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Photosynthetic light response in three carnivorous plant species: *Drosera rotundifolia, D. capensis and Sarracenia leucophylla*

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Abstract

Photosynthetic properties of carnivorous plants have not been well characterized and the extent to which photosynthesis contributes to carbon gain in most carnivorous plants is also largely unknown. We investigated the photosynthetic light response in three carnivorous plant species, *Drosera rotundifolia* L. (sundew; circumpolar and native to northern British Columbia, Canada), *Sarracenia leucophylla* Rafin. ('pitcher-plant'; S.E. United States), and *D. capensis* L. (sundew; Cape Peninsula, South Africa), using portable gas-exchange systems to explore the capacity for photosynthetic carbon gain in carnivorous plant species. Maximal photosynthetic rates (1.32–2.22 µmol m^{-2} s^{-1} on a leaf area basis) and saturating light intensities (100 to 200 µmol PAR m^{-2} s^{-1}) were both low in all species and comparable to shade plants. Field or greenhouse-grown *D. rotundifolia* had the highest rates of photosynthesis among the three species examined. Dark respiration, ranging from –1.44 (*S. leucophylla*) to –3.32 (*D. rotundifolia*) µmol m^{-2} s^{-1} was high in comparison to photosynthesis in the species examined. Across greenhouse-grown plants, photosynthetic light compensation points scaled with light-saturated photosynthetic rates. An analysis of gas-exchange and growth data for greenhouse-grown *D. capensis* plants suggests that photosynthesis can account for all plant carbon gain in this species.

Additional key words: carnivorous plants; *Drosera*; photosynthesis; respiration; *Sarracenia*; sundews.

Introduction

Carnivorous plants represent a uniquely interesting group of plants within the phylum *Anthophyta*. This group contains approximately 538 species occurring in 18 genera and 8 families found worldwide in both semi-terrestrial and aquatic habitats (Givnish 1989). Carnivorous plants have been known to grow in nutrient-poor environments where readily available nutrients (especially nitrogen) are limiting. Since the first meticulous experiments of Darwin (1875), it has often been proposed that carnivorous plants fulfill some of their basic nutrient requirements by insect prey capture and digestion. Nevertheless, it is now known that such plants are capable of growth without insect capture (Slack 2000). Many studies regarding carnivorous plants have focused on mineral nutrition and nutrient acquisition (Stewart and Nilsen 1992, Chapin and Pastor 1995, Adamec 1997, Thoren and Karlsson 1998). These studies suggest that carnivorous plants may benefit through increased biomass, increased nutrient concentrations, or increased reproduction capabilities from insect capture. However, less is known about the rates at which these plants photosynthesize and how carnivory may relate to photosynthesis.

Carnivorous plants possess the C_3 pathway of CO_2 fixation and it has been proposed that the impact of nutrient availability or habitat quality may affect the benefits and costs associated with photosynthesis (Givnish 1989). While growth of carnivorous plants has been generally shown to benefit from prey capture (Ellison 2006), net photosynthetic rate (P_N) may increase in some cases (Farnsworth and Ellison 2008, Pavlovič *et al.* 2009) but not in others (*e.g.* Méndez and Karlsson 1999, Wakefield *et al.* 2005). However, irrespective of

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Abbreviations: *E* – transpiration rate; g_{sw} – stomatal conductance to water vapour; k – convexity factor; P_N – net photosynthetic rate; P_{Nmax} – light saturated P_N; PPFD – photosynthetic photon flux density; $PPFD_{comp}$ – PPFD at the light compensation point for P_N; R_D – dark respiration; RH – relative humidity; α – apparent photosynthetic quantum yield.

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environmental or plant conditions, carnivorous plant P_N is generally lower, *e.g.* in the subarctic, relative to non-carnivorous plants (Mendéz and Karlsson 1999), at least in some cases because of relatively high dark respiration rates (Adamec 2010). The consequences of low P_N in leaves, and even lower P_N in traps (*e.g.* Adamec 2006), reflect the high inherent costs of the carnivorous strategy in plants (Karagatzides and Ellison 2009) and associated dark respiration (R_D).

The objectives of this study were two-fold, (*1*) to further characterize the photosynthetic light-response properties of three carnivorous plants: native (field- and greenhouse-grown) *D. rotundifolia*, and greenhouse-grown non-native *D. capensis* and *Sarracenia leucophylla*, and (*2*) to contrast the rate of carbon gain through absolute changes in aboveground biomass (top-down model) for one of these species (*D. capensis*) with a bottom-up modeling of net carbon gain (using measures of P_N and R_D) over a two-month interval. The last objective was specifically aimed at addressing the question of whether photosynthesis in *D. capensis* could reasonably account for the biomass gain observed for this species.

Materials and methods

Greenhouse plant material: *D. rotundifolia* and *D. capensis* are herbaceous perennials of the plant family *Droseraceae*. The former is found across the northern temperate regions of the world, including local bogs in the vicinity of Prince George, BC. Leaves of *D. rotundifolia* are borne on flat stalks and are arranged in a rosette with a diameter of 3 to 6 cm (Slack 2000). Six mature 1-year-old plants of the same seed source were selected. *D. capensis* is native to the Cape peninsula in South Africa, with total length of (petiole + leaf) between 7.5 and 15 cm arranged around a central stem (Slack 2000). Six mature 2-year-old plants were used. *S. leucophylla* is a herbaceous perennial from the plant family Sarraceniaceae. Its native range spans from north-west Florida into south-west Georgia and westward to the Mississippi border. The pitchers form from a central rhizome and generally grow to 75 cm in height when mature (Slack 2000). Six plants were grown from seed for 2 years and were of uniform health when measured in the present study.

All greenhouse-propagated plants representing all three species were grown in 10 cm^3 containers using a soil mixture consisting of 60% peat (*Premier Sphagnum* peat moss, Canada), 25% washed sand (*Kodies* sand pit, Prince George, BC, Canada), 10% 2–3 mm forestry sand (*Target products*, Abbotsford, BC, Canada) and 5% perlite (*Supreme* perlite, Portland, Oregon) from 2000 to 2002. Daytime greenhouse light conditions were a combination of natural sunlight supplemented with artificial lamps. Light levels at the apices of the carnivorous plants varied across the year from a lower winter average PPFD of 72 $\mu mol\ m^{-2}\ s^{-1}$ to a higher summer average of 125 $\mu mol\ m^{-2}\ s^{-1}$. Day- and night-time air temperatures were maintained at relatively constant levels throughout the year, 24 and 15 ± 2°C, respectively. Greenhouse humidity was generally between 60 and 70% relative humidity (RH) and plants were well-watered to simulate bog moisture conditions. Insect levels in the greenhouse were low but were occasionally found on plant traps. *Drosera* spp. produced healthy rosettes of mature leaves and *Sarracenia* had numerous mature traps (10–15 cm in height) at the time of sampling.

Field-collected *D. rotundifolia*: Field specimens of native *D. rotundifolia* plants were collected from a tamarack [*Larix laricina* (Du Roi) K. Koch], black spruce [*Picea mariana* (Mill.) BSP] dominated bog ~40km west of Prince George (53° 53' N, 122° 41' W) near Norman Lake Road on 1 and 13 July 2009, at the height of summer for this region. Plants were transported back to the University of Northern British Columbia and kept in a greenhouse as above until photosynthetic measurements were made within 5 days of the collection dates.

Gas-exchange measurements and light-response curve analysis: Gas-exchange properties of leaves of greenhouse grown plants were measured in the summer and fall of 2002 with a portable gas-exchange system (*LI-COR 6200*, Lincoln, NE, USA) with a 0.25-l chamber. For *S. leucophylla* and *D. capensis*, individual leaves were measured while the plant remained potted. For *D. rotundifolia*, because of small size, entire plants were removed from pots, measured for total area and placed in the chamber with bare roots externalized from the chamber for gas-exchange measurements, with roots kept moist for the duration. Each of the *S. leucophylla* and *D. capensis* plants were measured twice but *D. rotundifolia* plants could only be measured once due to its uprooting. External CO_2 concentrations were near-ambient (~400 ±15 $\mu mol\ mol^{-1}$) under both ambient light as well as from 0 to 600 μmol PAR $m^{-2}\ s^{-1}$ using a *QB6200 LED* light source (*Quantum Devices Inc*., Barneveld, WI, USA). After leaf dark acclimation and measurement of dark respiration, leaves were given a minimum of 2 min to stabilize to each new increasing light level before measurements were taken. Gas-exchange conditions of RH and temperature were maintained at greenhouse levels.

Gas-exchange for field-collected *D. rotundifolia* plants was measured using a portable gas-exchange system (*LI-COR 6400*, Lincoln, NE, USA) with a

LI-COR 6400-05 conifer chamber. Extracellular CO_2 concentrations were controlled at slightly above ambient levels (400 µmol mol^{-1}) and light levels were modulated by adjusting the amount of natural sunlight received starting with opaque cloth and transitioning to full sunlight by reductions in layers of neutral-density screen material. Plants remained rooted in natural, moist bog substrate for these measurements. Throughout all measurements, intracellular CO_2 concentrations (C_i), air temperature and RH did not deviate far from mean values of 385 ±5 µmol mol^{-1}, 28 ±2°C and 45 ±7% at all light levels, respectively.

Light-response curves were modeled by fitting non-rectangular hyperbolas to data as described by Prioul and Chartier (1977).

$$P_N = \frac{\mathrm{PPFD}\,\alpha + P_{\mathrm{Nmax}} - [(\alpha\ \mathrm{PPFD} + P_{\mathrm{Nmax}})^2 - 4\alpha\ P_{\mathrm{Nmax}}\ \mathrm{PPFD}\ k]^{0.5}}{2k} R_D$$

where P_{Nmax} is light-saturated net photosynthesis (µmol CO_2 m^{-2} s^{-1}); PPFD is photon flux density (µmol PAR m^{-2} s^{-1}); α is the initial slope or apparent photosynthetic quantum yield (P_N/PPFD at low PPFD), and k is the convexity or curvature factor (between 0 and 1). All parameters were computed using the empirical data with the exception of k, which was subjectively assigned for the best fit.

Carbon balance for *D. capensis*: To assess the importance of photosynthesis to carnivorous plant carbon balance, we assessed the aboveground biomass changes in *D. capensis* plants over 59 days, and contrasted this with an estimate of photosynthetic carbon gain over that same period of time. Leaf growth, total leaf area and number were measured in each of six replicate plants and converted to biomass based on area/mass ratios for these leaves in combination with final biomass measurements. Biomass was converted to carbon assuming a carbon fraction of 50%. This was contrasted with gas-exchange measurements for *D. capensis* performed under ambient light and growing conditions over typical 8-h photoperiods and in the dark. Twilight hours (~8h per day) had light levels that were very close to the light compensation point for *D. capensis*, and therefore only gas-exchange under ambient light and in dark conditions was considered for the calculation of CO_2 uptake rates for each plant over the 59-day period.

Statistical analysis: Single factor *ANOVA* was performed to assess the significance of effect of species on photosynthetic rates among the three carnivorous plant species and *t*-tests were performed to assess differences between means (*Excel v. 5.1, Microsoft Corp*., USA).

Results

Photosynthetic rates and response curves: The response of net photosynthesis to light (PFD) in greenhouse-grown *D. capensis, D. rotundifolia* and *S. leucophylla* is shown in Fig. 1. In all three species, non-rectangular hyperbolas provided good fits to the data, with linear responses at low PFD's < 80 µmol m^{-2} s^{-1} and light- saturated photosynthetic rates achieved at PFD's < 200 µmol m^{-2} s^{-1}. We also assessed the photosynthetic light response in native field-grown *D. rotundifolia* (Fig. 2). Interestingly, the photosynthetic light response of natural field-collected specimens of *D. rotundifolia* did not differ substantially from their greenhouse-grown counterparts, with the exception of a lower RD and higher PPFD (400–500 µmol m^{-2} s^{-1}) at photosynthetic light saturation (P_{Nmax}). Average transpiration rates (E) and stomatal conductances to water vapour (g_{swv}) for field grown *D. rotundifolia* were 1.13±0.33 (mmol m^{-2} s^{-1}) and 1.9 ±0.27 (mmol m^{-2} s^{-1}), respectively. Adaxial and abaxial stomatal densities for these same field-grown plants were 215 and 146 mm^{-2}, respectively.

Photosynthetic light-response curve characteristics for greenhouse-grown plants and field-grown *D. rotundifolia* are presented in Table 1. Leaf area- and mass-based photosynthetic rates (Table 1) were lowest in *S. leucophylla* and highest in native *D. rotundifolia*. Dark respiration (R_D), light compensation point ($\mathrm{PPFD}_{\mathrm{comp}}$) and the apparent photosynthetic quantum yield (α) all had similar species rankings. Area-based R_D was significantly higher in greenhouse-grown as opposed to field-collected specimens of *D. rotundifolia*, while no differences were observed in P_{Nmax}. Dark (daytime) respiration was uniformly ≥ light-saturated net photosynthesis in greenhouse-grown plants (Fig. 1, Table 1), with R_D: P_{Nmax} ranging from 1.45 in *D. rotundifolia* to 1.05 in *D. capensis*.

Carbon balance model results: *D. capensis* plants were grown for an additional 59 days under greenhouse conditions and their CO_2 uptake rates estimated in two ways, in top-down fashion after measuring the additional biomass-carbon produced over that time, and bottom-up by measuring P_N and R_D under ambient greenhouse conditions and multiplying by the leaf area (Table 2). With the assumptions provided, biomass gain and net CO_2 exchange methods resulted in similar values for net CO_2 uptake, 0.074 ± 0.024 versus 0.069 ±0.041 for this species.

Discussion

The responses of leaf photosynthesis in all three carnivorous species investigated in this study were well characterized by non-rectangular hyperbolas (Figs. 1, 2) typical of non-carnivorous plant leaves (Prioul and Chartier 1977), *i.e.* there were relatively linear increases in net photosynthesis with increasing light level (<100 µmol PFD m^{-2} s^{-1}) to a point of light saturation (100–500 µmol PFD m^{-2} s^{-1}) where net photosynthesis leveled off. Light-saturated photosynthetic rates found in this study for *S. leucophylla, D. rotundifolia*, and *D. capensis* [1.32–2.22 µmol m^{-2} s^{-1} on a leaf area basis; 29.4–47.1 nmol g^{-1} s^{-1} on a dry mass (DM) basis] were comparable to rates observed for *Pinguicula alpina*, *P. villosa*, *P. vulgaris*, and *D. rotundifolia* (Méndez and Karlsson 1999; 2.0–3.0 µmol m^{-2} s^{-1}), *D. capensis* and *S. psittacina* [Pavlovič *et al.* 2007, 31 and 36 nmol g^{-1}(DM) s^{-1}, respectively] and for the northern pitcher plant *S. purpurea* [Small 1972: 30 nmol g^{-1}(DM) s^{-1}].

The results of our study corroborate the prevalence of low maximal photosynthetic rates in carnivorous plants. While low photosynthetic rates in greenhouse-grown plants in this study (Fig. 1) could conceivably have been attributed to growth at lower than ambient light levels (Table 2), light-saturated photosynthetic rates of field-collected *D. rotundifolia* did not differ significantly from those of greenhouse-grown plants (Table 1), suggesting that photosynthesis is constitutively low, perhaps in coordination with low growth rates (*e.g.* Shipley 2006). However, photosynthetic rates in carnivorous plants may also be restricted externally. Stomatal densities or conductances did not appear to be limiting to gas exchange (Results section), but low photosynthetic rates among carnivorous plants could be due to low nutrient levels present in their native habitats, *i.e.* bogs. Ellison and Gotelli (2002) showed that by elevating soil nitrogen levels, pitchers of *S. purpurea* were reduced relative to phyllodia size resulting in an increase in the rate of

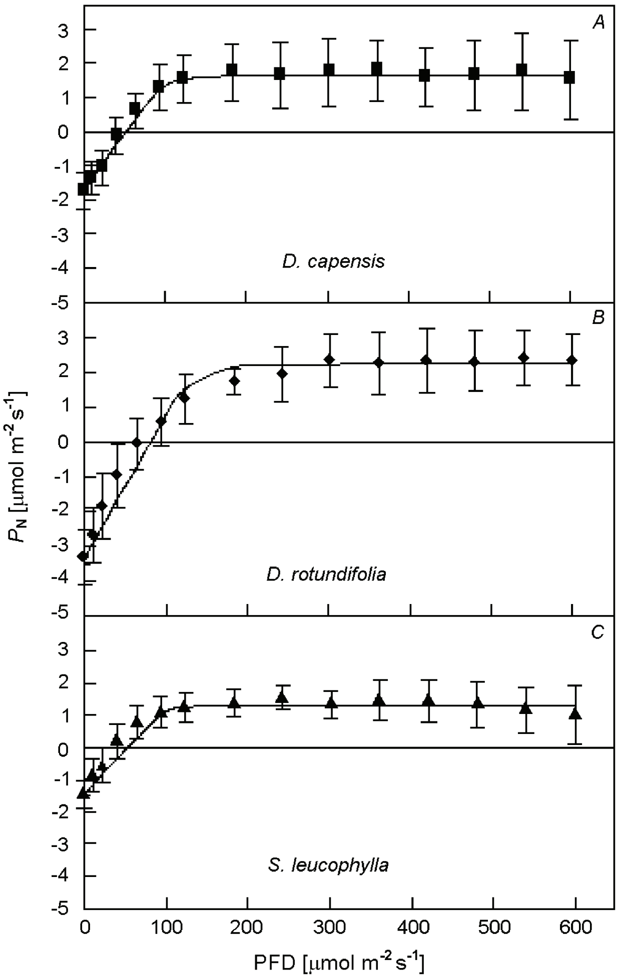

Fig. 1. Photosynthetic light-response curves for greenhouse-cultivated *D. capensis, D. rotundifolia* and *S. leucophylla* in 2002, each fitted with a non-rectangular hyperbolic function, $n = 6$. *Vertical bars* show the standard deviation.

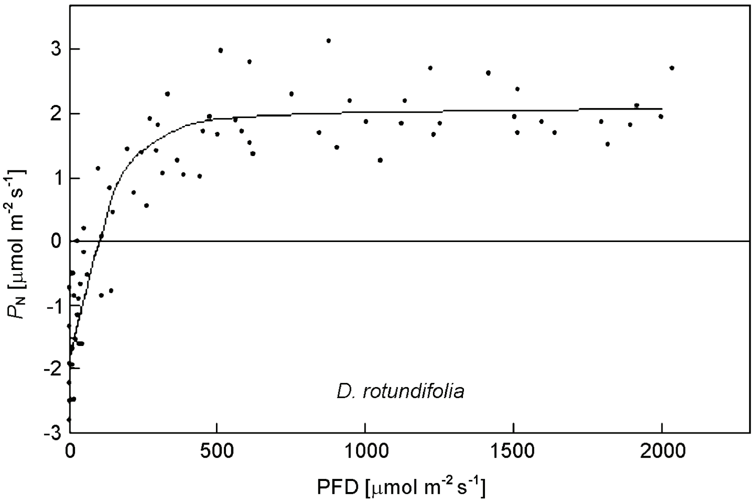

Fig. 2. Photosynthetic light-response curve for field-collected *D. rotundifolia* in 2009, fitted with a non-rectangular hyperbolic function, $n = 6$.

Table 1. Characteristics of photosynthetic light-response curves for *S. leucophylla, D. rotundifolia*, and *D. capensis* greenhouse-grown plants. Mean values (±SD, $n = 6$) of light-saturated area-based photosynthesis ($P_{\text{Nmax (area)}}$), light-saturated mass-based photosynthesis ($P_{\text{Nmax(mass)}}$), dark respiration (R_D), light compensation point ($\text{PPFD}_{\text{comp}}$), convexity factor ($k$), and apparent photosynthetic quantum yield (α, P_N/PPFD at low PPFD). Means followed by different letters indicate significant differences in $P_{\text{Nmax (area)}}$ and R_D between greenhouse- and field-collected *Drosera rotundifolia* (Student's *t*-test, $p < 0.05$).

Species	$P_{\text{Nmax (area)}}$ [µmol m^{-2} s^{-1}]	$P_{\text{Nmax(mass)}}$ [nmol g^{-1} s^{-1}]	R_D [µmol m^{-2} s^{-1}]	R_D:P_{Nmax}	$\text{PPFD}_{\text{comp}}$ [µmol PAR m^{-2} s^{-1}]	k	α
D. capensis	1.65 ± 0.1	36.9 ± 2.2	–1.73 ± 0.53	1.05	50.5	0.9	0.033
D. rotundifolia (greenhouse)	2.28 ± 0.39^a	47.0 ± 8.8	–3.32 ± 0.79^a	1.45	78.0	0.99	0.036
(field)	2.12 ± 0.48^a	–	–1.87 ± 0.77^b	0.88	92.1	0.9	0.020
S. leucophylla	1.32 ± 0.17	29.4 ± 3.7	–1.44 ± 0.43	1.09	43.6	0.99	0.027

Table 2. Empirically determined parameter values for aboveground carbon balance models (top-down; $n = 12$, versus bottom-up; $n = 6$) used to calculate instantaneous 24-h rates of net carbon gain for greenhouse-grown *Drosera capensis* plants over 59 days: mean±SD. [1]Net CO_2 uptake rate calculated by converting biomass gains over 59 days to instantaneous rates. Only aboveground processes were considered in the above models. [2]P_N measured under average greenhouse conditions: mean air temperature of 24°C, RH of 60–70%, and PPFD of 72 ±26 µmol m^{-2} s^{-1}. [3]R_D measured under daytime greenhouse conditions (24°C). [4]Dark respiration corrected to nighttime temperatures of 15°C assuming a Q_{10} of 2.5. [5]Net CO_2 uptake over 59 days was calculated by assuming P_N occurred over the ~9h photoperiod, corrected R_D occurred over the ~8h dark period, and no net CO_2 exchange occurred over the remaining ~7h of dawn and dusk. Mean plant leaf areas over the 59 days were 44.9 ±11.0 cm^2.

	Average increase in leaf number (59 d)	Average leaf mass [g(leaf DM)$^{-1}$]	Average plant biomass gains [g] (59 d)	Net CO_2[1] uptake rate [µmol(CO_2) m^{-2} s^{-1}] (top-down)
Net biomass production approach (top down)	5.66 ± 1.21	0.0088 ± 0.0027	0.052 ± 0.025	0.074 ± 0.024
	P_N[2]	R_D[3]	corrected R_D[4]	Net CO_2[5] uptake rate [µmol(CO_2) m^{-2} s^{-1}] (bottom-up)
Net CO_2 exchange approach (bottom-up)	0.66 ± 0.97	–1.07 ± 0.33	–0.47 ± 0.13	0.069 ± 0.041

photosynthesis. Similarly, Knight (1992) revealed that *U. macrorhiza* grew less in the presence of having leaves and bladders than those plants that produce leaves alone. Both studies suggest that there is a cost of carnivory and that photosynthesis is linked to the nutrient status of the habitat and investment in trapping structures. However, these studies only account for the effects of added nutrients to the substrate in which the plant grows. It is unclear to what extent nutrients obtained through prey capture contribute to photosynthetic performance. The cost-benefit modeling of Givnish *et al.* (1984) predicts that photosynthetic rates should increase as a result of prey-derived nutrient gain. However, Méndez and Karlsson (1999) did not find any significant increases in photosynthetic rates in prey-augmented carnivorous plants. They suggested instead that the nitrogen from prey was perhaps allocated to non-photosynthetic compounds.

Light-saturated photosynthesis based on leaf area and DM (Table 1) varied significantly between species. *Sarracenia leucophylla* exhibited the lowest rate of light-saturated photosynthesis (1.32 µmol m^{-2} s^{-1}). This rate could reflect the juvenile state of this species as pitchers were not fully expanded in our study. However, when comparing the mass-based photosynthetic rate of *S. leucophylla* (29.4 nmol g^{-1} s^{-1}) with that of the rate found in another pitcher-plant, *S. purpurea* (Small 1972), the values are similar, suggesting that photosynthetic rates may not differ significantly with age or size within this species. *Drosera rotundifolia,* field- or greenhouse-grown, had both the highest leaf area and mass-based photosynthetic rates (Table 1) among the three carnivorous species examined. It is interesting to note that although *D. rotundifolia* was the smallest in terms of size of the three species in this study, it possessed the higher area or mass-based rates.

Dark respiration rates, ranging from –1.44 (*S. leucophylla*) to –3.32 (*D. rotundifolia*) µmol m^{-2} s^{-1} in greenhouse-grown plants, were relatively high when compared to photosynthesis with the ratios of R_D:P_{Nmax} being above one for all greenhouse-grown plants and close to one (0.88) in field-grown plants (Figs. 1, 2; Table 1). Leaf respiration, normally 50% or less of light-saturated photosynthesis (*e.g.* Bazzaz and Carlson 1982), may have been higher in these carnivorous plants because plants limited by nitrogen tend to use a larger fraction of photosynthate for respiration than those with sufficient nitrogen (Lambers *et al.* 1998). The relatively low leaf nitrogen levels in *Drosera* spp. (Asada *et al.* 2005), combined with ^{15}N evidence for heavy reliance on insect as opposed to root-derived nitrogen (Millett *et al.* 2003), would support this contention. In addition, while respiration is generally higher in roots than in leaves (Lambers *et al.* 1998), this may not hold true for carnivorous plants that typically have reduced root systems (Juniper *et al.* 1989), as observed in our *Drosera* spp.; instead carbon allocation may be directed towards trapping mechanisms and associated stems and leaves. Thus, most carnivorous plant respiration in *Drosera* would likely be associated with growth (*i.e.* trap production) and maintenance (*e.g.* trap activity) respiration that is in part non-photosynthetic. Thoren *et al.* (2003) demonstrated a reduction of investment in carnivory in shade-grown or fertilized *D. rotundifolia* plants. However, the relatively low-light greenhouse *D. rotundifolia* plants had high R_D (not usual for shade plants and not consistent with reduction in carnivory and low insect capture) but a lower photosynthetic light compensation (characteristic of shade-grown plants). An explanation for these discordant results is not readily evident from this work or the literature and may warrant further attention.

Can photosynthesis explain biomass gain in carnivorous plants?

An ongoing question is whether photosynthesis provides enough carbon uptake to account for all of the observed biomass carbon gain in carnivorous plants? Despite the potential for considerable genetic and environmental control and variation in carbon metabolism within carnivorous plants, we performed a simple modeling exercise to assess whether net photosynthetic carbon uptake could potentially explain all of the biomass carbon gain observed for the carnivorous species, *D. capensis*. The average rate of aboveground biomass carbon gain for a 59-day period, disregarding any potential changes in root biomass, was found to 0.074 μmol(C) m^{-2} s^{-1}. Net photosynthesis and respiration rates measured in these plants under the ambient growing conditions were scaled up over the same 59-day period to yield an average C-gain of 0.069 μmol m^{-2} s^{-1}, lower but not significantly different from the biomass number above. While the latter required a considerable number of assumptions (Table 2), it does at least suggest that photosynthesis is capable of explaining all of the carbon gain in *D. capensis*. It should also be noted that the greenhouse environment used for this work, although not completely devoid of insect life, was unlikely to have provided *Drosera* with substantial inputs of insect carbon based on visual assessment of *Drosera* traps during the course of the experiment. Ultimately, experimental approaches such as feeding plants with isotopically labeled (*e.g.* ^{14}C or ^{13}C) insect material should ultimately provide a clearer picture of if or when (*e.g.* seasonally and under what environmental conditions) captured prey contribute to the carbon economy of different carnivorous plant species.

Overall, ambient rates of photosynthesis in one carnivorous plant (*D. capensis*) appeared to be sufficient to provide the carbon gain necessary to support the increases in plant biomass observed. A plausible explanation for the high ratios of 'dark' respiration to photosynthesis in the species evaluated in this study and in those of others, are the constitutive costs associated with building and maintenance of traps, relegating them to the "slow and tough" end of plant spectrum (Karagatzides and Ellison 2009).

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