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CONSTRUCTION COST AND INVASIVE POTENTIAL: COMPARING *LYTHRUM SALICARIA* (LYTHRACEAE) WITH CO-OCCURRING NATIVE SPECIES ALONG POND BANKS[1]

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Lythrum salicaria (purple loosestrife) is a nonindigenous invasive species characterized by prolific growth and abundance in marshy and riparian habitats across North America. Given its invasive success, we hypothesized this species may require less energy and/or use energy more efficiently for biomass construction than co-occurring noninvasive plant species. We measured leaf construction cost (CC), leaf mass per unit area (LMA), and leaf organic nitrogen and carbon content of *L. salicaria* and the five most abundant co-occurring species, *Parthenocissus quinquefolia, Erigeron philadelphicus, Asclepias syriaca, Spiraea latifolia,* and *Solidago graminifolia,* along dammed ponds in the Black Rock Forest, Cornwall, New York, USA. *Lythrum salicaria,* which was highly abundant (2.52 individuals/m^2), exhibited significantly lower area-based leaf CC (44.47 ± 4.24 g glucose/m^2 leaf) than relatively less abundant species, suggesting energetics may influence its invasive success. Conversely, least abundant *Solidago graminifolia* (0.67 individuals/m^2) exhibited the significantly highest leaf CC per unit leaf area (141.87 ± 39.21 g glucose/m^2 leaf). Overall, a negative correlation between species abundance and area-based leaf CC (r^2 = 0.73) indicated low energy requirements and/or high energy efficiency may influence relative abundance in the plant species studied. As it correlates with species abundance in this study, CC may be a useful tool for evaluating invasive potential.

Key words: abundance; construction cost; energetics; invasive species; *Lythraceae*; *Lythrum salicaria.*

Plant species have specific physiological pathways and rates by which they process resources, interact with other species, and impact their physical environment. Consequently, changes in species composition can alter ecosystem processes (Chapin et al., 1997), such as fire regimes, nutrient cycling, and energy budgets (Mack et al., 2000). A recent Florida study, for example, concluded 44–77% of invasive plants studied in that state potentially altered plant communities and/or ecosystem geomorphological, hydrological, and biogeochemical processes (Gordon, 1998). Given the many possible environmental and economic impacts of plant invasions, it is important to increase our understanding of the physiological and environmental factors that influence the invasive potential of plant species to facilitate preventative and remediation efforts.

Lythrum salicaria (purple loosestrife), a herbaceous perennial introduced from Europe and Asia, is thought to have arrived in North America during the early 1800s (Thompson, 1991). Since its introduction, this species has become particularly widespread across wetland, marshy, and riparian habitats in the northern tier states and provinces of North America. The spread of this species, along with that of other invasive plants, has altered the vegetation of many North American wetlands (Galatowitsch, Anderson, and Ascher, 1999), resulting in the decline of species diversity and the extinction of some rare species (Moore and Keddy, 1989). Invasions of *L. salicaria,* in particular, have been linked with the displacement of native plant species, including *Typha* spp. (cattail) (Mal, Louvett-Doust, and Louvett-Doust, 1997; Mullin, 1998) and *Scirpus* spp. (bulrush) (Mullin, 1998), as well as changes in ecosystem nitrogen cycling (Otto et al., 1999), sediment chemistry (Templer, Findlay, and Wigand, 1998), detrital input (Emery and Perry, 1996; Grout, Levings, and Richardson, 1997), and avian diversity (Whitt, Prince, and Cox, 1999).

The increasing abundance of *L. salicaria* suggests a high competitive advantage over many co-occurring native plants, yet this competitive success is not completely understood. While prolific seed production, high germination rates, and easy dispersal of its small seeds have been hypothesized to facilitate the spread of this species (Mal et al., 1992; Mullin, 1998), the continued success of *L. salicaria* also depends on its successful growth following establishment. Though it has been widely hypothesized that a lack of natural herbivores has given this species (Thompson, Stuckey, and Thompson, 1987; Rendall, 1989; Galatowitsch, Anderson, and Ascher, 1999) and other invasive species (Rejmánek, 1996; Mack et al., 2000) a competitive growth advantage over co-occurring native species, recent studies have indicated the vigor of *L. salicaria* cannot be explained entirely by either a lack of herbivory (Rachich and Reader, 1999; Willis and Blossey, 1999) or a reduced need for herbivory defense mechanisms (Willis, Thomas, and Lawton, 1999).

Habitat disturbance also has been cited as a factor influencing invasions of *L. salicaria* (Thompson, Stuckey, and Thompson, 1987; Mullin, 1998), and collectively, many studies have indicated there are positive correlations between disturbance and other species invasions in environments ranging from wetlands (e.g., Detenbeck et al., 1999) to grasslands (e.g., Rose, Platt, and Frampton, 1995) to roadsides (e.g., Dietz, Fischer, and Schmid, 1999). Based on these shared findings, it seems reasonable to conclude environmental disturbance does influ-

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ence the invasiveness of *L. salicaria* and numerous other plant species; ecosystem modeling results support this conclusion (Zalba et al., 2000). Yet the invasive species and their neighboring noninvasive species sharing these disturbed environments are subject to the same environmental conditions, regardless of the nature of the disturbance. Some components of plant physiology and/or morphology may, therefore, also influence the invasive potential of plant species by enabling them to establish populations capable of outcompeting other species in disturbed environments.

As a quantifiable measurement of the energy invested by a plant to construct biomass, construction cost (CC) can be related to both resource-use efficiency (Williams et al., 1987; Griffin, 1994) and growth rates (Lambers and Poorter, 1992; Poorter and Bergkotte, 1992; Griffin, Thomas, and Strain, 1993; Griffin, 1994; Poorter and Villar, 1997), with high CC typically being associated with slow-growing species (Lambers and Poorter, 1992; Poorter and Bergkotte, 1992; Griffin, Thomas, and Strain, 1993; Griffin, 1994; Poorter and Villar, 1997). Since every plant species has a resource requirement below which it cannot perform the functions necessary to grow and spread (Tilman, 1982), it has been hypothesized that a relatively low resource requirement could increase the competitive ability of plant species (Tilman, 1999). As it relates to CC, the resource requirement of a species could be influenced by the amount of energy required to perform growth functions, such that a plant requiring less energy to construct biomass may require less resources to generate that energy than a plant with more energetically expensive functions. Since a quantitative understanding of how different plants gain and allocate resources likely will facilitate predictions of their success in any given environment (Mooney, 1972) and plant energetics can be related to resource use, we consider CC as a general approach to evaluating invasive potential.

Researchers who recently studied 30 invasive and 34 native species in Hawaii found overall lower leaf CC for the invasive vs. native species (Baruch and Goldstein, 1999). Comparing native and invasive C_4 grasses in Venezuela, another study concluded a similar occurrence of low leaf CC in invasive plants when compared to their native counterparts (Baruch and Gomez, 1996). Given these recent findings and the association of CC with resource-use efficiency and growth rates, we hypothesize the invasiveness of *L. salicaria* over co-occurring native plants may be facilitated by relatively low energy requirements for leaf construction. Thus, *L. salicaria* may produce more photosynthetic leaf surface area and/or grow faster with lower energy expense to outcompete co-occurring native species. We investigated our hypothesis by comparing the leaf CC and related resource characteristics of field-collected *L. salicaria* and the five most abundant co-occurring native species along disturbed, dammed areas of three man-made ponds located in the Black Rock Forest, Cornwall, New York, USA.

MATERIALS AND METHODS

Leaf material—Vegetation surveys were conducted during the summer of 1999 around disturbed, dammed sections of three ponds—Upper Reservoir, Aleck Meadow Reservoir, and Sphagnum Pond—located in the Black Rock Forest, Cornwall, New York, USA. All three sites were in cleared areas of the forest and received direct sunlight. Along these dams, 1-m^2 plots were marked every 10 m along the pond banks, with the location of the first plot randomly assigned. The edge of the pond marked the boundary of one side of each plot. In total, 33 plots were marked. All dicot plant individuals within these plots were identified and counted. For *L. salicaria,* which can have many stems per individual (Mal et al., 1992), stems rising from the same rootstock were counted as one individual plant. Species relative abundance levels were determined on a density basis as the total number of individuals of each species divided by the total number of quadrants (in individuals per square meter). We have chosen to use this measure of abundance because it attests to the growth success as well as the establishment success of species.

Young, fully expanded sun leaves from one observably healthy individual of *L. salicaria* and the five most abundant co-occurring native species were collected from every plot where the respective species was present. To ensure enough leaf material was obtained for our analyses, ~50 cm^2 of leaf material was collected from each individual plant. Leaves were processed through a portable area meter (Model LI-3000A, LI-COR, Lincoln, Nebraska, USA) and then dried in a 60°C oven (Model 20 GC, Quincy Lab, Chicago, Illinois, USA) for 48 h and weighed to determine leaf mass per unit area (LMA) (in grams per square meter) for each individual. Following this measurement, all dried leaves were ground into a fine powder using a ball mill (Cianflone Scientific Instruments, Pittsburgh, Pennsylvania, USA) and stored with a desiccant to maintain dryness for construction cost analysis.

Leaf energy and resource investment—Organic nitrogen (N) (in grams per gram leaf dry mass) and carbon (C) (in grams per gram leaf dry mass) content of two 1–2 mg samples of leaf powder from each individual were determined using an elemental analyzer (ANCA-SL, ANCA, Crewe, UK). The duplicate samples for each individual were averaged. To calculate N and C per unit leaf area (in grams per square meter), these values were multiplied by the LMA for each individual.

Ash content (Ash) (in grams per gram leaf dry mass) was measured for each individual by burning preweighed leaf powder samples in a 400°C muffle furnace (Model 51844, Lindberg, Watertown, Wisconsin, USA) for 6 h to obtain ash and then dividing the ash mass by the sample mass. To obtain ash-free heats of combustion (H_C) (in kilojoules per gram leaf dry mass), three 6–20 mg pellets were pressed of the leaf powder from each individual. The pellets were combusted using a modified Phillipson microbomb calorimeter (Phillipson, 1964) (Gentry Instruments, Aiken, South Carolina, USA) calibrated with 6–20 mg benzoic acid standards of known energy values. The H_C values obtained for the triplicate pellets for each plant were then averaged.

The simplest measurement of CC involves quantifying the amount of resources allocated to a given vegetative structure's formation, which can be estimated accurately from measurements of H_C, Ash, and N content (Williams et al., 1987). The following equation (from Williams et al., 1987) was used to calculate CC as the amount of glucose required to synthesize plant biomass (equivalent to grams glucose per gram leaf dry mass): $CC = [(0.06968\triangle H_C - 0.065)(1 - \text{Ash}) + 7.5(k\text{N}/14.0067)](1/E_G)$, where k is the oxidation state of the nitrogen substrate and E_G is the growth efficiency. In terms of its deviation from 100%, E_G represents the fraction of cost required to provide reductant that is not incorporated into biomass (Penning de Vries, Brunsting, and van Laar, 1974). Penning de Vries, Brunsting, and van Laar (1974) calculated E_G as 0.87. Since k is +5 for nitrate and −3 for ammonium and the form of N was not known in our samples, CC for each individual was calculated twice, once with $k = 5$ and once with $k = -3$, providing a range of possible N substrate-dependent CC values. To calculate leaf CC per unit leaf area (equivalent to grams glucose per square meter), these values were multiplied by the LMA for each individual. Species means were obtained for all measured factors by averaging the values of all individuals for each species.

Statistical analyses—After homogeneity of sample variances was verified using a Levene statistic test, a one-way analysis of variance (ANOVA) model adjusted for unbalanced experimental design (in which species was defined as the fixed independent variable) was used to compare means between species for all measured leaf variables (SPSS for Windows, release 7.5.1, 1996, SPSS, Chicago, Illinois, USA). Mean values were considered significantly different if $P \leq 0.05$. When ANOVA results were significant, least significant difference (LSD) post-hoc analysis was performed to further compare species means. Linear regressions were made to determine the relationship between mean leaf CC and other leaf variables for all species. The average of the leaf

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TABLE 1. Summary of one-way analysis of variance (ANOVA) results for all measured leaf physiological variables, where species was considered the fixed independent variable.

Leaf variable	Sum of squares	df	Mean square	*F*	*P*
Density (individuals/m^2)					
Between groups	160.4	5	32.08	14.89	0.00
Within groups	413.76	192	2.16		
Total	574.16	197			
CC[a] (g/g)					
Between groups	7.7	5	1.54	16.9	0.00
Within groups	5.83	64	0.09		
Total	13.53	69			
CC (g/m^2)					
Between groups	68 886.44	5	13 777.29	13.81	0.00
Within groups	59 846	64	997.43		
Total	128 732.4	69			
LMA[b] (g/m^2)					
Between groups	14 316.45	5	28363.29	8.76	0.00
Within groups	19 618.29	64	326.97		
Total	33 934.74	69			
C (mg/g)					
Between groups	114 013.2	5	22 802.63	9.68	0.00
Within groups	148 384.2	64	2355.31		
Total	262 397.4	69			
C (g/m^2)					
Between groups	4453.5	5	890.7	11.73	0.00
Within groups	4478.75	64	75.91		
Total	8932.25	69			
N (mg/g)					
Between groups	638.49	5	127.7	5.89	0.00
Within groups	1387.81	64	21.69		
Total	2026.31	69			
N (g/m^2)					
Between groups	2.78	5	0.56	2.59	0.04
Within groups	12.87	64	0.21		
Total	15.64	69			
C : N					
Between groups	2014.92	5	402.98	18.5	0.00
Within groups	1372.66	64	21.79		
Total	3387.58	69			

[a] CC = construction cost.
[b] LMA = leaf mass per unit area.

CC values considering ammonium and nitrate each as the primary source of leaf N were used in regression analysis.

RESULTS

Relative abundance, area- and mass-based leaf CC, leaf N and C, and C : N were all significantly different between sampled species (Table 1). Overall, 39 species were identified along the dammed areas of the pond perimeters. Of the species sampled, *Parthenocissus quinquefolia* (Virginia creeper), *L. salicaria,* and *Erigeron philadelphicus* (common fleabane) were significantly more abundant than *Asclepias syriaca* (common milkweed), *Spiraea latifolia* (meadowsweet), and *Solidago graminifolia* (lance-leaved goldenrod) (Fig. 1). Collectively, these species included a vine (*P. quinquefolia*), a shrub (*Spirea latifolia*), and four herbs. All are common in the region of this study, and all but *L. salicaria* are native to North America. Sample sizes were reflective of the relative abundance of the species and were consistent for all analyses (n = 19 for *L. salicaria,* n = 17 for *P. quinquefolia,* n = 16 for *E. philadelphicus,* n = 7 for *A. syriaca* and *Spirea latifolia,* and n = 4 for *Solidago graminifolia*).

Mean leaf CC, considering either ammonium or nitrate as the primary source of organic N, was generally lower in the more relatively abundant species and higher in the less relatively abundant species (Fig. 2). Both *P. quinquefolia* and *L. salicaria,* as well as *Spirea latifolia,* had significantly lower mass-based leaf CC than the other sampled species, with least-abundant *Solidago graminifolia* exhibiting the greatest mass-based leaf CC (Fig. 2A). When expressed per unit area, *P. quinquefolia* and *L. salicaria* exhibited significantly lower mean leaf CC values than all other sampled species, including *Spirea latifolia,* while both *Solidago graminifolia* and *A. syriaca* had the statistically highest mean area-based leaf CC. (Fig. 2B). Linear regression analysis revealed a significant negative correlation between area-based mean leaf CC and species relative abundance (Fig. 3), but only a weak degree of correlation when leaf CC was expressed per unit leaf dry mass (r^2 = 0.31).

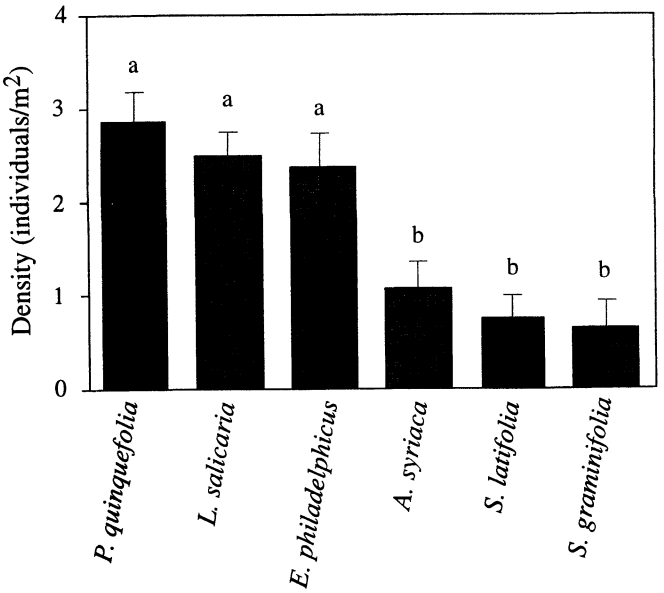


Fig. 1. Abundance of invasive *L. salicaria* and the five most abundant co-occurring species along dammed sections of three ponds in the Black Rock Forest, New York, USA. Error bars represent 1 SE of the mean. Means shown below the same letter are not significantly different at the $P \leq 0.05$ level of significance.

Figure Abbreviations: C, organic carbon content; CC, construction cost; LMA, leaf mass per unit area; N, organic nitrogen content.

Other leaf characteristics also varied significantly according to species relative abundance. In general, LMA increased with increasing relative abundance, with *P. quinquefolia* and *L. salicaria* exhibiting significantly lower mean LMA values than the other sampled species (Table 2). Both of these species also had significantly lower mean leaf C per unit leaf area than the other sampled species, though *L. salicaria* alone exhibited the significantly lowest mass-based leaf C value. Conversely, the three least abundant species, *A. syriaca, Spirea latifolia,* and *Solidago graminifolia,* exhibited the highest area- and mass-based mean leaf C values (Table 2). Expressed per unit leaf area, mean leaf N was significantly lower in *P. quinquefolia, L. salicaria,* and *E. philadelphicus* than in least-abundant *Solidago graminifolia,* while mass-based mean leaf N was relatively high and significantly no different in *P. quinquefolia, L. salicaria,* and *Solidago graminifolia* (Table 2). Mean leaf C : N appeared to exhibit an interspecific trend opposite to that of mass-based mean leaf N, with *P. quinquefolia, L. salicaria,*

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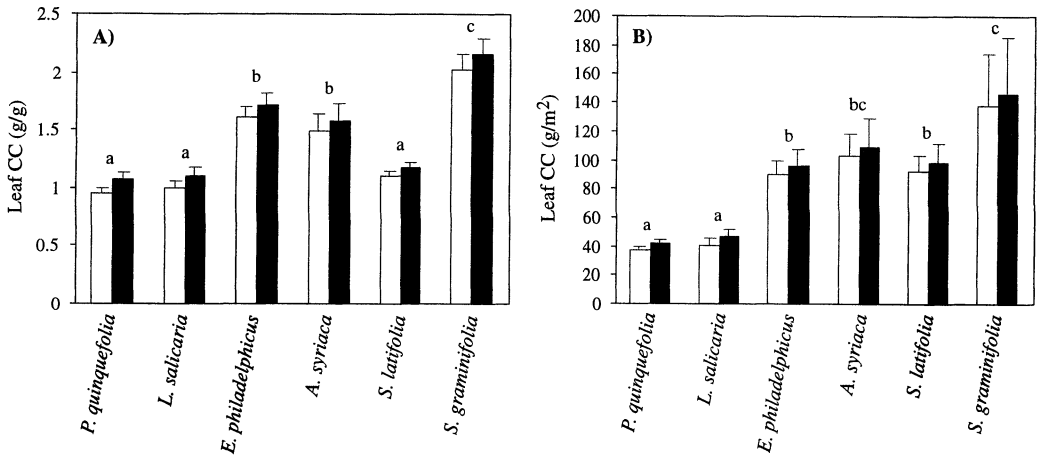


Fig. 2. Mean leaf CC of *L. salicaria* and the five most abundant co-occurring species in the study sites (A) expressed per unit leaf dry mass and (B) expressed per unit leaf area. Construction cost was calculated considering each ammonium (open bars) and nitrate (shaded bars) as the primary source of leaf N. Species are listed along the *x*-axis in order of decreasing abundance (left to right). Error bars represent 1 SE of the mean. Means shown below the same letter are not significantly different at the $P \leq 0.05$ level of significance.

and *Solidago graminifolia* exhibiting the significantly lowest values (Table 2).

A combination of these leaf characteristics seemed to be associated with area-based leaf CC, while leaf CC expressed per unit dry leaf mass was not correlated significantly with any of the measured leaf variables. Specifically, both LMA (Fig. 4A) and area-based leaf C (Fig. 4B) were moderately correlated with area-based mean leaf CC, while mean leaf N per unit leaf area was strongly correlated with this factor (Fig. 4C). However, there was no significant degree of correlation between mean leaf C : N and area-based leaf CC.

DISCUSSION

Since leaves are the primary site of photosynthetic carbon gain, leaf CC, in particular, could have profound impacts on species growth and abundance. Specifically, a relatively low area-based leaf CC that allows the construction of more leaf surface area with low energetic expense, such as that exhibited by both invasive *L. salicaria* and weedy *P. quinquefolia* in this study, may provide some species with a competitive advantage over others. More indirectly, low energy requirements for leaf construction could allow such species to invest more energy in other strategies, such as reproductive efforts or root growth.

Area-based leaf CC estimates provide information on processes influenced by leaf surface area, such as those driven by light interception or those limited by diffusion to the plant surface (Griffin, 1994). The stronger association of species relative abundance with area-based leaf CC than mass-based leaf CC in this study suggests processes dependent on leaf surface area may influence competitive success of these species to some extent. In fact, we found LMA to be slightly more strongly correlated with species relative abundance than is area-based leaf CC in this study ($r^2 = 0.81$). However, because LMA is not a cause but rather the result of a change in physiology, while leaf CC may be considered a more mechanistic approach to understanding plant growth, we emphasize leaf CC and related factors.

Here, a positive correlation between LMA and area-based mean leaf CC (Fig. 4A) illustrates the association of leaf CC and leaf thickness or cell density. Typically, plants with a high LMA have been found to contain more lignin (Austin and Vitousek, 1998; Groeneveld, Bergkotte, and Lambers, 1998) and cell-wall components (Groeneveld, Bergkotte, and Lambers, 1998), which tend to be energetically expensive. In our study, this association seemed characteristic of two of the less abundant species, *A. syriaca* and *Solidago graminifolia,* which exhibited relatively high mean LMA values associated with both high mass- and area-based leaf CC, while both *P. quinquefolia* and *L. salicara* exhibited the opposite characteristics.

The relatively low mean LMA of the most abundant sampled species in this study (Table 2) could indicate these species have a higher capacity for light interception and carbon assimilation with a limited amount of energetic expense, while rel-

TABLE 2. Leaf resource investment of six species along pond banks in the Black Rock Forest. Leaf mass per unit area (LMA), organic carbon (C) and nitrogen content (N), and carbon-to-nitrogen molar ratio (C : N) of invasive *Lythrum salicaria* and its five most abundant neighboring species within the study sites. Species are presented in order of decreasing abundance (left to right). Values presented are species means ±1 SE. Values followed by the same superscript letter are not significantly different at the $P = 0.05$ level of significance.

Leaf variable	*Parthenocissus quinquefolia*	*Lythrum salicaria*	*Erigeron philadelphicus*	*Asclepias syriaca*	*Spiraea latifolia*	*Solidago graminifolia*
LMA (g/m²)	38.9 ± 2.8^{A}	42.9 ± 3.6^{A}	58 ± 4^{B}	68.8 ± 10.1^{BC}	82.8 ± 8.5^{C}	66.7 ± 17.7^{BC}
N (mg/g)	24.8 ± 1.1^{C}	21.7 ± 0.9^{BC}	20.8 ± 1.7^{B}	18.6 ± 1.1^{AB}	14.9 ± 0.6^{A}	26.2 ± 2.4^{C}
N (g/m²)	1 ± 0.1^{A}	0.9 ± 0.1^{A}	1.2 ± 0.2^{A}	1.3 ± 0.2^{AB}	1.2 ± 0.1^{AB}	1.7 ± 0.4^{B}
C (mg/g)	416.8 ± 3.6^{B}	349.8 ± 15.6^{A}	428.5 ± 15.9^{B}	441.5 ± 9.4^{BC}	476.6 ± 10.5^{C}	445.2 ± 8.7^{BC}
C (g/m²)	16.3 ± 1.2^{A}	15.1 ± 1.8^{A}	23.8 ± 1.7^{B}	30.6 ± 4.6^{BC}	39.9 ± 4.8^{C}	29.8 ± 8.2^{BC}
C : N	20.7 ± 1^{A}	19.7 ± 1.4^{A}	25.2 ± 1.1^{B}	28.1 ± 1.9^{B}	37.5 ± 1.4^{C}	19.4 ± 1.9^{A}

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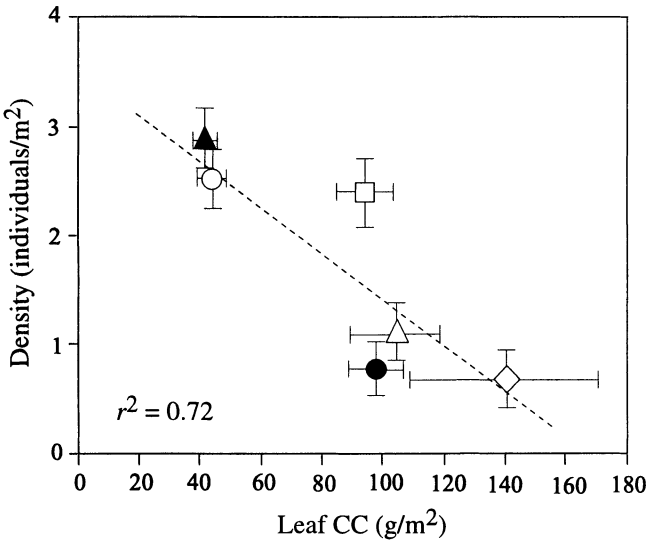


Fig. 3. Negative correlation between species abundance and mean leaf CC expressed per unit leaf area. Herbaceous species are represented by open symbols; shrub and vine species are represented by shaded symbols. ▲ = *Parthenocissus quinquefolia*; ○ = *Lythrum salicaria*; □ = *Erigeron philadelphicus*; △ = *Asclepias syriaca*; ● = *Spirea latifolia*; ◇ = *Solidago graminifolia.* Error bars represent 1 SE of the mean.

atively higher mean LMA could have the opposite effect in co-occurring species. Though photosynthesis was not measured in our study, researchers who examined photosynthesis of invasive plants with lower LMA and leaf CC than co-occurring native plants concluded the invasive species had overall higher average rates of mass-based photosynthesis (Baruch and Goldstein, 1999).

Nitrogen, which is contained in many of the more expensive biochemical plant compounds (Penning de Vries, Brunsting, and van Laar, 1974) such as proteins and amino acids (Williams et al., 1987), typically exhibits a positive correlation with leaf CC (Miller, Eddleman, and Kramer, 1990; Sims and Pearcy, 1991; Griffin, Thomas, and Strain, 1993; Griffin, Winner, and Strain, 1996). The relatively high mass-based leaf N and low mass-based leaf CC in both *L. salicaria* and *P. quinquefolia* in this study suggests these species have a low energetic expense per unit N, which could increase photosynthetic capacity at minimal cost. Yet the strong positive correlation between area-based leaf N and CC (Fig. 4C) reflects the influence of interspecific differences in LMA. Like area-based leaf N, leaf C also seemed to be influenced by LMA (Fig. 4B). Relating both N and C content, the significantly low leaf C : N of *L. salicaria* could indicate reduced herbivory defense in the form of low amounts of structural carbon compounds, such as cellulose and lignin (Herms and Mattson, 1992), which have an energetic cost.

In *L. salicaria,* low leaf CC may be indicative of high resource-use efficiency and growth rates, both of which could facilitate its invasiveness. As it correlates with species abundance in this study, leaf CC could provide a useful evaluation of invasive potential that may be applicable in other settings. While past research has suggested there may be little interspecific variation in this factor (e.g., Merino, 1987; Chapin, 1989; Williams, Field, and Mooney, 1989), a more recent review has found a twofold range in mass-based leaf CC and an even greater range in area-based leaf CC between species

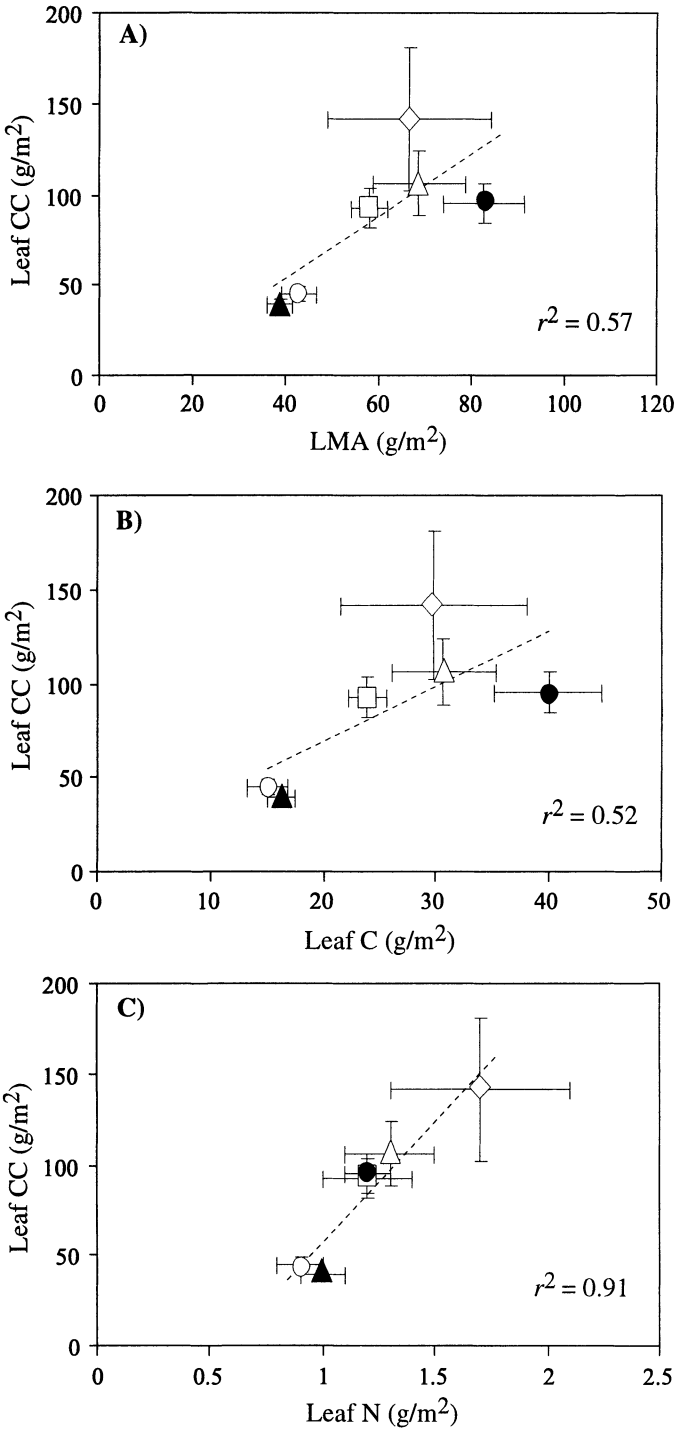


Fig. 4. Positive correlations (A) between LMA and mean leaf CC, (B) between mean leaf C and CC, and (C) between mean leaf N and CC. All factors are expressed per unit leaf area. ▲ = *Parthenocissus quinquefolia*; ○ = *Lythrum salicaria*; □ = *Erigeron philadelphicus*; △ = *Asclepias syriaca*; ● = *Spirea latifolia*; ◇ = *Solidago graminifolia.* Error bars represent 1 SE of the mean.

(Griffin, 1994). Our findings, while contributing only a small piece to the complex puzzle of species invasions, support those of a very limited number of other studies examining leaf CC and species invasiveness (e.g., Baruch and Gomez, 1996; Baruch and Goldstein, 1999).

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While more specific physiological and morphological characteristics may contribute to the relative competitive ability of a species, it often is difficult to draw conclusions regarding the influence of these specific characteristics on invasive potential due to a lack of commonality. For example, while some invasive species may have high seed production or the ability to fix nitrogen, other invasive species may not share these characteristics. However, since every growth strategy has an energy consequence, energy can be considered a basic unit of comparison between organisms (Griffin, 1994). As such, CC measurements reflect specific growth strategies, while allowing for a more general comparison of resource-use efficiency between species. We propose examining leaf CC of native and invasive species in other settings to further evaluate the application of this factor for assessing invasive potential. Furthermore, we suggest evaluating CC measurements for other plant structures, such as roots, stems, and seeds, to gain insight into patterns of energy use and resource allocation within invasive and co-occurring native plants.

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