genotype hypothesis (Baker 1965). Plastic responses of photosynthesis to temperature were high in *B. davidii* (unpublished data). A high phenotypic plasticity is considered to be an important trait of invasive species (Daehler 2003). However, our results do not negate the role of rapid evolution in the invasion of *B. davidii* because populations from the native range were not included in this study. Further studies with populations from both native and introduced ranges are necessary to test the role of evolution in the invasion of *B. davidii*.

On nitrogen-poor soils, *B. davidii* can outcompete *B. pendula* (Humphries and Guarino 1987). The soil on which the invader was grown in this study was not fertile, as its mass-based leaf nitrogen content was lower than that of the same species (Cornelissen et al. 1997) and many other species (Reich et al. 1997; He et al. 2006). In these unfertile conditions, the invader showed ecophysiological advantages over the native species. It has long been recognized that increased resource availability often differentially increases

the performance of invasive species over that of native species (Daehler 2003), and increases the invasibility of a community (Davis et al. 2000). For example, the photosynthetic rate of an invasive forb was higher than those of native species at high plant water potential but not at low water potential (Hill et al. 2006). Therefore, it is reasonable to conclude that *B. davidii* may have universal performance advantages over the co-occurring native species. Further studies conducted in more environments are necessary to test the context-dependent performance of the invader and to explore whether the leaf-level ecophysiological advantages of the invader can scale up to whole-plant-level advantages.

In summary, *B. davidii* allocated more leaf nitrogen to the photosynthetic machinery than the five native species. This was the most important difference between the invader and the natives, leading to a higher resource capture ability (P_{\max} , V_{\max} , CE and J_{\max}) and utilization efficiency (PNUE and RE) in the invader. The different responses of P_{\max} to C_i between the invasive and native species again confirmed the importance of the higher nitrogen allocation to photosynthesis in the invader. The higher nitrogen allocation to the photosynthetic machinery, V_{\max} , CE, J_{\max} , P_{\max} , PNUE and RE may facilitate *B. davidii* invasion. No difference in any of the physiological traits evaluated was detected among the eight populations of *B. davidii*, indicating that the invader did not evolve in these traits during range expansion, thus providing support to the general-purpose genotype hypothesis. Our study highlights the need for further comparative research on a wide range of invasive and native species to fully assess the generality of the ecophysiological features found in *B. davidii* among invasive plants and to determine the extent of the competitive advantages provided by them.

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