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THE COST OF CARNIVORY FOR *DARLINGTONIA CALIFORNICA* (SARRACENIACEAE): EVIDENCE FROM RELATIONSHIPS AMONG LEAF TRAITS[1]

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Scaling relationships among photosynthetic rate, foliar nutrient concentration, and leaf mass per unit area (LMA) have been observed for a broad range of plants. Leaf traits of the carnivorous pitcher plant *Darlingtonia californica*, endemic to southern Oregon and northern California, USA, differ substantially from the predictions of these general scaling relationships; net photosynthetic rates of *Darlingtonia* are much lower than predicted by general scaling relationships given observed foliar nitrogen (N) and phosphorus (P) concentrations and LMA. At five sites in the center of its range, leaf traits of *Darlingtonia* were strongly correlated with elevation and differed with soil calcium availability and bedrock type. The mean foliar N : P of 25.2 ± 15.4 of *Darlingtonia* suggested that these plants were P-limited, although N concentration in the substrate also was extremely low and prey capture was uncommon. Foliar N : P stoichiometry and the observed deviation of *Darlingtonia* leaf traits from predictions of general scaling relationships permit an initial assessment of the ‘‘cost of carnivory’’ in this species. Carnivory in plants is thought to have evolved in response to N limitation, but for *Darlingtonia*, carnivory is an evolutionary last resort when both N and P are severely limiting and photosynthesis is greatly reduced.

Key words: carnivorous plants; *Darlingtonia californica*; fens; leaf mass area; leaf traits; photosynthesis; nitrogen; serpentine.

A central goal of plant ecology is to understand fundamental relationships among common processes required by living plants: the fixation of carbon via photosynthesis, the acquisition and use of mineral nutrients, and the use of carbon and mineral nutrients in the construction of plant organs (Givnish, 1986; Reich et al., 1997, 1999; Sterner and Elser, 2002; Wright et al., 2004). Recent analyses of data from thousands of species have suggested that physiological and stoichiometric constraints are the primary controls on relationships between leaf traits such as photosynthetic rate, nutrient and mineral content, specific leaf area, and leaf longevity (Reich et al., 1999; Castro-Diéz et al., 2000; Shipley and Lechowicz, 2000; Ellison, 2002; Wright et al., 2004). These interspecific relationships appear to be altered only modestly by climate or habitat characteristics (Reich and Oleksyn, 2004; Wright et al., 2004), life form (Craine et al., 2001; Wright and Westoby, 2001; Reich et al., 2003), or by evolutionary history (Ackerly and Reich, 1999).

Wright et al. (2004, p. 821) called the observed scaling relationships among leaf traits among >2500 species of plants a ‘‘universal spectrum of leaf economics.’’ This spectrum defines scaling relationships among photosynthetic rate, foliar N and P, and leaf mass area, encompasses a broad continuum of plant functional types, and includes species that range from low to high growth rates and photosynthetic efficiencies. This model is useful for identifying plants that have unique adaptations (Reich et al., 1999). It may also be used to elucidate how intraspecific adaptations to local site conditions occur within the context of these broad constraints set by leaf-level trade-offs.

Plants in marginal habitats, such as bogs, fens, and other wetlands, often have a suite of unique characteristics that allow them to persist in strongly nutrient-limiting conditions. For example, two studies have shown that scaling relationships among leaf traits of wetland plants differ substantially from predictions based on the broad syntheses of plants from terrestrial biomes (Shipley and Lechowicz, 2000; Ellison, 2002). Mangroves (Ellison, 2002) and freshwater wetland herbs (Shipley and Lechowicz, 2000) have lower photosynthetic rates and lower diffusive conductance for given levels of leaf nitrogen than do terrestrial plants. Leaf nitrogen content, photosynthetic rate, and diffusive conductance are all lower in mangroves than are expected given the lifespan of the leaves (Ellison, 2002). High salinities and anoxic soil conditions result in slow transpiration rates and high water use efficiencies in mangroves (Ball and Passioura, 1994) and entail a high carbon cost of water uptake by roots (Ball and Sobrado, 1998) that may explain their position as outliers in the general spectrum of leaf traits (Ellison, 2002). Similarly, low redox potentials brought on by waterlogging may contribute to relatively low photosynthetic rates in freshwater wetland plants (Talbot and Etherington, 1987; Talbot et al., 1987; Crawford and Braendle, 1996). The wetland herbs studied by Shipley (2000) tend to occur in phosphorus-limited systems (Bedford et al., 1999), whereas mangroves are known to be limited either by nitrogen, phosphorus, or both (Onuf et al., 1977; Alongi et al., 1992; Clough, 1992; Feller, 1995; Ellison and Farnsworth, 2001).

The combination of extremely low nutrient concentrations, high light, and waterlogged soils in bogs, fens, tepuis, and

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inselbergs (Givnish et al., 1984, 1989; Barthlott et al., 1998; Porembski and Barthlott, 2000; Ellison and Gotelli, 2001) is hypothesized to favor the evolution of carnivory in plants (Givnish et al., 1984; Benzing, 1987, 2000). The 600 or so species of carnivorous plants share a convergent capacity to derive mineral nutrients directly from capture and digestion of animal prey (Benzing, 1987; Givnish, 1989; Ellison and Gotelli, 2001; Ellison et al., 2003) that supplements nutrient uptake from soil (Chapin and Pastor, 1995; Schulze et al., 1997; Ellison and Gotelli, 2001). The relationship between low nutrient concentrations and potentially high photosynthetic rates in these habitats is the foundation for the cost-benefit model for the evolution of carnivory in plants (Givnish et al., 1984). This model asserts that carnivory should be favored if the marginal ''costs'' associated with constructing carnivorous organs are less than the marginal photosynthetic ''benefits'' derived from the additional nutrients obtained from carnivory. The cost-benefit model has been supported with data showing that carnivorous plants can reduce their production of carnivorous organs when nutrients are more abundant in the peat, ponds, or streams in which these plants grow (Knight and Frost, 1991; Knight, 1992; Zamora et al., 1998; Guisande et al., 2000; Ellison and Gotelli, 2002; Thorén et al., 2003), as well as in shady conditions (Zamora et al., 1998; Brewer, 2003; Thorén et al., 2003). This flexibility in carnivorous investment also suggests that leaf traits of these plants, notably nutrient content and photosynthetic rates, could be quite variable among habitats, especially if either soil nutrients or prey availability vary widely. Based on findings in other wetland systems (Shipley and Lechowicz, 2000; Ellison, 2002), we hypothesized that the spectrum of leaf traits in a carnivorous plant might be an outlier with respect to the universal spectrum, indicating trade-offs between deployment of leaf mass, leaf area, and nutrients towards prey capture and away from photosynthesis.

In all carnivorous taxa, the carnivorous organs are modified leaves, leaf parts such as tendrils, or glands occurring on leaves (Juniper et al., 1989), but few data on leaf traits of carnivorous plants are available. The data set of 2548 species at 175 sites compiled by Wright et al. (2004) includes three carnivorous plant species: two records of *Sarracenia purpurea* L. (Sarraceniaceae) from Wisconsin, USA (Reich et al., 1999), and Ottawa, Canada (Small, 1972); one record of *Drosera rotundifolia* L. (Droseraceae) from Abisko, Sweden (Kudo et al., 2001); and unpublished data for an unidentified *Drosera* species from Western Australia.

The original publications of these data also provide no information on intraspecific variability in leaf traits. *Darlingtonia* is a geographically narrow endemic, and hence we further expect low variability within and among populations in leaf-trait relationships. A recent comparative study of leaf traits in endemics and congeneric widespread species showed that endemics did not differ in leaf traits from their widespread congeners (Lavergne et al., 2004), but neither wetland plants nor carnivorous plants were included in their study.

In this study, we examined leaf traits of the carnivorous plant *Darlingtonia californica* Torrey (Sarraceniaceae). We addressed four questions: (1) What is the intraspecific variation in photosynthetic rates, specific leaf area, and leaf nutrient and mineral content? (2) Is the observed variation associated with habitat characteristics such as ambient nutrient availability or elevation? (3) Where does *Darlingtonia* fit in the universal spectrum of leaf traits defined by Wright et al. (2004)? (4) What does the placement of *Darlingtonia* in this universal spectrum tell us about the ecological costs of carnivory?

Study species—*Darlingtonia californica* is a long-lived, rhizomatous, perennial, carnivorous pitcher plant endemic to southern and coastal Oregon and northern California, USA (Torrey, 1853; Schnell, 2002). It is the only species in the genus and the only pitcher plant native to North America west of the Rocky Mountains. *Darlingtonia* grows in fens and along seeps and streams generally associated with ultramafic rocks and serpentine soils (Whittaker, 1960; Becking, 1997; Coleman and Kruckeberg, 1999), although it appears more to tolerate rather than require soils with high metal content, and it does not hyperaccumulate metals in its tissues (Reeves et al., 1983). The 50–100 cm tall pitchers of *Darlingtonia* are modified (epiascidiate) leaves (Arber, 1941; Franck, 1974, 1976) that are produced every 2–4 wk throughout the growing season (April/May–September/October at our sites) and senesce over the winter; their lifespan is generally 6 mo or less. The pitchers have a prominent, nearly spherical ''hood'' with a ''mouth'' at the base of the hood that faces downward (Fig. 1). From the far edge of the mouth hangs a ''fishtail appendage.'' Allometry of the tube, hood, and fishtail appendage differs between seedling (nonfeeding) and adult (feeding) pitchers but is generally consistent within life stages (Franck, 1976). Wasps and other prey are attracted to nectar secreted by extrafloral nectaries along the hood, mouth, and fishtail appendage; only approximately 2% of the potential prey visiting the nectaries is caught by the pitchers (Dixon et al., 2005). *Darlingtonia* does not possess digestive enzymes (Hepburn et al., 1927); captured prey is broken down by a food web of bacteria, protozoa, mites, and fly larvae (Naeem, 1988; Nielsen, 1990). The plant absorbs the mineral nutrients excreted by this food web.

Darlingtonia is locally common in appropriate habitats, but regionally it is threatened by mining, logging, collection by carnivorous plant hobbyists and commercial growers, and housing development. Although *Darlingtonia* was de-listed from CITES appendix II in 2000 (http://www.traffic.org/bulletin/cop11decisions.pdf, accessed 5 April 2005), it is ''watch-listed'' in both California and Oregon (http://international.fws.gov/animals/darlingt.html, accessed 5 April 2005). Therefore, it was also of interest to gather basic data on growth patterns and their variability within and among populations that are of conservation concern.

Study sites—We studied *Darlingtonia* at five sites in the Siskiyou Mountains along the California–Oregon border (Table 1). These sites are all within the Klamath Ranges (KR) subregion of the northwestern (NW) region of the California floristic province (Hickman, 1993). The bedrock is peridotite or granodiorite (Kruckeberg, 1984), and all five sites are characterized by serpentine soils (Kruckeberg, 1984; Becking, 1997) and circumneutral pH (6.9–7.3; see Materials and Methods) in the seeps and flowing streams along which *Darlingtonia* grows. The sites span an elevational range from 411 m above sea level (a.s.l.) at T. J. Howell's fen to 1241 m a.s.l. at Hobson Horn. At three of the sites (Days Gulch, Hawk Creek, and L. E. Horton), *Darlingtonia* grows on rocky terrain alongside continuously flowing streams, whereas at the other two sites (T. J. Howell, Hobson Horn), the plants grow in vegetated fens underlain by 10–30 cm of peat. Common co-occurring herbaceous plant species (nomenclature follows Hickman,

1993) include *Rudbeckia californica* A. Gray (Asteraceae), *Lotus oblongifolius* (Benth.) E. Greene (Fabaceae), and *Narthecium californicum* Baker (Liliaceae). At the higher elevation sites, the ericaceous shrubs *Rhododendron occidentale* (Torrey & A. Gray) A. Gray and *Ledum glandulosum* Nutt. and the trees *Pinus monticola* Douglas (Pinaceae) and *Chamaecyparis lawsoniana* A. Murray (Cupressaceae) form a patchy canopy over the *Darlingtonia* populations.

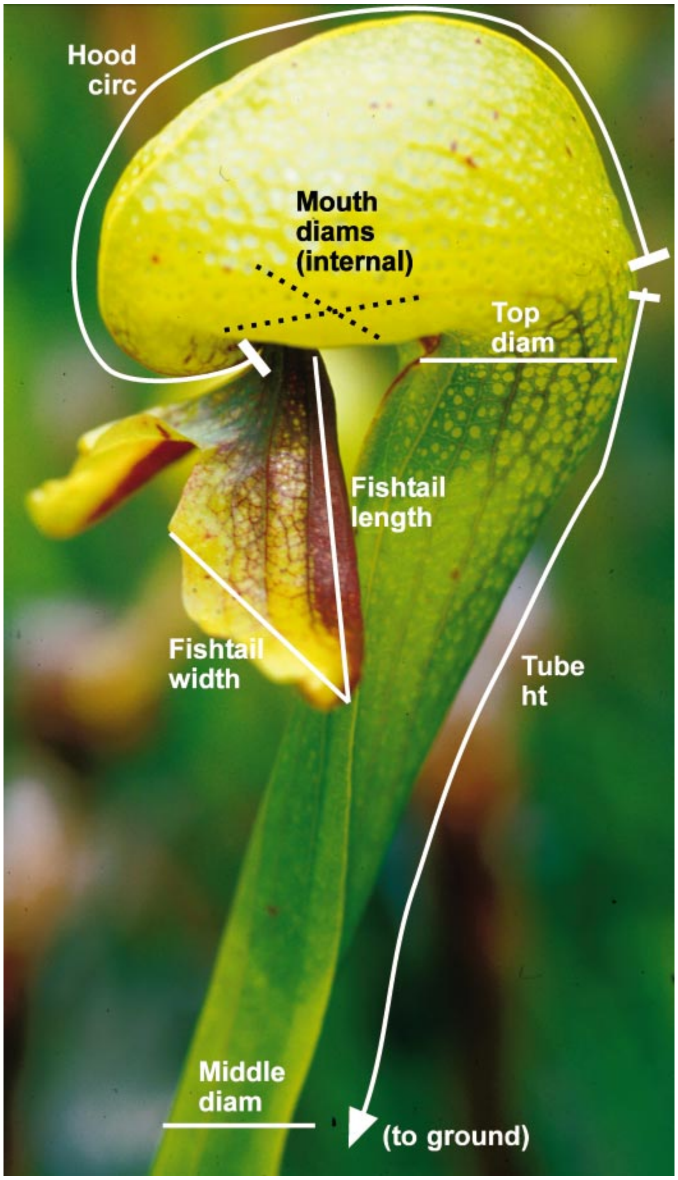

Fig. 1. Photograph of a *Darlingtonia californica* pitcher with morphological measurements indicated (lower diameter at ground level not shown). Note the translucent hood and the pronounced fishtail appendage attached to the proximal side of the mouth.

MATERIALS AND METHODS

Site characterization—All fieldwork was conducted from 3 to 13 August 2001. Elevation and location of each site was determined using a handheld Trimble GPS (Trimble Navigation, Sunnyvale, California, USA). Bedrock type was determined from field forms provided by the U.S. Bureau of Land Management and the U.S. Forest Service, published sources (Kruckeberg, 1984), and field observations. At each site, five 50-mL surface water samples were collected in sterile plastic tubes, frozen, and shipped frozen to our laboratory in Massachusetts for chemical analysis. There, water pH and calcium concentration were measured with an Orion model 290A portable pH/ISE meter and Orion pH and calcium electrodes (Thermo Electron, Waltham, Massachusetts, USA). Nitrogen (both NO_3-N and NH_4-N) and phosphorus (PO_4-P) concentrations were determined spectrophotometrically using standard methods (Bledzki and Ellison, 1998; Clesceri et al., 1998).

Field and laboratory measurements of plants—At each site, we measured size and shape of the largest mature, fully expanded pitcher on 10–12 distinct plants (genets) haphazardly chosen from among a stand of 500–10 000 plants growing in full sun. The sample size was limited by federal collecting permits, and we were permitted to collect only leaves (pitchers), not whole plants (i.e., we could not excavate roots and rhizomes). For each leaf, we used a flexible fabric tape to measure the height (±1 mm) of the pitcher's tube from ground level to the base of the hood; the circumference (±1 mm) of the hood from its base, around the top, and down to the mouth; and the length and height (±1 mm) of each half of the fishtail appendage (Fig. 1). Dial calipers were used to measure the two diameters (±0.1 mm) of the mouth and the diameter of the tube at its base, halfway up its length, and just below the hood. After measuring the leaf, we determined maximum photosynthetic rate (A_{area} in micromoles of CO_2 per square meter per second) using a LI-COR 6200 infrared gas analysis system (LI-COR, Lincoln, Nebraska, USA) with a custom-built 4-L chamber that enclosed the hood, fishtail appendage, and upper 20 cm of the pitcher tube. The chamber was constructed of Lexan (General Electric Plastics, Pittsfield, Massachusetts, USA) and included two fans (LI-COR) to ensure adequate mixing of air. All measurements of A_{area} were taken between 0930 and 1430 hours and photosynthetic photon flux density (PPFD) always exceeded 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Chlorophyll contents of the pitcher tube, hood, and fishtail appendage were then assayed in the field using a CCM-200 chlorophyll content meter (Opti-Sciences, Tyngsboro, Massachusetts, USA). The CCM-200 reports relative

TABLE 1. Environmental variables measured at the five *Darlingtonia californica* sites. Latitude and longitude are given imprecisely to protect sensitive sites and habitats. Water chemistry values are means of five samples; standard deviation in parentheses; values with different superscripted letters are significantly different ($P < 0.05$, Tukey's HSD test for post-hoc comparisons among means).

Site	Latitude (°N)	Longitude (°W)	Elevation (m a.s.l.)	Bedrock	Peat?	Surface stream?	NO_3-N (mg/L)	NH_4-N (mg/L)	PO_4-P (mg/L)	Ca (mg/L)	pH
T. J. Howell	42.2	122	411	Peridotite	Yes	No	0.004^{A} (0.010)	$0.39^{A,B}$ (0.24)	0.21^{A} (0.08)	7.89^{A} (3.73)	6.75^{B} (0.06)
Days Gulch	42.2	123	470	Peridotite	No	Yes	0.007^{A} (0.010)	0.19^{A} (0.01)	0.32^{B} (0.05)	3.92^{A} (0.39)	7.13^{C} (0.17)
L. E. Horton	42.5	124	540	Peridotite	No	Yes	0.004^{A} (0.009)	$0.39^{A,B}$ (0.01)	0.12^{A} (0.03)	3.95^{A} (0.77)	$6.81^{B,C}$ (0.09)
Hawk Creek	42.5	124	1100	Granodiorite	No	Yes	0.007^{A} (0.012)	0.74^{B} (0.44)	0.15^{A} (0.05)	48.05^{C} (23.03)	6.44^{A} (0.20)
Hobson Horn	41.9	124	1241	Granodiorite	Yes	No	0.009^{A} (0.012)	0.27^{A} (0.12)	0.10^{A} (0.09)	26.72^{B} (7.81)	6.47^{A} (0.14)

units (0–100), which we converted to actual units (μg chlorophyll [$a + b$]/m²) after calibrating the device with direct measures of chlorophyll content using the acetone extraction procedure of Porra et al. (1989) (the conversion equation was μg chlorophyll/m² = 391.8 + 16.78 × CCM units; $r^2 = 0.89$). The pitchers were then cut at the base, pressed in the field to prevent drying and loss of area (Shipley and Lechowicz, 2000), and returned within 24 h to our laboratory in Massachusetts where we used a LI-COR 3000 leaf area meter to determine the total area (±1 mm²) of the pitcher and the area of the portion of the pitcher that had been enclosed in the photosynthesis measurement chamber. The tube and hood were cut lengthwise and laid flat to get accurate measures of their area, and the area of the flat fishtail appendage was measured separately. We then dried the pitchers at 70°C to constant mass, and weighed (±0.001 g) the hood, fishtail appendage, and tube (sections inside and outside the photosynthesis chamber separately). The areas and masses were used to calculate leaf mass area (LMA, in grams per square meter) and mass-based photosynthetic rates (in nanomoles of CO_2 per gram per second). Each portion of the pitcher—hood, fishtail appendage, and tube—was ground in a Wiley mill prior to sending the samples to the University of Vermont Agricultural and Environmental Testing Laboratory where the C, N, and mineral content (P, Ca, Mg, K, Na, Al, Mn, Cu, Zn, Cr, Co, and Ni) of the leaves was determined. Carbon and N content of the finely ground, dried samples were determined using a Leeman Lab model 440 CHN elemental analyzer (Teledyne Technologies, Los Angeles, California, USA). Mineral content was determined on microwave-digested samples using a Perkin-Elmer Optima 3000 DV inductively-coupled plasma (ICP) atomic emission spectrometer (PerkinElmer, Wellesley, Massachusetts, USA).

Statistical analyses—All data analyses were performed using S-Plus version 6.1 (Insightful, Seattle, Washington, USA). We used linear regression to examine relationships between plant size and shape characteristics, and one-way analysis of variance (ANOVA) to examine differences among sites. Composite measures of morphology and tissue mineral content were constructed using principal components analysis (PCA). Because these data were measured on different scales and varied across orders of magnitude (from millimeter-diameter mouths to nearly meter-tall pitchers), before conducting the PCAs, we standardized all the morphological data to Z scores, $Z_i = (Y_i - \bar{Y}/s)$, where Y_i is the value of the measurement, $\bar{Y}$ is the mean of all values of that measurement, and s is the estimated standard deviation (Gotelli and Ellison, 2004). The Z scores are expressed in standard deviation units; for example a Z-score = +4 means that the value measured is four standard deviations larger than the observed mean.

We examined relationships between key leaf traits using reduced major axis regression on logarithmically transformed data (Reich et al., 1997, 1999; Wright et al., 2004). These relationships were compared with the leaf trait data used to construct the universal spectrum of leaf economics (Wright et al., 2004). Finally, we compared our measured values of mass-based photosynthesis (A_{mass}) with those predicted by the universal equation given in supplement 4 of Wright et al. (2004): $\log_{10}(A_{mass}) = 0.74 \times \log_{10}(N_{mass}) - 0.57 \times \log_{10}(LMA) + 2.96$.

RESULTS

Sites—Surface water at the sites did not differ in concentration of NO_3-N ($P = 0.9$, ANOVA), but did differ in pH ($P = 1.2 \times 10^{-6}$), NH_4-N concentration ($P = 0.01$), PO_4-P concentration ($P = 0.001$), and Ca concentration ($P = 6.3 \times 10^{-6}$). The two highest elevation sites, characterized by granodiorite bedrock, had significantly higher Ca concentration in the surface water, significantly lower PO_4-P in the surface water, and significantly lower pH than the other three sites underlain by peridotite bedrock (Table 1). NH_4-N concentrations varied significantly among the sites, but were not related to bedrock type, either of the two physiognomic characteristics, or elevation.

Plant morphology—Pitcher size measurements (tube height, diameter, hood circumference, and mouth diameter) were highly correlated with each other (all covariances >0.4). The first two principal components of pitcher size and shape accounted for 75% of the variance in the data and primarily reflected characteristics of the hood and of the height of the pitcher. Plants with large scores on the first principal component were larger in all characteristics than plants with small scores (Fig. 2A), and we used PC-1 scores in our subsequent analyses of plant size. The size of the whole plant (Fig. 2A) and the area of the fishtail appendage, a measure of the display used to attract prey (Fig. 2B), increased from low-elevation sites to the second highest one, but then declined at the highest site to a size equal to that found at the lower elevation sites. However, the allometric relationship between plant size and area of the fishtail appendage was similar across the five sites ($r^2 = 0.31$, $P < 1 \times 10^{-6}$). Leaf mass area increased steadily from low elevations to high elevations (Fig. 2C).

Chlorophyll and photosynthesis—Chlorophyll was not evenly distributed in *Darlingtonia* pitchers (Fig. 1, Fig. 2E); the green tube contained significantly ($t_{54} = 10.4$, $P < 1 \times 10^{-6}$) higher concentrations of chlorophyll (0.5–0.8 mg/g) than either the hood, with its many translucent aureoles (0.41–0.47 mg/g), or the fishtail appendage (0.40–0.45 mg/g). Photosynthetic rates of the pitchers were quite low, ranging from 10 to 50 nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$ (Fig. 2D). Both chlorophyll content and photosynthetic rate increased with increasing elevation (Fig. 2D and E).

Foliar nutrient and mineral content—Leaf nitrogen was quite low (overall average of 11.1 (=1.11%) ± 3.2 [SD] mg/g), but in parallel with chlorophyll content and photosynthetic rates, N content increased markedly with elevation (Fig. 2F). Leaf carbon content was consistently high among sites (488 ± 11 mg/g), and the combination of low N and high C yielded high C : N ratios (overall, 48.7 ± 10.9) in these plants. As N content increased with elevation, C : N ratios declined significantly ($F_{4,51} = 49.2$, $P = 1 \times 10^{-16}$). The three low-elevation sites had similar ($P > 0.05$) C : N ratios (T. J. Howell, 51.9 ± 3.12; Days Gulch, 56.8 ± 5.85; L. E. Horton, 56.0 ± 4.76), much higher than the C : N ratios at the two high-elevation sites (Hawk Creek, 41.0 ± 4.62; Hobson Horn, 32.1 ± 6.66), which also differed significantly from one another ($P < 0.05$).

Neither foliar P (0.6 ± 0.4 mg/g) nor foliar K (6.5 ± 3.9 mg/g) differed among the sites ($P = 0.07$ and $P = 0.10$, respectively). Key stoichiometric relationships, N : P ratios (25.2 ± 15.4) and N : K ratios (2.5 ± 1.6), did not differ among sites ($P = 0.97$ and $P = 0.36$, respectively).

Although all sites had serpentine soils, there were significant differences among sites in the metal content of pitchers. Principal components analysis revealed correlated groups of metals. Most notably, magnesium content was highest at low-elevation sites (low scores for PC-1; Fig. 2G), whereas calcium (low scores for PC-3; Fig. 2H), aluminum, and manganese (high scores for PC-1; Table 3 and Fig. 2G) content were highest at the high-elevation sites.

Scaling relationships among leaf traits—Mass-based maximal net photosynthetic rate (A_{mass}), leaf nitrogen (N_{mass}), leaf phosphorus (P_{mass}), and LMA of *Darlingtonia* were all significantly correlated with each other (Fig. 3). There was pronounced variability in all these traits among *Darlingtonia* in-

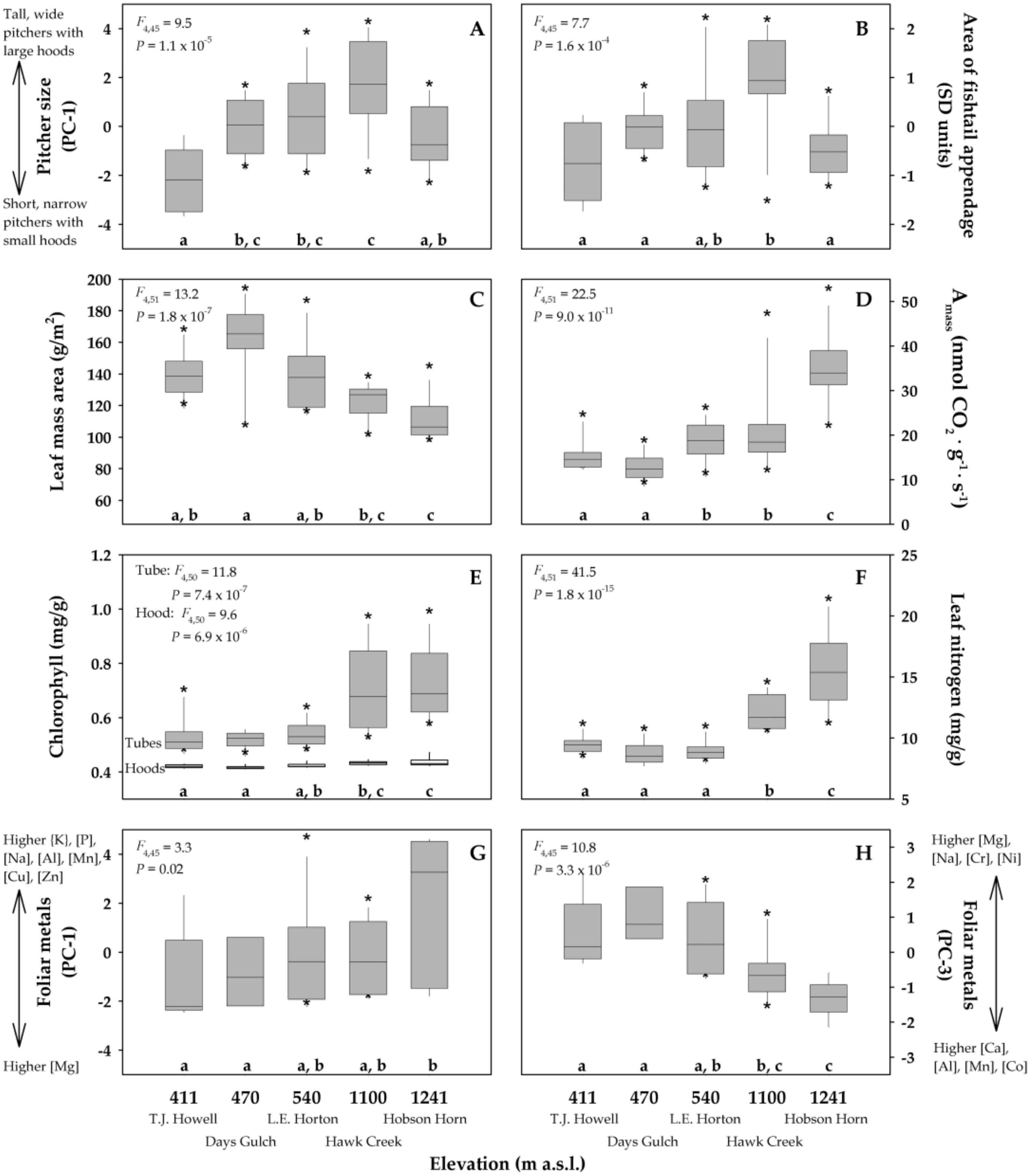

Fig. 2. Differences among sites in plant size (A), area of the fishtail appendage (B), leaf mass area (C), photosynthetic rate (D), chlorophyll content (E), leaf nitrogen content (F), and leaf metal content (G and H). Each panel illustrates box plots of 10–12 measurements per site (whiskers extend to the upper and lower deciles, and observations beyond these percentiles are indicated with an asterisk). The *F* statistics and associated *P* values are from one-way ANOVAs; sites with different letters are significantly different for the measured variable ($P < 0.05$, Tukey's honestly significant difference [HSD] test for a posteriori comparisons). Both chlorophyll content in the tube and chlorophyll content in the hood are shown in panel E.

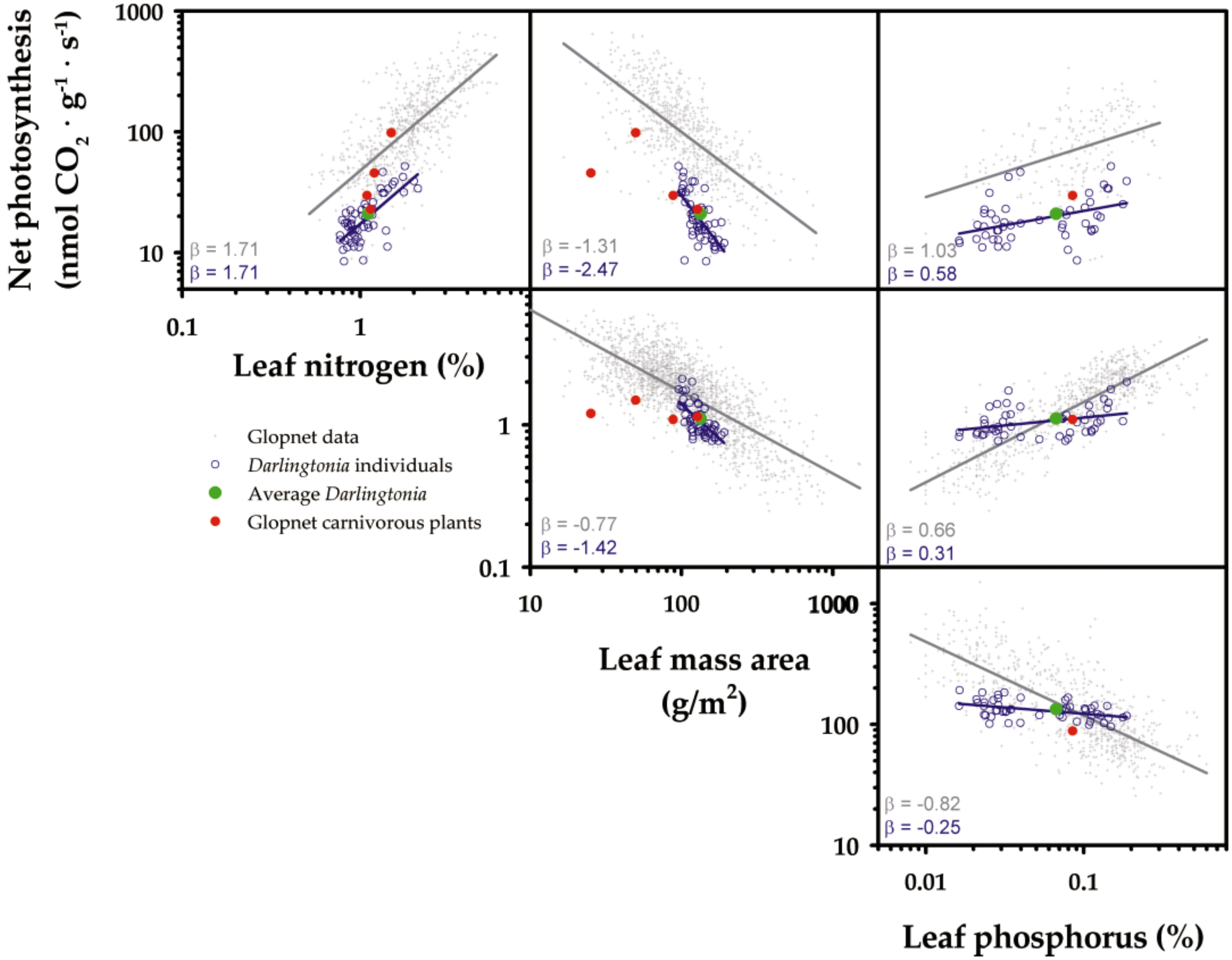

Fig. 3. Relationships between mass-based photosynthetic rate, leaf mass area, leaf nitrogen (%), and leaf phosphorus (%). The light grey points are data used to generate the universal spectrum of leaf traits (the Glopnet data set: Wright et al., 2004), the red circles are the four carnivorous plant species in the Glopnet data set (only one *Sarracenia* record has a value for P_{mass}), the light blue points are the 56 *Darlingtonia* individuals (this study), and the green point is the average *Darlingtonia* individual (this study). The slopes (scaling relationships) from the reduced major axis regressions of the Glopnet data (grey) and the *Darlingtonia* data (blue) are given in the lower left corner of each panel.

dividuals, and the average A_{mass}, N_{mass}, and LMA of *Darlingtonia* were similar to those of the Wisconsin *Sarracenia purpurea*, but much lower than those of the Ottawa *S. purpurea* or the two *Drosera* spp. in the Glopnet data set (Wright et al., 2004). The average P_{mass} of *Darlingtonia* was similar to that of the Ottawa *S. purpurea*, the only carnivorous plant in the Glopnet data set with reported P concentrations. The general scaling equations of Wright et al. (2004) overestimated A_{mass} in *Darlingtonia* by over twofold (Fig. 4); the multiple regression equation for the *Darlingtonia* data was: $\log_{10}(A_{mass}) = 0.91 \times \log_{10}(N_{mass}) - 0.77 \times \log_{10}(LMA) + 2.88$ ($r^2 = 0.60$, $N = 56$). Among *Darlingtonia* plants, A_{mass} increased half as quickly per unit increase in P and decreased ≈50% more rapidly per unit increase in LMA than did the plants in the Wright et al. (2004) data set.

DISCUSSION

Our intent in this study was to explore scaling relationships between leaf mass, photosynthetic rate, morphology, and foliar chemistry for a little-studied and highly unusual endemic carnivorous plant species and to compare these scaling relationships to the ‘‘universal spectrum of leaf traits’’ (Wright et al., 2004, p. 821) developed using data from noncarnivorous plants. In addition, to our knowledge, this is the first combined study of the physiology and morphometrics of *Darlingtonia californica*, and we documented substantial intraspecific variation in these traits within and among populations.

In terms of environmental conditions, the two high-elevation sites (Hawk Creek and Hobson Horn) differed most markedly from the other sites in surface water pH and phosphorus and calcium concentrations (Table 1). This may in part reflect the chemistry of the granodiorite bedrock at these two sites, which contrasts with the peridotite bedrock at the lower elevation sites. Ultramafic peridotite bedrock tends to be high in magnesium and relatively low in calcium, whereas igneous granodiorite tends to be somewhat enriched in calcium relative to magnesium (Strahler and Strahler, 1992). Although absolute

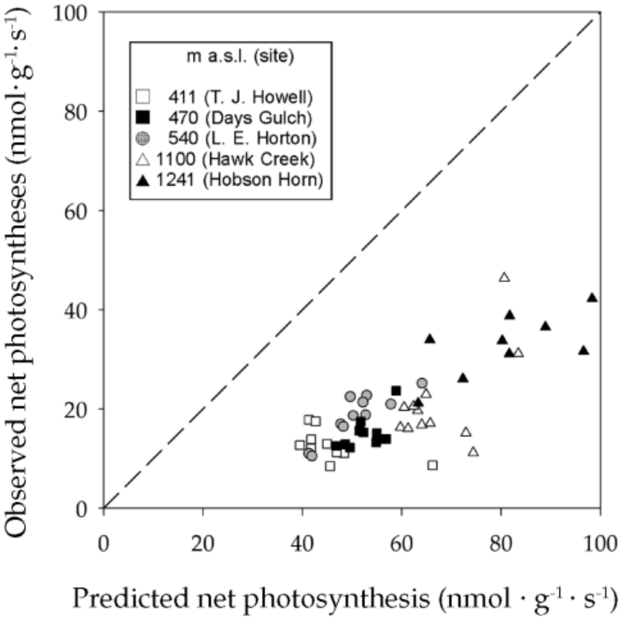

Fig. 4. Difference between the observed net photosynthetic rate of *Darlingtonia* (*y*-axis) and that predicted by the multiple regression equation of Wright et al. (2004) of photosynthetic rate on leaf nitrogen content and leaf mass area (*x*-axis). An accurate prediction would have the points falling on or close to the 1 : 1 diagonal, dashed reference line.

nitrate and ammonium concentrations in the substrate did not differ significantly among sites, increased soil calcium concentration is associated with enhanced mobilization of N by plants and could contribute to the higher foliar N observed in plants at Hawk Creek and Hobson Horn.

We investigated whether plants growing in these contrasting habitats differed in their relative allocation to photosynthetic vs. carnivorous structures (Gotelli and Ellison, 2002). However, we did not find significant differences in the allometric relationships between pitcher size and fishtail appendage size among the five sites, despite the fact that overall plant size varied widely among the populations. This result accords with data presented by Franck (1976), who found pronounced allometric differences between juveniles and adult *Darlingtonia* pitchers, but relatively constant allometric relationships among adult pitchers. Our observations and Franck's data suggest that *Darlingtonia* has little morphological flexibility in balancing photosynthesis and prey capture, even when soil N is more readily available to the plant. These data differ from results of other studies on carnivorous species that have demonstrated flexibility in relative allocation of carnivorous structures in response to N availability (Knight and Frost, 1991; Knight, 1992; Zamora et al., 1998; Guisande et al., 2000; Ellison and Gotelli, 2002; Thorén et al., 2003).

We observed high variability among plants in leaf traits, both within and among populations of *Darlingtonia*. As predicted by the universal spectrum of leaf traits, N_{mass}, A_{mass}, and LMA were all tightly correlated. *Darlingtonia* has similar scaling relationships of N_{mass}, LMA, and P_{mass} to those reported for noncarnivorous taxa (Reich et al., 1999; Wright et al., 2004). However, on average *Darlingtonia* had a much lower A_{mass} for its N_{mass}, P_{mass}, and LMA relative to the species studied by Wright et al. (2004) (Figs. 3, 4). Likewise, A_{mass} also was lower as a function of LMA than that of the two *Drosera* and one of the *Sarracenia* species reported in that study, and low relative to its N content compared with three species of *Pinguicula* and one species of *Drosera* not included in the Glopnet data set (Mendéz and Karlsson, 1999). Indeed, photosynthetic rates were very low relative to most plant species (see also Mendéz and Karlsson, 1999), although they did vary significantly among sites, with the plants at the high-elevation sites showing the highest rates of the five populations. This implies that A_{mass} is highly constrained as a function of LMA in this species, even though both traits are quite variable among sites. It is possible that the observed low A_{mass} is a consequence of low amounts of C stored in (or translocated to) belowground tissues. Although carnivorous plants are normally described as having small root systems, *Darlingtonia* develops extensive rhizomes (A. M. Ellison, personal observation). Because we were not permitted to excavate plants, we could not quantify root : shoot ratios of *Darlingtonia*, but we suspect that the low A_{mass} in this species is not a by-product of small allocation to root and rhizome production.

The concentrations of N, P, and K in foliar tissue were quite low, in the lower decile of ranges reported in broad reviews of vascular plants (Aerts and Chapin, 2000). The values of foliar N concentration we found in *Darlingtonia* are similar to those found for a range of other carnivorous plant species, including sundews (*Drosera*), flytraps (*Dionaea*), and pitcher plants (*Nepenthes*, *Cephalotus*, *Darlingtonia*, and *Sarracenia*) (Karlsson and Carlsson, 1984; Schulze and Schulze, 1990; Schulze et al., 1991, 1997; Chapin and Pastor, 1995; Mendéz and Karlsson, 1999; Ellison and Gotelli, 2002; Thorén et al., 2003; Wakefield et al., 2005). In particular, N_{mass} values reported by Schulze et al. (1997) for greenhouse-grown *Darlingtonia* are almost identical to the values we found for field-grown plants, and N_{mass} for carnivorous plans in the Glopnet data set (Wright et al., 2004) were similarly low (Fig. 3).

Because N has been assumed to be the limiting nutrient for carnivorous plants (but see Karlsson and Carlsson, 1984), P and K have not been measured routinely in studies of carnivorous plant stoichiometry, but P values in *Sarracenia* pitchers (Chapin and Pastor, 1995; Wakefield et al., 2005) and *Pinguicula* leaves (Karlsson and Carlsson, 1984) are as low or lower than those we observed in *Darlingtonia*. The N : P and N : K ratios we observed suggest that *Darlingtonia* is P-limited or P + K co-limited, based on comparisons with other wetland plants for which nutrient limitation has been derived based on stoichiometric relationships (Olde Venterink et al., 2003).

Preliminary evidence from other carnivorous plants (Karlsson and Carlsson, 1984; Wakefield et al., 2005) suggests that they may preferentially absorb P from prey. Our data on N : P ratios of common prey for *Darlingtonia* (N : P = 14; A. M. Ellison, unpublished data), and the very low rate of prey capture at all our study sites (Dixon et al., 2005) suggest that prey are not a significant source of P for these plants. Thus, the high and variable N : P ratios of pitchers at the different sites most likely reflects differences among sites in soil and water nutrient availability. Photosynthesis, leaf N, and plant size of *Darlingtonia* are highly sensitive to N availabilities, and photosynthetic rates in carnivorous plants are more responsive to additions of inorganic N (Ellison and Gotelli, 2002) than to additions of prey (Mendéz and Karlsson, 1999; Wakefield et al., 2005). All these studies suggest that in the field, the majority of foliar N is derived from substrate sources rather than carnivory, but absolute concentrations in soil and surface water are extremely low (Table 1). However, the relationship between observed nutrient concentrations and actual nutrient availability is unknown; we do not yet know the mechanisms by which carnivorous plants take up nutrients from prey or soil. The considerable investment in carnivorous traps may reflect as much a need for P as for N. Taken together, these observations suggest that carnivory in plants is Hobson's choice—an evolutionary ''last resort''—when concentrations of both N and P are extremely low in the soil.

Detailed investigation of this unusual species has allowed us to detect the morphometric and physiological axes along which it deviates from the universal spectrum of leaf traits. This deviation may allow us to more accurately assess the costs of carnivory in *Darlingtonia*. Construction costs associated with the elaborate pitcher, including the hood and fishtail appendage with their extrafloral nectaries and relatively low chlorophyll content, appear to be reflected in the relatively high LMA values and C : N ratios we observed. With a moderate leaf lifespan of less than 6 mo and a low photosynthetic rate, *Darlingtonia* exemplifies a species that Wright et al. (2004) would characterize as giving a ''slow return'' on investments of nutrients and dry mass in leaves and could perhaps be considered as an extreme along this continuum.

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