

CONSTRUCTION COSTS, PAYBACK TIMES, AND THE LEAF ECONOMICS OF CARNIVOROUS PLANTS¹

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Understanding how different plant species and functional types “invest” carbon and nutrients is a major goal of plant ecologists. Two measures of such investments are “construction costs” (carbon needed to produce each gram of tissue) and associated “payback times” for photosynthesis to recover construction costs. These measurements integrate among traits used to assess leaf-trait scaling relationships. Carnivorous plants are model systems for examining mechanisms of leaf-trait coordination, but no studies have measured simultaneously construction costs of carnivorous traps *and* their photosynthetic rates to determine payback times of traps. We measured mass-based construction costs (CC_{mass}) and photosynthesis (A_{mass}) for traps, leaves, roots, and rhizomes of 15 carnivorous plant species grown under greenhouse conditions. There were highly significant differences among species in CC_{mass} for each structure. Mean CC_{mass} of carnivorous traps (1.14 ± 0.24 g glucose/g dry mass) was significantly lower than CC_{mass} of leaves of 267 noncarnivorous plant species (1.47 ± 0.17), but all carnivorous plants examined had very low A_{mass} and thus, long payback times (495–1551 h). Our results provide the first clear estimates of the *marginal* benefits of botanical carnivory and place carnivorous plants at the “slow and tough” end of the universal spectrum of leaf traits.

Key words: carnivorous plants; construction costs; cost–benefit analysis of botanical carnivory; photosynthesis; plant economics; payback time; universal spectrum of leaf economics.

Understanding how the investment (or allocation) of carbon and mineral nutrients varies in different plant organs and among species, plant functional types, and the vegetation of different biomes is a major goal for plant ecology (Wright et al., 2004). A synthesis of global data on plant traits—leaf nitrogen (N), phosphorus (P), and potassium (K) content (%), leaf mass area (LMA: g/cm²), leaf lifespan, and maximal leaf photosynthetic rates (A_{mass} : nmol CO₂ g⁻¹ s⁻¹)—of 2548 species (the Glopnet data set; Wright et al., 2004) illustrated and quantified the bivariate scaling relationships between traits (e.g., A_{mass} as a function of %N) and revealed a “universal spectrum of leaf economics” (Wright et al., 2004, 2005). This spectrum defines trade-offs in plant allocation when changes in one trait co-vary consistently with changes in a second trait. Additional research has identified carnivorous plants (Ellison and Farnsworth, 2005; Farnsworth and Ellison, 2008), mangroves (Ellison, 2002), and lianas in tropical forests (Santiago and Wright, 2007) as notable outliers relative to the universal spectrum of leaf traits. These exceptions to the rule have reinforced the importance of trade-offs in our understanding of why leaf traits consistently scale with one another.

Shipley et al. (2006) proposed that the trade-off between allocation of nutrients to structural tissues and long-term storage vs. their immediate use in boosting photosynthetic rates is a potential mechanism for the observed coordination among leaf traits. Such trade-offs can be observed easily with carnivorous plants

because carnivorous plants inhabit open environments (e.g., bogs and other wetlands) where light and water are not limiting but nutrients are in extremely short supply, and therefore it is relatively easy to separate out experimentally the effects of nutrient limitation from effects of limitation of light or water (Butler and Ellison, 2007; Farnsworth and Ellison, 2008).

Plants respond to resource imbalances by allocating new biomass (carbon) to acquisition of resources that most strongly limit plant growth (Bloom et al., 1985). Economic models have been used successfully to examine resource allocation and performance of plants (Givnish, 1986), and in these models carbon most often is the currency used because it is straightforward to measure the cost in grams or energy-equivalents of carbon needed to produce and maintain a structure. However, it is not just the total construction cost (CC, usually as g glucose/g dry mass [DM]), but the *marginal* costs and benefits of an investment in any particular structure that must be determined. The payback time (hours or days) to recover the carbon investment can be calculated easily as $CC_{\text{mass}}/A_{\text{mass}}$ when both cost and net photosynthesis (A_{mass}) are expressed as nmol C/g DM, and A_{mass} is measured per unit time. Payback time can be thought of as the time span that a leaf must photosynthesize to recover (amortize) the carbon investment used in its construction (Poorter et al., 2006).

Carnivorous plants have elaborate traps (e.g., pitfall traps, sticky pads, snap-traps) that they use to catch prey; associated glandular hairs and secretory cells subsequently dissolve the prey and release nutrients that are absorbed by the plant (Darwin, 1875; Lloyd, 1942). These traps are thought to be physiologically costly structures, and it has been hypothesized that constructing elaborate traps would be selected for only if they provide a net marginal benefit to the plant by capturing prey that provides essential nutrients (e.g., N, P) required for photosynthesis (Givnish et al., 1984; Benzing, 2000). An explicit test of this hypothesis requires simultaneous measurements of both marginal costs and marginal benefits (photosynthesis) of carnivory. Here, we provide for the first time a simultaneous assessment of both the costs and benefits of botanical carnivory.

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These data allow us to further assess trade-offs between allocation of nutrients to structural tissues and their immediate use for enhancing photosynthesis; i.e., to test Shipley et al.'s (2006) proposed mechanism underlying the universal spectrum of leaf economics.

The majority of previous studies of costs and benefits of botanical carnivory have used feeding experiments to examine the response of plant growth or photosynthesis to addition of prey or nutrients (e.g., N, P; reviewed by Ellison, 2006; Ellison and Gotelli, 2009). Our previous work has shown that carnivorous plants have unexpectedly low A_{mass} for their leaf N and P content (Ellison and Farnsworth, 2005; Ellison, 2006; Ellison and Gotelli, 2009), and these scaling relationships do not change significantly when plants are given supplemental prey (Wakefield et al., 2005; Farnsworth and Ellison, 2008). Low rates of A_{mass} by carnivorous plants have been suggested to be one cost of carnivory (Ellison and Farnsworth, 2005; Ellison, 2006; Pavlovič et al., 2007). For pitcher plants (*Sarracenia* spp.), this latter result is thought to result from allocation of excess nutrients to storage and subsequent growth, rather than to immediate syntheses of enzymes required for photosynthesis (Butler and Ellison, 2007).

Osunkoya et al. (2007) examined the cost of building carnivorous traps for eight species of *Nepenthes* pitcher plants in Borneo. These species have a flat photosynthetic lamina (modified from the leaf base: Lloyd, 1942) and an attached cylindrical trap (pitcher) that is a modified, episcidiate leaf (Arber, 1941; Owen and Lennon, 1999). Pitchers should have lower construction costs than leaves or evolution would not have favored this extra pathway for nutrient uptake/assimilation (Osunkoya et al., 2007). Pavlovič et al. (2007) found similar rates of respiration for traps and conjoined laminae of *Nepenthes alata* and *N. mirabilis* but lower rates of photosynthesis for traps, and they concluded that reduced photosynthesis is a cost of multiple functions (digesting prey, absorbing nutrients and transferring nutrients to other plant parts). However, as Givnish et al. (1984) outlined, it is the marginal gain that needs to be measured because high costs can have high benefits or low costs can have low benefits. That is, the measurements of construction cost (e.g., Osunkoya et al., 2007) and photosynthesis (e.g., Pavlovič et al., 2007) need to be undertaken on the same individuals. This analysis is currently lacking for carnivorous plants and is the focus of the work presented here.

We asked four questions in this study. First, what is the CC_{mass} of traps of 15 carnivorous plant species? Second, how does CC_{mass} of carnivorous plants compare with CC_{mass} of noncarnivorous species? Third, how does CC_{mass} of traps compare with CC_{mass} of roots and rhizomes (underground stems) for carnivorous plants that produce rhizomes? Fourth, what is the payback time (i.e., $CC_{\text{mass}}/A_{\text{mass}}$ in hours or days) for a carnivorous trap? The answers to these questions allowed us to address the following three hypotheses.

First, for carnivorous plants in which the trap is modified from a leaf and when the trap simultaneously fixes carbon (through photosynthesis) and acquires nutrients (through carnivory), we hypothesized that traps should be relatively expensive structures with high construction costs. Second, for carnivorous species, such as those in the genus *Nepenthes*, that have separate photosynthetic leaves and traps, we hypothesized that the CC_{mass} of a trap should be lower than the CC_{mass} of the associated leaf. Third, we hypothesized that roots would be less expensive than leaves because of lower concentrations in the roots of expensive compounds such as lipids and proteins (Poorter and Villar, 1997).

To our knowledge, this is the first study to measure, on the same plant and at the same time, both the construction costs and photosynthetic rates for carnivorous plants. These measurements permit the calculation of marginal gain as payback time and integrate traits used to calculate leaf trait scaling relationships (Wright et al., 2004) with construction costs. This integration allowed us to test a fourth hypothesis: that there should be clear and significant trade-offs between A_{mass} and CC_{mass} as proposed by Shipley et al. (2006).

MATERIALS AND METHODS

Study species—We examined construction costs of 15 carnivorous plant species in three plant families and two orders (Sarraceniaceae [Ericales]; Nepenthaceae and Droseraceae [Caryophyllales]) grown in a climate-controlled (25°C daytime, 15°C nighttime, 80% humidity) greenhouse at Harvard Forest, Massachusetts, USA. These included 11 species of North American pitcher plants (*Sarracenia alabamensis*, *S. alata*, *S. flava*, *S. jonesii*, *S. leucophylla*, *S. minor*, *S. oreophila*, *S. purpurea*, *S. rosea*, *S. rubra*, and *Darlingtonia californica*; Sarraceniaceae); two Asian pitcher plants (*Nepenthes × coccinea*, a Victorian-era hybrid of [*N. rafflesiana* × *N. ampullaria*] × *N. mirabilis*, and *N. × miranda*, a modern hybrid of *N. maxima* × [*N. northiana* × *N. maxima*]; Nepenthaceae); the sundew *Drosera filiformis* (Droseraceae), and the Venus fly trap *Dionaea muscipula* (Droseraceae). *Sarracenia*, *Darlingtonia*, *Drosera filiformis*, and *Dionaea* are native to North America, whereas the *Nepenthes* species are hybrids of species native to the Southeast Asian tropical lowlands. The modified leaves of *Dionaea*, *Drosera*, and North American *Sarracenia* and *Darlingtonia* both photosynthesize and trap prey, although some *Sarracenia* spp. also produce photosynthetically more efficient phyllodia (flat, nontrapping leaves; Ellison and Gotelli, 2002). *Nepenthes* spp., by contrast, have a flat lamina (a modified petiole) and an attached cylindrical trap that is modified from a leaf or leaflet (Arber 1941). Previous work has shown that A_{mass} of the laminae of *Nepenthes* is the primary source of photosynthate and that A_{mass} of *Nepenthes* pitchers is near zero (Pavlovič et al., 2007). Thus, we measured construction costs of both laminae and pitchers of *Nepenthes* and phyllodia when present on *Sarracenia*. All plants used in our study had reached reproductive maturity; by excluding juvenile plants, we minimized the potential confounding effects of nonfunctional traps that are too small to capture prey (common in juvenile plants) and heterophylly relative to adult plants (Franck, 1976).

Photosynthesis—Among the pitcher plants, we measured plants with at least three mature, fully expanded pitchers. There were six replicate plants for each species with the exception of *N. × coccinea* ($N = 4$) and *Darlingtonia californica*, *N. × miranda*, and *S. rosea* ($N = 2$ each). The Venus fly trap *Dionaea muscipula* and the sundew *Drosera filiformis* were flowering at the time of measurement, but the other species were not. Maximum photosynthetic rate (A_{area} , as $\mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of one trap (and lamina for *Nepenthes*) on each plant was determined using a LI-COR 6400 IR gas analysis system (LI-COR, Lincoln, Nebraska, USA) fitted with a 3 cm × 2 cm cuvette that was clamped onto the central portion of a pitcher or leaf. We also measured A_{area} of phyllodia that were produced by *S. flava*, *S. leucophylla*, and *S. oreophila* during our study. All measurements were taken between 0900 and 1400 hours at a photosynthetic photon flux density (PPFD) of 1200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ during 23–25 July 2006. Measurement of A_{area} for *Dionaea* included both its snap-trap and the attached petiole. In those few instances when the sample did not cover the entire surface area of the cuvette (i.e., *Dionaea*, *Drosera*, *N. × coccinea*), photosynthetic rates were adjusted for the proportion of the cuvette covered by leaf tissue. In those cases where only two plants were available, 2–4 pitchers were sampled from a plant and averaged for that individual.

Harvest—Plants were harvested immediately after photosynthetic rates were measured. Pitchers were cut longitudinally with a stainless steel razor blade and washed with tap water to remove any prey, detritus, or extrafloral nectar. Pitchers were subsequently rinsed with distilled-deionized water, patted dry with a paper towel, and spread on the conveyer belt of a Li-Cor 3000 to measure leaf area ($\pm 1 \text{ mm}^2$). Leaf areas and associated masses were used to calculate leaf mass per unit area (LMA: g m^{-2}) and to re-express A_{area} as A_{mass} ($\text{nmoles CO}_2 \text{ g}^{-1} \text{ s}^{-1}$). Roots and rhizomes were washed separately with tap water and rinsed with distilled-deionized water. Traps, phyllodia, roots, and rhizomes were dried separately at 70°C to constant mass, weighed ($\pm 0.001 \text{ g}$ dry

mass [DM]) and ground to a fine powder with a stainless steel capsule and ball bearing in a Wig-L-Bug grinder (Bratt Technologies, LCC, East Orange, New Jersey, USA).

Estimation of construction cost—Tissue construction costs (CC_{mass} ; g glucose/g DM) were estimated for roots, rhizomes, and the leaf tissue on which A_{area} had been measured using the heat-of-combustion method (Williams et al., 1987):

$$CC = [(0.06968 \Delta H_c - 0.065) \times (1 - \text{Ash}) + (kN)] \times (1/E_g),$$

where ΔH_c is the heat of combustion (energy as kJ/g ash-free dry mass [AFDM]), Ash is the ash content (g ash/g DM), k is the oxidation state of the nitrogen substrate (nitrate = +5, ammonium = -3), N is the organic nitrogen content (g N/g DM), and E_g is the growth efficiency (the proportion of energy used to produce reductant that is consumed during the formation of tissue but not contained within the biomass). An $E_g = 0.87$ incorporates cost of transport and gives a good fit against the detailed biochemical analysis used as the standard (Griffin, 1994).

Heat of combustion was determined using a microbomb calorimeter (construction details available online at <http://harvardforest.fas.harvard.edu/personnel/web/aellison/research/stoichiometry/calorimetry/Micro-bomb%20Home%20Page.htm>) calibrated with benzoic acid pellets of known calorific values. The calibration was verified with a spinach reference standard (NIST 1570a; National Institute of Standards and Technology, Gaithersburg, Maryland, USA) with a noncertified calorific value of 3500 cal/g DM. Analysis of $N = 35$ spinach pellets during our assay yielded an average calorific value of 3536 cal/g DM (i.e., +1% of the expected value). In almost all cases, we had sufficient carnivorous plant tissue so that each sample could be analyzed in triplicate as 2–12 mg pellets pressed from the ground sample. The H_c values obtained for the triplicate pellets of each sample were then averaged. Because of the large number of analyses (>1000), we used Ni-Cr ignition wire (which contributes a small amount of heat during the reaction) rather than the more expensive Pt wire that does not give off heat from combustion. Therefore, five samples of Ni-Cr wire and no sample pellet were combusted to obtain the heat given off by the Ni-Cr wire and to determine the intercept of the calibration line.

Total nitrogen was substituted for organic N (Nagel et al., 2005) and measured on a Carlo-Erba Model 2500CN elemental analyzer. Nagel et al. (2005) found that the substitution of total N for organic N overestimated CC by only 0.03–0.06%. Ash content was determined by combusting a 10–100 mg subsample of the powdered plant tissue in a muffle furnace at 550°C for 6 h. Construction costs were calculated using both $k = +5$ and -3 , and the average value reported on a dry mass basis.

We estimated CC per gram DM rather than per plant biomass because of the differing sizes of plants used in the analysis. Dry mass per structure is provided in Appendix S1 (see Supplemental Data with online version of article) to allow for scaling up the results to the whole-plant level. Payback time was calculated as $CC_{\text{mass}}/A_{\text{mass}}$ after conversion of CC_{mass} from g glucose/g DM to nmol C/g DM and conversion of A_{mass} from nmol $\text{CO}_2 \cdot \text{g}^{-1} \cdot \text{DM} \cdot \text{s}^{-1}$ to nmol $\text{C} \cdot \text{g}^{-1} \cdot \text{DM} \cdot \text{h}^{-1}$. Calculations for payback times of pitcher construction for *Nepenthes* also were made using A_{mass} of the attached lamina. We estimated payback time on an hourly rather than daily basis because of the differing light levels during a daily period and across the growing season. Thus, our estimate of payback time represents the minimum amortization.

Statistical analysis—We tested for differences in CC_{mass} of traps, roots, and rhizomes among species using a nested analysis of variance (plant structure nested within species) using the program SPSS, release 14.0.0 for Windows (SPSS, 2005). Significant ($P < 0.05$) differences for the ANOVA model were followed by Tukey's (HSD) post hoc test to compare CC_{mass} of organs among species. A paired t -test was used to test for differences in CC_{mass} for species with traps and phyllodia/laminae. We used an unpaired t -test to test for differences in CC_{mass} of traps against leaves of 267 noncarnivorous species compiled from a search of the published literature (Griffin, 1994; Isagi, 1994; Mitchell et al., 1995; Baruch and Gomez, 1996; Dai and Wiegert, 1996; Isagi et al., 1997; Marquis et al., 1997; Niinemets, 1997; Spencer et al., 1997; Wullschlegel et al., 1997; Baruch and Goldstein, 1999; Eamus et al., 1999; Baruch et al., 2000; Nagel and Griffin, 2001; Villar and Merino, 2001; George et al., 2003; Suarez, 2003, 2005; Nagel et al., 2004, 2005; Oikawa et al., 2004, 2007; Osunkoya et al., 2004, 2007; Barthod and Epron, 2005; Brunt et al., 2006; J. D. Karagatzides, unpublished data). We tested for a relationship between A_{mass} and CC_{mass} using reduced major axis regression on logarithmically transformed data using custom code written for the R statistical software package, version 2.6.1 (R Devel-

opment Core Team, 2007; our code is available online Appendix S2). All raw data collected during this study are available online from the Harvard Forest Data Archive (<http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id=hf112>).

RESULTS

Trap traits—With the exception of A_{mass} , there were significant differences among species for all variables measured (Table 1). Mean ash concentration of carnivorous traps ranged more than sixfold from 1.4 to 9.5%. Mean N concentration, by comparison, was more constrained (range 0.58–1.31% N). On average, the greatest ash and N concentrations were measured in *N. ×coccinea* pitchers. All the carnivorous plants examined in this study had low mean maximal net photosynthesis when expressed on a mass basis (A_{mass} range = 1.1–64.0 nmol $\text{CO}_2 \cdot \text{g}^{-1} \cdot \text{s}^{-1}$). Pitchers of both *Nepenthes* species had the lowest, and *S. rubra* had the highest A_{mass} . Although N concentrations observed among species varied only about threefold, rates of photosynthetic nitrogen-use efficiency (PNUE_N ; $\mu\text{mol CO}_2 \cdot \text{mol}^{-1} \text{N} \cdot \text{s}^{-1}$) varied over sixfold from 13.4 for *N. ×coccinea* lamina to a maximum of 89.3 for *S. flava* pitchers (Table 1). The mean energy content (kJ/g AFDM) of the carnivorous traps ranged from 12.8 in *S. minor* to 22.5 in *S. purpurea*. Traps of *S. flava* had energy content similar to *S. purpurea*, and traps of all other species had an energy content less than 17.4 kJ/g AFDM. The lowest LMA (40 g/m²) was measured for traps of *N. ×coccinea* compared to a maximum LMA of 118 g/m² for sticky pads of *Drosera filiformis*. The ratio of dry mass to fresh mass was lowest in the species with the smallest pitchers and lowest LMA (*N. ×coccinea*). Low dry mass to fresh mass ratios were also found for *N. ×miranda* and for some of the smaller carnivorous traps including *Drosera filiformis* and *Dionaea muscipula* (range dry : fresh mass = 0.10–0.14). *Sarracenia purpurea* and *Darlingtonia californica* had intermediate ratios of dry to fresh mass, while the remaining species of *Sarracenia* had ratios ≥ 0.20 up to a maximum of 0.26.

Construction costs—Differences among species for energy, nitrogen, and ash content led to highly significant differences among species for CC_{mass} of traps, roots, and rhizomes. The overall nested analysis of variance model (whole-plant analysis pooling traps, roots, and rhizomes with structures nested within species) was highly significant ($F_{26, 149} = 9.385$; $P = 2.49 \times 10^{-20}$). Pooled across all species, CC_{mass} of traps, roots, and rhizomes were similar (1.15 ± 0.28 , 1.15 ± 0.13 , and 1.16 ± 0.16 g glucose/g DM, respectively; $F_{2, 149} = 1.353$; $P = 0.262$). There were, however, significant differences in construction costs of particular structures among species (Table 2). Similar to the trend for energy content, significantly greater CC_{mass} was measured for traps of *S. purpurea* ($P < 0.0003$) and *S. flava* ($P < 0.006$) than for the other species measured in this study. A group comprised of *S. minor*, *S. alabamensis*, *S. oreophila*, *S. leucophylla*, and *S. jonesii* had the lowest CC_{mass} for traps. There were fewer significant differences among species for the construction of belowground structures. For roots, CC_{mass} of *S. alabamensis* was significantly greater than *S. minor* ($P = 0.0001$), *S. oreophila* ($P = 0.0001$), and *Dionaea muscipula* ($P = 0.04$; Table 2). Construction costs of rhizomes for *S. flava* and *S. minor* were significantly lower ($P < 0.0014$) than for *S. oreophila* and *S. purpurea* (Table 2).

Carnivorous traps had significantly lower ($t = 3.35$, $df = 12$, $P = 0.006$) CC_{mass} (1.29 ± 0.20 g glucose/g DM) than did the

TABLE 1. Mean (± 1 SD; unless pooled into one composite sample or not available [n/a]) for traits of carnivorous plants with (A) traps or (B) lamina/phyllodia. Different lowercase letters indicate significant differences among species for each trait ($P < 0.05$, Tukey's HSD post hoc test for multiple comparisons among means). No post hoc comparisons were done on the data for laminae/phyllodia because the overall ANOVA was not significant for any of the traits ($F_{5,16} < 3.0$; $P > 0.1$). Values presented are N : sample size; Ash: ash content following combustion (g ash/g dry mass); N: nitrogen content (g N/g dry mass), PNUE_N: photosynthetic nitrogen use efficiency ($\mu\text{mol CO}_2 \cdot \text{mol}^{-1} \text{N} \cdot \text{s}^{-1}$), Energy: energy content measured by bomb calorimetry (kJ/g ash-free dry mass); LMA: mass of leaves/m² leaf area); and the ratio of dry mass to fresh mass.

Species	N	Ash	N	A _{mass}	PNUE _N	Energy	LMA	Dry : Fresh Mass
A) Traps								
<i>Darlingtonia californica</i>	2	5.6 e	1.31 e,f	27.5	30.5 ab	16.2 ab	70 ab	0.16
<i>Sarracenia alabamensis</i>	6	1.6 \pm 0.4 a,b,c	1.13 \pm 0.11 c,d,e,f	53.0 \pm 23.0	67.2 \pm 31.8 b	13.1 \pm 0.5 a	59 a,b \pm 12	0.23 \pm 0.04 e,f
<i>Sarracenia alata</i>	6	1.7 \pm 0.3 a,b,c	0.89 \pm 0.13 a,b,c,d,e	47.7 \pm 17.6	76.0 b \pm 27.6	16.0 a,b \pm 1.1	73 \pm 11 b,c	0.25 \pm 0.03 e,f
<i>Sarracenia flava</i>	6	3.0 \pm 0.9 c,d	0.71 \pm 0.02 a,b	45.5 \pm 7.3	89.3 \pm 14.0 b	22.0 \pm 2.0 c,d	100 \pm 4 c,d,e,f	0.21 \pm 0.04 d,e,f
<i>Sarracenia jonesii</i>	6	1.6 \pm 0.5 a,b,c	1.00 \pm 0.06 b,c,d,e,f	55.2 \pm 16.9	77.3 \pm 23.4 b	13.1 \pm 0.7 a	61 \pm 6 a,b	0.22 \pm 0.03 e,f
<i>Sarracenia leucophylla</i>	6	2.4 \pm 0.2 a,b,c,d	0.79 \pm 0.10 a,b,c,d	36.5 \pm 10.1	65.5 \pm 21.0 b	13.9 \pm 1.5 a,b	104 \pm 16 d,e,f	0.22 \pm 0.03 e,f
<i>Sarracenia minor</i>	6	1.7 \pm 0.2 a,b,c	0.73 \pm 0.09 a,b	41.7 \pm 11.0	81.3 \pm 21.1 b	12.8 \pm 2.2 a	78 \pm 6 b,c,d,e	0.26 \pm 0.04 f
<i>Sarracenia oreophila</i>	6	1.4 \pm 0.1 a	1.04 \pm 0.09 b,c,d,e,f	53.7 \pm 16.4	73.3 \pm 25.0 b	14.6 \pm 1.1 a,b	76 \pm 10 b,c,d	0.21 \pm 0.02 d,e,f
<i>Sarracenia purpurea</i>	6	1.5 \pm 0.4 a,b	1.22 \pm 0.47 d,e,f	40.3 \pm 19.2	51.2 \pm 24.5 a,b	22.5 \pm 2.8 d	66 \pm 8 a,b	0.17 \pm 0.03 b,c,d
<i>Sarracenia rosea</i>	2	2.7 a,b,c,d	0.98 b,c,d,e,f	37.0	54.0 ab	14.9 ab	62 ab	n/a
<i>Sarracenia rubra</i>	6	2.9 \pm 1.0 b,c,d	1.14 \pm 0.14 c,d,e,f	64.0 \pm 28.3	80.2 \pm 34.6 b	17.4 \pm 0.9 b,c	66 \pm 5 a,b	0.20 \pm 0.03 c,d,e
<i>Nepenthes x coccinea</i>	2	9.5 f	1.80 g	2.5	1.5 a	14.1 ab	40 a	0.10 a
<i>Nepenthes x miranda</i>	2	5.7 e	0.58 a	1.1	3.0 ab	16.2 ab	108 e,f	0.12 a,b
<i>Drosera filiformis</i>	6	5.5 \pm 0.6 e	1.33 \pm 0.15 f,g	30.7 \pm 2.9	32.8 \pm 4.0 a,b	13.7 \pm 1.3 a,b	118 \pm 11 f	0.12
<i>Dionea muscipula</i>	6	3.9 \pm 0.8 d,e	0.76 \pm 0.08 a,b,c	26.3 \pm 10.8	48.7 \pm 20.8 a,b	13.5 \pm 1.9 a	113 \pm 17 f	0.14 \pm 0.01 a,b,c
$F_{14,58}$		32.086	11.946	1.684	3.013	18.064	18.263	16.255
P		2.3×10^{-22}	1.9×10^{-12}	0.084	0.002	2.5×10^{-16}	1.9×10^{-16}	8.6×10^{-13}
B) Laminae/phyllodia								
<i>Nepenthes x coccinea</i>	5	8.5 \pm 1.7	3.44 \pm 1.10	29.8 \pm 23.1	13.4 \pm 10.7	16.8 \pm 1.4	67 \pm 10	0.14 \pm 0.02
<i>Nepenthes x miranda</i>	2	5.8	0.91	36.0	51.5	16.5	103	0.14
<i>Sarracenia flava</i>	5	2.8 \pm 0.3	0.83 \pm 0.13	43.0 \pm 10.1	74.0 \pm 20.9	18.6 \pm 3.6	154 \pm 23	0.20 \pm 0.02
<i>Sarracenia leucophylla</i>	5	2.5 \pm 0.2	1.06 \pm 0.16	35.8 \pm 24.1	48.5 \pm 30.0	17.7 \pm 1.9	132 \pm 30	0.20 \pm 0.03
<i>Sarracenia oreophila</i>	3	2.4 \pm 1.3	1.38 \pm 0.12	n/a	n/a	16.5 \pm 0.4	n/a	0.17 \pm 0.01

TABLE 2. Mean (± 1 SD; unless pooled into one composite sample or not available [n/a]) construction costs (g glucose/g dry mass) for phyllodia/laminae (noncarnivorous leaves), traps, roots, and rhizomes of 15 carnivorous plants. The overall nested analysis of variance model (structures nested within species) was highly significant ($F_{18,133} = 14.97$, $P = 2.49 \times 10^{-20}$), but there were no significant differences among traps, roots, and rhizomes ($F_{2,149} = 1.353$; $P = 0.262$). Different lowercase letters indicate differences among species in the construction cost of a given plant part ($P < 0.05$, Tukey's HSD post hoc test for multiple comparisons among means).

Species	N	Phyllodia/laminae	Traps	Roots	Rhizomes
<i>Darlingtonia californica</i>	2	n/a	1.17 \pm 0.18 a,b	1.15 \pm 0.04 a,b	1.30 \pm 0.01 a,b
<i>Sarracenia alabamensis</i>	6	n/a	0.97 \pm 0.04 a	1.36 \pm 0.05 b	1.22 \pm 0.06 a,b
<i>Sarracenia alata</i>	6	n/a	1.19 \pm 0.09 b	1.19 \pm 0.12 b	1.12 \pm 0.13 a,b
<i>Sarracenia flava</i>	6	1.40 \pm 0.31	1.64 \pm 0.16 c	1.11 \pm 0.07 a,b	0.94 \pm 0.10 a
<i>Sarracenia jonesii</i>	6	n/a	0.97 \pm 0.06 a	1.21 \pm 0.08 a,b	1.17 \pm 0.15 a,b
<i>Sarracenia leucophylla</i>	6	1.32 \pm 0.15	1.02 \pm 0.12 a,b	1.17 \pm 0.06 a,b	1.12 \pm 0.05 a,b
<i>Sarracenia minor</i>	6	n/a	0.94 \pm 0.18 a	1.02 \pm 0.09 a	1.00 \pm 0.09 a
<i>Sarracenia oreophila</i>	6	1.22 \pm 0.03	1.08 \pm 0.09 a,b	1.02 \pm 0.10 a	1.34 \pm 0.10 b
<i>Sarracenia purpurea</i>	6	n/a	1.71 \pm 0.22 c	1.19 \pm 0.14 a,b	1.31 \pm 0.18 b
<i>Sarracenia rosea</i>	2	n/a	1.12 \pm 0.11 a,b	1.23 a,b	1.27 a,b
<i>Sarracenia rubra</i>	6	n/a	1.29 \pm 0.07 b	1.13 \pm 0.10 a,b	1.11 \pm 0.04 a,b
<i>Nepenthes \timescoccinea</i>	2	1.18 \pm 0.02	0.96 \pm 0.06 a,b	1.16 a,b	1.31 a,b
<i>Nepenthes \timesmiranda</i>	2	1.19 \pm 0.01	1.16 \pm 0.08 a,b	1.28 \pm 0.07 a,b	n/a
<i>Drosera filiformis</i>	6	n/a	0.98 \pm 0.09 a	1.06 a,b	1.09 a,b
<i>Dionaea muscipula</i>	6	n/a	0.97 \pm 0.15 a	0.88 a	n/a

associated lamina or phyllodia (1.41 \pm 0.14 g glucose/g DM) for the five carnivorous plants in this study and eight species of *Nepenthes* in Borneo (Osunkoya et al., 2007) that have both traps and phyllodia or laminae (Fig. 1). Construction costs of traps were also significantly lower than construction costs of leaves of 267 noncarnivorous species compiled from a search of the published literature ($t = 6.32$, $df = 288$, $P = 9.87 \times 10^{-10}$; Fig. 2). Six carnivorous species were at the lower extreme of the overall distribution, including plants with snap-traps (*Dionaea muscipula*), sticky pads (*Drosera filiformis*), and pitfall traps (*Sarracenia alabamensis*, *S. jonesii*, *S. minor*, *N. \times miranda*). The two species with the greatest CC_{mass} for traps measured in this study (*S. purpurea*, *S. flava*) were $\sim 20\%$ below the maximum of 2.10 g glucose/g DM found in the literature for leaves. Construction costs of roots of carnivorous plants were also significantly lower than CC_{mass} of roots of 20 noncarnivorous species ($t = 3.20$, $df = 34$, $P = 0.003$; Fig. 2). Construction costs of rhizomes were also lower than CC_{mass} of bamboo, the only noncarnivorous species for which rhizome CC_{mass} has been reported (Fig. 2).

Payback time—We found no significant relationship between A_{mass} and CC_{mass} ($r = 0.17$, $df = 54$, $P = 0.51$), but differences in payback time to recover (amortize) the carbon cost of constructing carnivorous traps were significantly different among species ($F_{14,54} = 4.980$, $P = 8.02 \times 10^{-6}$; Table 3). The longest times were for *S. purpurea* (1551 h) and *Darlingtonia californica* (1370 h). *Sarracenia flava* had a payback time (1262 h) similar to *Darlingtonia californica*, and four other species (*S. leucophylla*, *S. rosea*, *Drosera filiformis*, and *Dionaea muscipula*) had payback times exceeding 900 h. The *Nepenthes* and six remaining *Sarracenia* species recovered pitcher CC_{mass} in about one-third to one-half the time (range 495–849 h) required by *S. purpurea*.

DISCUSSION

The goal of this study was to use carnivorous plants to examine mechanisms underlying the universal spectrum of leaf traits (Wright et al., 2004; Shipley et al., 2006) by testing four specific hypotheses about construction costs, photosynthetic rates, and payback times: (1) carnivorous traps that both photosynthe-

size and capture prey should be relatively costly structures (have high CC_{mass}), (2) when separate structures for photosynthesis and prey capture occur on the same plants, CC_{mass} of traps should be lower than CC_{mass} of laminae and phyllodia, (3) construction costs of roots and rhizomes should be less than leaves (traps, phyllodia, lamina), and (4) there should be a clear trade-off between A_{mass} and CC_{mass} . To our knowledge, this is the first time that both construction costs and photosynthetic rates for carnivorous traps have been measured simultaneously, and our results provide further insights into hypothesized mechanisms underlying the universal spectrum of leaf traits (Wright et al., 2004; Shipley et al., 2006).

Our data did not support our first hypothesis. As a group, traps of carnivorous plants had significantly lower average CC_{mass} than did leaves of noncarnivorous plants (Fig. 2). But our data

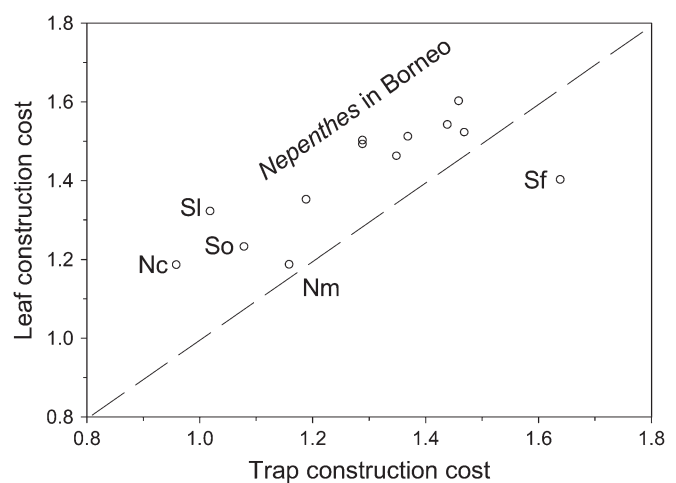


Fig. 1. Construction costs (g glucose/g dry mass) for five carnivorous plants (this study) and *Nepenthes* in Borneo (Osunkoya et al., 2007) that have both traps and phyllodia or laminae, with broken line representing a 1:1 relationship. Abbreviations: Nc = *Nepenthes \times coccinea*, Nm = *N. \times miranda*, Sf = *Sarracenia flava*, Sl = *S. leucophylla*, So = *S. oreophila*.

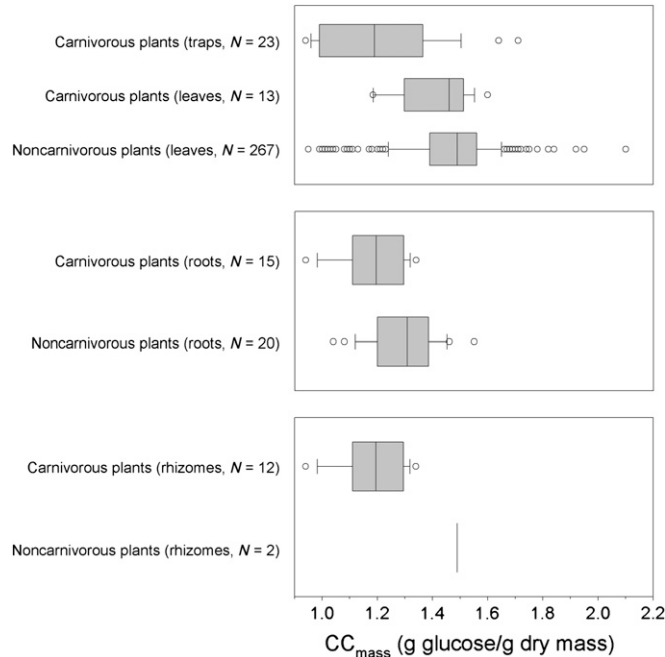


Fig. 2. Tissue construction cost for 15 carnivorous plants (this study), eight species of *Nepenthes* in Borneo (Osunkoya et al., 2007) and 267 noncarnivorous plants (data from Griffin, 1994; Isagi, 1994; Mitchell et al., 1995; Baruch and Gomez, 1996; Dai and Wiegert, 1996; Isagi et al., 1997; Marquis et al., 1997; Niinemets, 1997; Spencer et al., 1997; Wullschlegel et al., 1997; Baruch and Goldstein, 1999; Eamus et al., 1999; Baruch et al., 2000; Nagel and Griffin, 2001; Villar and Merino, 2001; George et al., 2003; Suárez, 2003, 2005; Nagel et al., 2004, 2005; Oikawa et al., 2004, 2006; Osunkoya et al., 2004, 2007; Barthod and Epron, 2005; Brunt et al., 2006; J. D. Karagatzides, unpublished data).

did support our second hypothesis. Traps were less costly to build than phyllodia in *Sarracenia* and laminae in *Nepenthes* (our data and data of Osunkoya et al. [2007]; Fig. 1). Similar to

TABLE 3. Mean (± 1 SD) payback time (h/g DM) for traps. Different lowercase letters indicate significant differences among species in payback time ($P < 0.05$, Tukey's HSD post hoc test for multiple comparisons among means). Note that payback for *Nepenthes* is for the mass-weighted cost of the lamina plus the trap, but is based on A_{mass} by the lamina alone (A_{mass} of *Nepenthes* pitchers ≈ 0).

Species	N	Trap payback time (h/g DM)
<i>Darlingtonia californica</i>	2	1370 \pm 446 c,d
<i>Sarracenia alabamensis</i>	6	682 \pm 299 a,b,c
<i>Sarracenia alata</i>	6	705 \pm 142 a,b,c,d
<i>Sarracenia flava</i>	6	1262 \pm 395 b,c,d
<i>Sarracenia jonesii</i>	6	495 \pm 58 a
<i>Sarracenia leucophylla</i>	6	932 \pm 507 a,b,c,d
<i>Sarracenia minor</i>	6	737 \pm 179 a,b,c,d
<i>Sarracenia oreophila</i>	6	694 \pm 231 a,b,c,d
<i>Sarracenia purpurea</i>	6	1551 \pm 614 d
<i>Sarracenia rosea</i>	2	1019 \pm 424 a,b,c,d
<i>Sarracenia rubra</i>	6	565 \pm 105 a,b
<i>Nepenthes \times coccinea</i>	2	815 \pm 118 a,b,c,d
<i>Nepenthes \times miranda</i>	2	849 \pm 246 a,b,c,d
<i>Drosera filiformis</i>	6	1052 \pm 126 a,b,c,d
<i>Dionea muscipula</i>	6	1087 \pm 191 a,b,c,d
Overall $F_{14,54}$		4.613
P		2.09×10^{-5}

our results, Pavlovič et al. (2007) measured near-zero A_{mass} for pitchers of *Nepenthes alata* and *N. mirabilis* and higher rates of A_{mass} for laminae. Together, these results suggest long payback times based on pitcher CC_{mass} measured by Osunkoya et al. (2007), although Pavlovič et al. (2007) did not measure A_{mass} of the *Nepenthes* spp. studied by Osunkoya et al. (2007). Overall, the low CC_{mass} of carnivorous traps is associated with low A_{mass} ; traps have small marginal gains and long payback times.

Our data neither clearly supported nor failed to support our third hypothesis. Contrary to the findings of previous studies that measured costs for individual compounds in structures of herbaceous plants (e.g., Poorter and Villar, 1997), we found that traps (modified from leaves) were not consistently more costly to build than roots or rhizomes (Table 2). We note that Poorter and Villar (1997) found that construction costs of stems in herbaceous plants were similar to those of roots. It may be that traps of carnivorous plants have high concentrations of total structural carbohydrates that are relatively cheap compounds (Poorter and Villar, 1997), but have low concentrations of the expensive compounds used for photosynthesis (hence the low A_{mass} measured for carnivorous plants). Similar to traps, average CC_{mass} for carnivorous plant roots (Table 2) was lower in all but one case (*S. alabamensis*) than the average CC_{mass} of roots of 20 noncarnivorous species (Fig. 2). Rhizome CC_{mass} for carnivorous plants in the current study is similar to tubers of *Potamogeton pectinatus* but 10–37% lower than for bamboo (*Phyllostachys bambusoides* and *P. pubescens*, both with a cost of 1.49 g glucose /g DM), the only other studies we found reporting CC_{mass} for rhizomes (Fig. 2).

Payback time of traps ranged threefold (495–1551 h) and differed significantly among the carnivorous plants we studied. Energy content was significantly greater in the two *Sarracenia* species with the highest CC_{mass} and payback times (*S. purpurea* and *S. flava*; Table 1), suggesting that these two species invest in expensive compounds (e.g., lipids, soluble phenolics, protein, lignin; Poorter et al., 2006). This observation lends credence to the hypothesized trade-offs between investments in liquid-phase processes such as photosynthesis and structural processes required to construct leaves, roots, and rhizomes (Shipley et al., 2006). Several carnivorous plants in the current study had relatively similar (and low) CC_{mass} but substantially different LMA (e.g., *Drosera filiformis*, *Dionea muscipula*, *S. minor*, *S. alabamensis*, *S. jonesii*). Leaf mass area increases with added cell layers, but CC_{mass} remains unchanged if these layers are of similar biochemical composition (Griffin, 1994). Leaf mass area also increases with an investment in less costly compounds (e.g., structural and nonstructural carbohydrates; Poorter et al., 2006). The generally observed pattern in our data of decreasing N concentration with increasing LMA (Wright et al., 2004) further supports the notion of an investment in non-N-based compounds as leaf density increased.

All carnivorous plants examined in the current study had long payback times to recover carbon invested in traps. As the number of functions of an organism or organs increases, the efficiency of performance of any particular function may decline (Read and Stokes, 2006). Pavlovič et al. (2007) suggested that reduced photosynthesis of *Nepenthes* traps was a cost of multiple functions—digesting prey, absorbing nutrients, and transferring nutrients to other plant parts. The long payback times we measured for carnivorous plants (Table 3) also may reflect the inefficiency of a modified leaf in fulfilling these multiple roles in addition to photosynthesizing. Kikuzawa and

Lechowicz (2006) found a near constant lifetime carbon gain for leaves of 25 species. If carbon gain similarly is equal across all carnivorous plants (and A_{mass} is low across all carnivorous plants studied to date: Table 1 and Ellison, 2006), then a longer lifespan could offset differences in carbon cost and gain (A_{mass}) in the current study. This trade-off between lifespan, carbon cost, and carbon gain is an example of the “many-to-one mapping relationship in functional design” that reflects different ways to achieve a constant lifetime carbon gain for individual leaves (Kikuzawa and Lechowicz, 2006, p. 381). However, for 20 of the 25 species in the study by Kikuzawa and Lechowicz (2006), they used only the mean value of CC_{mass} (1.5 g glucose/g DM) based on 79 species compiled in Griffin (1994); therefore the constant lifetime carbon gain hypothesis needs further testing with species-specific values of CC_{mass} .

Finally, our data did not support our fourth hypothesis, Shipley et al.'s (2006) prediction concerning trade-offs between A_{mass} and CC_{mass} . Our data do show that carnivorous plants overall have low construction costs, but their very low photosynthetic rates led to long payback times. However, it is difficult to compare our estimates of payback time (in hours) with those for noncarnivorous plants reported in the literature (in days); accurate estimates of payback time require information on the daily hours of maximal A_{mass} for these species (e.g., mean labor time; Kikuzawa and Lechowicz, 2006) because light is not available 24 h per day. For example, a generous assumption of 10 h/d of maximal A_{mass} for the carnivorous plants in our study that are found in open environments would require ~50–150 d to recover the carbon used to construct a trap. This range exceeds estimates for noncarnivorous plants growing in open, well lit areas (e.g., 4–30 d for *Piper* spp. (Williams et al., 1989); 15–20 d for sun leaves of six adult tree species (Poorter et al., 2006)). Actual payback times could be lower, however, because early returns on foliar investment can offset later losses (Westoby et al., 2000), and carnivorous plants translocate nutrients from trap to trap (Butler and Ellison, 2007). Thus, traps may have higher rates of A_{mass} early in the growing season, particularly before they open and actively trap and digest prey, which may reduce the payback time estimated from our calculations. Pavlovič et al. (2007), for example, found that phylloids (emerging in spring) of *Sarracenia psittacina* had significantly greater A_{mass} than pitchers (which formed later in the growing season). Ellison and Gotelli (2002) also found that phylloids of *S. purpurea* had photosynthetic rates 25% higher than those of pitchers. Additionally, prolonged tissue life is a major mechanism by which the efficiency of resource use is maximized in resource-poor environments (Bloom et al., 1985), and measurements of leaf lifespan of carnivorous plants would provide the additional data needed to complete their carbon budgets.

Our results of low CC_{mass} for carnivorous traps are contrary to the common expectation that the construction of elaborate carnivorous traps should be costly (Givnish et al., 1984). Furthermore, carnivorous plants are poorly represented in the universal spectrum of leaf economics data set (four of 2548 observations; Wright et al., 2004) and are outliers because they have very low photosynthetic rates (Ellison and Farnsworth, 2005; Farnsworth and Ellison, 2008). Our use of payback time, integrating traits used to assess leaf-scaling relationships with construction costs, yields better estimates for total costs and benefits of carnivorous structures to place carnivorous plants at the “slow and tough” end of the universal spectrum of leaf economics.

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