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Leaf traits of natural populations of *Adiantum reniforme* var. *sinensis*, endemic to the Three Gorges region in China

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Abstract

Leaf mass per unit area (LMA), carbon and nitrogen contents, leaf construction cost, and photosynthetic capacity (P_{max}) of *Adiantum reniforme* var. *sinensis*, an endangered fern endemic to the Three Gorges region in southwest China, were compared in five populations differing in habitat such as soil moisture and irradiance. The low soil moisture and high irradiance habitat population exhibited significantly higher LMA, area-based leaf construction (CC_A), and carbon content (C_A), but lower leaf nitrogen content per unit dry mass (N_M) than the other habitat populations. The high soil moisture and low irradiance habitat populations had the lowest CC_A, but their cost/benefic ratios of CC_A/P_{max} were similar to the medium soil moisture and irradiance habitat population due to their lower leaf P_{max}. Hence *A. reniforme* var. *sinensis* prefers partially shaded, moist but well-drained, slope habitats. Due to human activities, however, its main habitats now are cliffs or steeply sloped bare rocks with poor and thin soil. The relatively high energy requirements and low photosynthetic capacity in these habitats could limit the capability of the species in extending population or interspecific competition and hence increase its endangerment.

Additional key words: carbon content; construction cost; endangerment; energy requirement; fern; leaf mass per unit area; nitrogen content; photosynthetic capacity.

Introduction

Leaf traits are often related to the habitat and microhabitat of a particular species (Merino *et al.* 1984, Ellsworth and Reich 1992, Prior *et al.* 2003, Suárez 2003). For example, plants grown at low altitude or dry habitats generally have lower leaf nitrogen content (Friend *et al.* 1989, Westbeek *et al.* 1999, Suárez 2005), while leaf mass per unit area (LMA) tends to increase with increasing drought and irradiance (Evans and Hughes 1961, Kremer and Kropff 1999, Vats *et al.* 2002, Suárez 2005, Poorter *et al.* 2006). Many previous studies have revealed that these variations in leaf traits among populations within the same species are the results of adapting to growth habitats. However, such leaf traits are achieved at different energetic expense (Williams *et al.* 1987, Griffin 1994). Leaf construction cost, a quantifiable measurement of energy invested by a plant to construct biomass (Griffin 1994, Nagel and Griffin 2001), varies with the chemical composition of the leaf tissue (Suárez 2005, Poorter *et al.* 2006) and is strongly influenced by irradiance (Sims and Pearcy 1991, Poorter *et al.* 2006) and soil water (Suárez 2005). The ratio of leaf construction cost to photosynthetic capacity (P_{max}) reflects the cost-benefit relationship of leaf biomass construction and/or energy use efficiency, which can have important ecological implications for species survival, growth, and distribution (Zhang and Luo 2004, Nagel *et al.* 2005). Thus, studies of the differences in leaf traits among populations within the same species from the perspective of leaf cost-benefit relationship contribute to the understanding of the optimum habitat and population distribution of this species. If the species is endangered, findings from such studies can assist in the development of management approaches to conserve it.

Adiantum reniforme var. *sinensis*, an evergreen medicinal fern of the family Adiantaceae which has therapeutic effects on jaundice hepatitis, urinary infection, and otitis media (Xie 1993), is only distributed at altitudes 80–480 m in Wanzhou District and Shizhu County

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Abbreviations: C_A – carbon content per unit area; C_M – carbon content per unit dry mass; CC_A – construction cost per unit area; CC_M – construction cost per unit dry mass; C/N – carbon-to-nitrogen ratio; LMA – leaf mass per unit area; N_A – nitrogen content per unit area; N_M – nitrogen content per unit dry mass; P_{max} – photon saturated photosynthetic rate.

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of Chongqing Municipality within the Three Gorges region of Yangtze River, China (Xie 1993, Shi *et al.* 2005). Environmental conditions in the Three Gorges have changed greatly in recent years due to overexploitation for medicine and the Three Gorges Project construction for impoundment. Consequently, populations of *A. reniforme* var. *sinensis* have decreased rapidly and this species is now listed as endangered in the Chinese red data book (Fu 1992). *A. reniforme* var. *sinensis*, a variety of *A. reniforme* from the Azores in the northern Atlantic Ocean, is also the most primitive and the only unifoliate plant of the family Adiantaceae in Asia. Consequently, the species is very important for studying the origin, evolution, and geological change of ferns, especially for studying the theory of continental drift (Lin 1980).

To date, studies of *A. reniforme* var. *sinensis* have focused mainly on biological features, spore propagation, and genetic diversity (Xie 1993, Xu *et al.* 1998, Pan *et al.* 2005). Little is known about leaf traits and the causes of its endemic endangerment. In this study, we compared the leaf traits of five populations of *A. reniforme* var. *sinensis* differing in habitat (such as soil moisture and irradiance) and focused on their cost-benefit relationships. The objectives were to investigate the relationships between leaf traits and habitats and to elucidate possible ecophysiological mechanisms influencing the endangerment of this species.

Materials and methods

Study sites and plants: The study sites were located between Wanzhou District and Shizhu County (30º30'–30º51'N, 107º50'–108º21'E), Chongqing, Southwest China, and have a subtropical monsoon humid climate. Mean annual precipitation is approximately 1 206 mm and rainfall occurs primarily in spring and summer, with little rainfall in autumn and winter. Mean temperature is strongly seasonal, ranging from 7 °C in January to 28 °C in July.

A. reniforme var. *sinensis* is a single-leaf fern, 5–20 cm tall. The leaves are circular or kidney-shaped, 2–6 cm in diameter, and emerge from rhizomes in late February. The species is found mainly on thin soil on sloped rocks or rocky crevices in the lowland of valleys and the plant community can be divided into 4 types, *i.e.* *Platycarya strobilacea-Quercus aliena-Miscanthus sinensis* sparse forest community, *Rhus chinensis-Iris japonica* shrubbery community, *Debregeasia edulis-Veronicastrum stenostachyum* weeds community, *Vitex negundo-Lygodium japonicum* shrubbery community (Shi *et al.* 2005). In this study, five experimental sites with *A. reniforme* var. *sinensis* populations were chosen: Q, S, Y, F, and E (Fig. 1) and their localities and habitats are presented in Table 1. Irradiances at the population height were measured at different time of six rainless days during the experimental period (February 25, April 16, June 26, August 17, November 14, and December 22, 2004). The measurements were made using a digital luxmeter (*TES 1332*, Taiwan), and reference irradiance above the population (open sky irradiance) was measured simultaneously at the height of 3 m near the habitat. Relative irradiance, which is the ratio of irradiance at the population height to the open sky irradiance, was calculated and used for irradiance availability of each population. The soil water availability at 5 cm below-ground, where *A. reniforme* var. *sinensis* roots are densely distributed, was calculated from field-fresh and oven-dried (105 °C) mass.

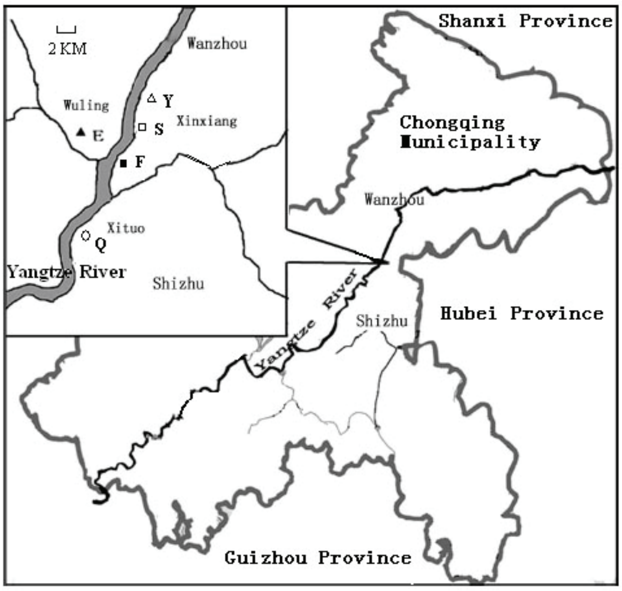

Fig. 1. Location of five *A. reniforme* var. *sinensis* populations. Population abbreviations are the same as in Table 1.

Leaf measurements: Five–six plants were randomly chosen from each population and their all newly sprouting leaves were tagged on February 25, 2004. Ten months later (22 December 2004), all the selected plants were dug up, potted, and brought into the laboratory in the evening. Photosynthetic capacity ($P_{\max}$) was determined with a portable gas exchange systém (*LI-6400*, *Li-Cor*, Lincoln, USA) in the next morning. The saturating photon flux density in the leaf chamber was provided at 400 μmol m^{-2} s^{-1} according to Liao *et al.* (unpublished), and ambient CO_2 and air temperature were maintained at 360 μmol mol^{-1} and 24 °C, respectively. Five–six healthy, tagged leaves from each selected plant were used and leaf area was measured using a portable leaf area meter (*Li-Cor 3000*, Lincoln, NE, USA). Harvested leaf material was then dried in an oven at 60 °C for at least 72 h and weighed to determine leaf mass per unit area (LMA). Following this measurement, all dried leaves were ground and homogenized. Construction costs (CC_M) [kg(glucose) kg^{-1}] were calculated using the method proposed by Vertregt and Penning de Vries (1987) and modified by Navas *et al.* (2003):

$$CC_M = [-1.041 + 5.077\ C_M/(1\,000 - \text{Min})][(1\,000 - \text{Min})/1\,000] + [5.325\ N_M/1\,000]$$

where C_M, Min, and N_M are, respectively, the contents of carbon, minerals, and organic nitrogen [g kg^{-1}].

The contents of total carbon and nitrogen were determined with an elemental analyzer (*2400 II CHNS/O, PerkinElmer*, USA), and mineral content was calculated by taking the fraction of minerals in ash, which is estimated gravimetrically after combustion in a muffle furnace at 550 °C for 4 h, as equal to 0.67 (Vertregt and Penning de Vries 1987). To calculate leaf carbon, nitrogen, and construction costs per unit leaf area (C_A, N_A, and CC_A), these values were multiplied by the LMA for each leaf.

Statistical analysis was conducted using *SPSS 13.0* for windows (*SPSS*, Chicago, USA). Leaf traits (LMA, P_{max}, C_A, C_M, N_A, N_M, C/N (carbon-to-nitrogen ratio), CC_A, CC_M, and CC_A/P_{max}) at different populations were compared using one-way ANOVA followed by least significant difference (LSD) *post-hoc* analysis ($p<0.05$).

Results

Q, the population growing at low soil water availability and high irradiance habitat (Table 1), had significantly higher leaf CC_A than all other populations, while both F and E, the two populations growing at high soil moisture and low irradiance habitats, had the statistically lowest mean leaf CC_A (Fig. 2*A*). When expressed per unit leaf mass, however, there were no significant differences among Q, F, and E, but the two medium irradiance habitat populations (Table 1) S and Y had significantly lower CC_M than the population Q (Fig. 2*B*).

Table 1. Localities and habitats of five *A. reniforme* var. *sinensis* populations. Data for soil moisture and irradiance are the means ± SE. *Different letters* in each row indicate significant differences ($p<0.05$).

Population	Q	S	Y	F	E
Locality	Qinjiaogou, Xituo, Shizhu County	Shanshulin, Xinxiang, Wanzhou District	Youchangba, Xinxiang, Wanzhou District	Fujiaping, Xinxiang, Wanzhou District	Ermianyan, Wuling, Wanzhou District
Habitat	On exposed rocks	On rocks under sparse forest	In weeds	In shrubbery	On cliff or in rock seams
Altitude [m]	240	205	270	220	210
Slope aspect	NW 10°	SW 12°	SE 30°	SW 58°	SE 55°
Slope gradient	45°	65°	60°	35°	75°
Soil moisture [%]	10.1 ± 0.6^c	11.3 ± 1.2^c	12.8 ± 1.1^b	14.5 ± 0.9^a	15.4 ± 1.3^a
Irradiance [%]	28.1 ± 3.7^a	19.3 ± 2.8^b	15.5 ± 4.1^b	10.4 ± 2.2^c	7.8 ± 1.9^c

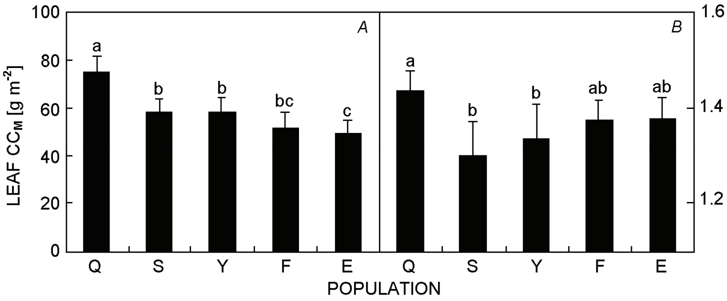

Fig. 2. Leaf construction cost per unit area (CC_A) (*A*) and per unit dry mass (CC_M) (*B*) of five populations of *A. reniforme* var. *sinensis*. Population abbreviations are the same as in Table 1. Means ± SE. *Different letters* in each graph indicate significant differences ($p<0.05$).

LMA of Q was significantly higher than those of F and E, but the differences among Q, S, and Y were insignificant (Table 2). Q exhibited the highest mean leaf C_A and C_M. F and E had the statistically lowest mean leaf C_A, though they had no significantly lower mean leaf C_M than S and Y (Table 2). Leaf N_A tended to decrease with decreased growth altitude, and Y, the highest altitude population (Table 1), had significantly higher leaf N_A than S, the lowest altitude population. Leaf N_M, however, was independent of altitudes of populations. Q and S, the two low soil moisture habitat populations, had significantly lower mean leaf N_M than the other three populations. Conversely, Q and S exhibited significantly higher mean leaf C/N than Y, F, and E (Table 2).

Y, the medium soil moisture and irradiance habitat population (Table 1), had the highest leaf P_{max}, but the

Table 2. Leaf mass per unit area (LMA), photon saturated photosynthetic rate (P_{max}), carbon content per unit area and per unit dry mass (C_A, C_M), nitrogen content per unit area and per unit dry mass (N_A, N_M), and carbon-to-nitrogen ratio (C/N) of five populations of *A. reniforme* var. *sinensis*. Population abbreviations are the same as in Table 1. Means ± SE. *Different letters* in each row indicate significant differences ($p<0.05$).

Leaf traits	Q	S	Y	F	E
LMA [g m^{-2}]	52.18±3.97^{a}	45.10±5.68^{ab}	43.93±6.97^{ab}	37.45±4.88^{bc}	36.08±3.04^{c}
P_{max} [μmol m^{-2} s^{-1}]	1.04±0.14^{b}	1.09±0.19^{b}	1.42±0.22^{a}	1.20±0.13^{ab}	1.10±0.17^{b}
C_A [g m^{-2}]	23.32±1.94^{a}	18.87±2.82^{b}	18.50±2.41^{b}	16.02±2.12^{bc}	15.49±1.62^{c}
C_M [g kg^{-1}]	446.76±9.21^{a}	420.62±15.53^{b}	422.18±9.30^{b}	427.90±7.96^{b}	429.37±9.60^{b}
N_A [g m^{-2}]	0.95±0.17^{ab}	0.79±0.13^{b}	1.01±0.16^{a}	0.92±0.15^{ab}	0.85±0.12^{ab}
N_M [g kg^{-1}]	18.18±3.02^{b}	17.70±0.83^{b}	23.50±2.90^{a}	24.58±1.46^{a}	23.67±4.37^{a}
C/N	25.19±3.14^{a}	23.77±0.52^{a}	18.16±1.99^{b}	17.46±1.04^{b}	18.64±3.62^{b}

differences in P_{max} among the other populations were not statistically significant (Table 2). As concerns the ratio CC_A/P_{max}, Q and Y had the highest and lowest values, respectively (Fig. 3).

Discussion

Since leaves are the primary site of photosynthetic carbon gain, leaf construction cost, in particular, could have profound impacts on species growth and abundance (Nagel and Griffin 2001). Specifically, a relatively low leaf CC_A in some populations of a species, allowing the construction of more leaf surface area with low energetic expense, may invest more energy in other strategies, such as reproductive efforts or inter-specific competition (Tilman 1999, Nagel and Griffin 2001). Therefore, the high soil moisture and low irradiance habitat populations of *A. reniforme* var. *sinensis*, F and E, which exhibited lower leaf CC_A, could have physiological and growth advantage over others.

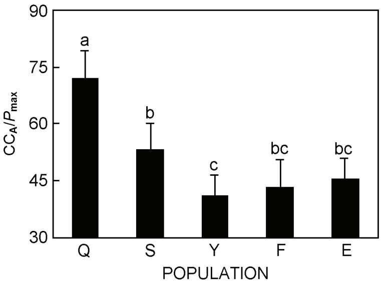

Fig. 3. The energetic cost/benefit ratio of mean leaf construction cost (CC_A) to mean leaf photon saturated photosynthetic rate (P_{max}) expressed per unit leaf area of *A. reniforme* var. *sinensis*. Population abbreviations are the same as in Table 1. Means ± SE. *Different letters* indicate significant differences ($p<0.05$).

Typically, plants with high LMA contain more lignin (Austin and Vitousek 1998, Groeneveld *et al.* 1998) and cell-wall components (Groeneveld *et al.* 1998), which tend to be energetically expensive (Griffin 1994). In our study, LMA of *A. reniforme* var. *sinensis* exhibited similar trends as leaf CC_A with population habitats, illustrating that differences of leaf CC_A could depend on leaf structural saccharides (such as lignin and cellulose).

In the three lower soil moisture habitat populations of *A. reniforme* var. *sinensis*, the higher irradiance population Q had significantly higher leaf CC_A than the other two populations (S and Y), but no significant differences were found in LMA. This suggested leaf CC_A in *A. reniforme* var. *sinensis* is more sensitive to habitat or microhabitat than LMA. LMA is probably not a cause but rather the result of a change in physiology, while leaf CC_A may be a more mechanistic approach to understanding plant growth (Nagel and Griffin 2001).

Leaf C_A exhibited the same trends as leaf CC_A when comparing populations from different habitats. However, leaf nitrogen, which is contained in many of the more expensive biochemical plant compounds such as proteins and amino acids (Williams *et al.* 1987), showed different trends from C_A and CC_A. This revealed further that changes in structural carbon compounds, rather than expensive organic nitrogen compounds, could be the main factors responsible for the differences in leaf construction cost in this study.

Leaf construction cost reflects the energy that a plant must invest in the construction of leaf biomass, whereas P_{max}, the leaf benefit, is a measure of the potential energy supply of a leaf (Nagel *et al.* 2002). As such, the relationship between them reflects a trade-off between leaf energetic gains and costs. Q, the low soil moisture and high irradiance habitat population, had the highest energy requirements and lower photosynthetic capacity for carbon gain. The high soil moisture F and E populations had lower CC_A than the other populations, but the low irradiance reduced their photosynthetic capacity and their cost/benefit ratios of CC_A/P_{max} were similar to Y, the medium soil moisture and irradiance habitat population, which had higher leaf CC_A than F and E but the highest leaf P_{max}.

Muraoka *et al.* (2002) suggested a "suitable" environment for plant growth partially depends on the cost-benefit relationship. Thus, in *A. reniforme* var. *sinensis*, the high soil moisture and medium irradiance could be the optimum habitat, and low soil moisture and high irradiance is stress-inducing. This conclusion is consistent with previous investigation, which showed that *A. reniforme* var. *sinensis* grew better in partially shaded, warm, and moist, but well-drained slope habitats than others (Xie 1993, Shen *et al*. 1999, Shi *et al*. 2005). The favourite habitats, however, are few and dispersed, and are disturbed by human activities and the ongoing construction of the Three Gorges Project. So *A. reniforme* var. *sinensis* now is mainly distributed on cliffs or steeply sloped bare rocks with thin and poor soil, water stress of which and few human disturbances appear frequently (Pan *et al*. 2005, Shi *et al*. 2005). According to the above analysis, *A. reniforme* var. *sinensis* has relatively high energy requirements and low photosynthetic capacity at these habitats, which could limit its capability in extending population or inter-specific competition and hence increase its endangerment.

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Sixteen review articles describing the carbon side of photosynthesis appeared in volumes 36–66 of the book series entitled "Progress in Botany". From 1974 till 2004 the readers of this series had the immense possibility of getting well balanced information what happened in this field of research mainly in the previous two years (only exceptionally the interval was one or three years). The reviews were written by two well-known scientists—one from Germany and another one from Australia. This fact ensured a good balance of information originated all over the world. Their cooperation functioned for twelve long two-year periods, only once (1986) J.A.M. Holtum was a third co-author. Last four reviews were prepared by the sole Grahame J. Kelly because of retirement of Erwin Latzko.

The reviews reprinted in original form in this Volume had various subtitles characterizing the most important pool of information or anniversary. They are a good illustration of the history of photosynthetic carbon research and therefore let me present all of them here: Carbon Metabolism; Biochemical and Physiological Aspects of Carbon Metabolism; Control of Carbon Metabolism Through Enzyme Regulation and Membrane Mediated Metabolite Transport; Chloroplast Capability and the Uncertain Fate of CO_2; The Profound Effects of Illumination on the Metabolism of Photosynthetic Cells; On Land and at Sea; By Day and by Night; New Regulators of CO_2 Fixation, the New Importance of Pyrophosphate, and the Old Problem of Oxygen Involvement Revisited; On Regulation at the Cellular Level and at the Whole Plant Level, and Some Considerations Concerning the Interactions of These Regulatory Events with the Increasing Level of Atmospheric CO_2; Twenty Years of Following Carbon Cycle in Photosynthetic Cells; The Chloroplast's Sesquicentenary, and Some Thoughts on the Limits to Plant Productivity; The Carbon Metabolisms of Unstressed and Stressed Plants; In and Beyond the Chloroplast; Carbon Metabolism from DNA to Deoxyribose; Quantification and Manipulation; The Calvin Cycle's Golden Jubilee.

Of course, almost every review explained new facts on the C_3, C_4, and CAM cycles and the respective models, enzymes, and reactions, dealt with experiments using chloroplasts and *in vitro* systems, with effects of stresses and ecological influences, regulation by environmental factors and pH, with photorespiration, chlororespiration, and mitochondrial respiration, starch, sucrose, and glycollate biosynthesis and metabolism, various primary and secondary photosynthates, with regulation of their production and features of their transport, CO_2 release and recapture, specific features in algae and higher aquatic plants, with resulting plant productivity, advances in used methods, *etc*. Every review was accompanied with hundreds of references; I regret only that full references (with titles of articles) started to be presented as late as in volume 60.

Even if this fine series of reviews reached now its end, it is a welcome source of information for young scientists who—I hope—will not only look at internet, but also read books printed on paper. Their lecture will be lead by a brief but good Subject Index. And I hope together with both authors that in a near future the idea of their beloved author Jonathan Swift (his Gulliver is mentioned in three mottos!), that photosynthesis will "be able to supply the Governor's gardens with [condensed] sunshine at a reasonable rate", will be realised. Or will there be more pigs transformed with a spinach gene (see p. 381) instead?

Z. ŠESTÁK (*Praha*)