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Biomass allocation patterns in terrestrial, epiphytic and aquatic species of *Utricularia* (Lentibulariaceae)

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Abstract

Utricularia forms the largest genus of carnivorous plants and is characterized by the possession of typical traps ("bladders"). Total biomass allocation was examined in three aquatic, six terrestrial and one epiphytic species of *Utricularia* from natural habitats in West Africa and from the Botanical Gardens, Bonn. Total biomass of aquatic species was considerably higher than that of terrestrial or epiphytic species. Epiphytic *Utricularia* accumulate about 35% of their biomass in green leaves, in contrast to 65% of nearly chlorophylless reproductive structures and traps. Aquatic species allocated more than 85% of their total biomass to stolons, leaves and traps, but only 10–13% to reproductive structures. This is in stark contrast to the allocation patterns of terrestrial bladderworts. These species allocate nearly 90% of their total biomass in reproductive structures, and only about 10% to stolons, leaves and traps. This reduction of photosynthetically active plant tissue strongly suggests that as a consequence of the alternative resource of chemical energy, the carnivorous habit might have partly replaced autotrophy in certain terrestrial *Utricularia* species, especially in some smaller ones.

Keywords: Allocation patterns; Biomass; Carnivorous plants; *Utricularia*; Protozoa

Introduction

Containing about 320 species, the Lentibulariaceae is the most species rich family of carnivorous plants (Barthlott et al., 2004). It comprises the genera *Pinguicula*, *Genlisea* and *Utricularia* (bladderworts), with the latter representing the largest genus (214 spp.). Morphologically (e.g. Brugger and Rutishauser, 1989; Goebel, 1891; Juniper et al., 1989) and taxonomically (Taylor, 1989), *Utricularia* is one of the best studied genera of carnivorous plants, with terrestrial species accounting for the majority of species, far outnumbering the aquatic members. All species of this genus are characterised by the presence of traps which are borne in large numbers on stems and leaves. These traps, or "bladders", operate by sucking in prey which subsequently is digested (Lloyd, 1942; Lollar et al., 1971; Sydenham and Findlay, 1973). Information on the prey of *Utricularia,* including a large variety of organisms (e.g. Tardigrada, Gastropoda, Crustacea, see Andriakovics et al., 1988; Darwin, 1875; Mette et al., 2000) are only available for aquatic

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species from northern temperate regions. A number of quantitative studies have been devoted to cost-benefit analyses of aquatic *Utricularia* species (e.g. Friday, 1992; Knight and Frost, 1991; Knight, 1992; Richards, 2001), and have demonstrated that the percentage of biomass invested in traps may be as high as 60%. However, surprisingly little is known on cost-benefit ratio and the prey of terrestrial bladderworts. It has been shown recently that these species possess significantly smaller traps than aquatic members of this genus (Seine et al., 2002). Similar to the related genus *Genlisea* (Barthlott et al., 1998), it appears as if the terrestrial species are highly specialized to trap protozoa (Seine et al., 2002). Moreover, terrestrial *Utricularia* species are remarkable because of their often tiny leaves compared to the size of their inflorescences.

In this study, allocation of biomass to reproductive structures (including leafless, flower-bearing stalks) and vegetative structures (leaves, stolons and traps) are quantified for several tropical aquatic and terrestrial species of *Utricularia*. We hypothesize that aquatic and terrestrial bladderworts have strongly contrasting investment strategies, which may be indicative of fundamental differences in nutrient uptake and energy supply.

Material and methods

In this study, three aquatic (*Utricularia australis* R.Br., *U. gibba* L., *U. reflexa* Oliver), six terrestrial (*U. blanchetii* A.DC, *U. juncea* Vahl, *U. micropetala* Sm., *U. parthenopipes* P. Taylor, *U. pubescens* Sm., *U. subulata* L.), and one epiphytic species (*U. quelchii* N.E.Br.) were examined. The aquatic plants – except for *U. australis* from the Botanical Gardens Bonn – were collected from small seasonal ponds located in the Comoé National Park (NE Ivory Coast). Specimen of two terrestrial species – *U. blanchetii* and *U. parthenopipis* – were taken from cultivations at the Botanical Gardens Bonn. The remaining terrestrial species were collected at Mt. Niangbo, a granite rock outcrop (‘‘inselberg’’) in the north of Ivory Coast. The terrestrial *Utricularia* species were found growing in large numbers in ephemeral flush communities on wet, shallow soil. All flowering plants were collected at the peak of the rainy season in September 2000 in 14-day intervals in Ivory Coast. At the Botanical Gardens Bonn the samples were taken between March and October 2001. For each species, 10 plants were randomly collected and dried at 40 °C for 48 h. Substrate particles attached to terrestrial plants were carefully removed using a dissecting needle. The plants were separated into flowers/scape and leaves, stolons and traps, and then weighted.

Results

All three aquatic *Utricularia* species had fleshy stolons, between 20 and 30 cm in length (e.g. *U. australis*, Fig. 1). Their leaves were 0.6–1.5 cm long and subdivided into further segments. Between the segments, 1–5 mm long traps were inserted. The inflorescences were erect, and up to 15 cm in length. The terrestrial species had subterranean stolons, and few to numerous leaves. These were 0.3–0.9 cm long and up to 3 mm in width. Traps occurred on stolons and leaves, and were between 0.2 and 1.3 mm in length. The height of the erect inflorescences was about 12.6–25.2 cm.

The biomass of the aquatic species was considerably higher (*U. australis* 19.2 + 2.2 g, *U. gibba* 16.8 ± 1.7 g, *U. reflexa* 22.1 ± 2.7 g) than that of the terrestrial ones (*U. blanchetii* 0.013 ± 0.004 g, *U. juncea* 0.011 ± 0.004 g, *U. micropetala* 0.011 ± 0.004 g, *U. pubescens* 0.0074 ± 0.0003 g, *U. subulata* 0.007 ± 0.0003 g). Significant differences ($p < 0.00001$) between the two groups of species were observed regarding the distribution of biomass to reproductive versus vegetative structures (Table 1; Fig. 4). In the aquatic members, the largest portion of the biomass was allocated to leaves, stolons and traps (*U. gibba* 86.66%, *U. reflexa* 89.53%), whereas the amount of biomass allocated to reproductive structures was only 13.44% in *U. gibba*, and 10.47% in *U. reflexa*. In marked contrast, only a small fraction of the total biomass was allocated to leaves, stolons and traps within the terrestrial species, whereas about 90% of the biomass was invested in reproductive structures.

All three aquatic species invested most of their biomass in leaves (ca. 60%), whereas the terrestrial species generally allocated less than 9% of their total biomass to leaves, only *U. subulata* (Fig. 3) invested about 10%. *U. juncea* allocated the smallest fraction of total biomass to leaves, stolons and traps (8.82%). In the terrestrial species, subterranean stolons and traps accounted for between 2% and 3.5% of the vegetative biomass, with the traps themselves contributing only between 0.14% and 0.21%. Aquatic *Utricularia* plants invested far more biomass in traps, amounting to about 17–20% of total dry weight. The results were similar for the epiphytic species *U. quelchii* (Fig. 2) with about 0.401 g (35.5%) allocated in green leaves and stolons versus 0.961 g (64.5%) in chlorophylless traps and flowers.

Discussion

The results indicate that a clear distinction can be drawn between biomass allocation in aquatic and terrestrial *Utricularia* species. According to Friday