

TURION DEVELOPMENT IS AN ECOLOGICAL TRAIT IN ALL POPULATIONS
OF THE AQUATIC CARNIVOROUS PLANT
ALDROVANDA VESICULOSA (DROSERACEAE)

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Aldrovanda vesiculosa L. is a globally rare aquatic carnivorous plant, recently listed as Endangered by the International Union for the Conservation of Nature (IUCN) in light of significant population decline worldwide over the last century (Cross 2012a). Fewer than 50 extant natural populations are now believed to exist worldwide (Cross 2012b). However, despite the recent focus afforded to the species in the face of its decline, several aspects of its ecology and biology remain unclear. As part of a concerted global effort to conserve, restore, and increase awareness of the threats faced by *A. vesiculosa*, this paper discusses population differentiation in the context of coloration and the production of turions (hibernacula).

The expansive distribution of *A. vesiculosa* encompasses almost a dozen climatic zones from tropical monsoonal to subarctic (see Peel *et al.* 2007), and extends some 84° in latitude from the Limpopo River in southern Africa to Lake Ladoga in northern Russia (Fig. 1), and over 160° in longitude from eastern Ghana to Bundaberg on the eastern coast of Australia (Cross 2012b). This range represents one of the most expansive climatic tolerances known for any angiosperm species. In order to persist in such a wide variety of climates, *A. vesiculosa* must rely on one of two physiological characters: either 1) the possession of an extraordinarily broad ecological tolerance (plasticity) for abiotic factors such as temperature and seasonality, particularly in relation to the timing and success of reproduction and overwintering, or 2) the development of specific tolerances or adaptation to climatic and seasonal conditions at a regional or local scale. Both of these scenarios have differing implications for population genetics, dispersive and colonization capacity, and the ability of populations to respond to environmental alteration through human activity or climate change.

Habitat degradation and fragmentation are believed to be among the principal causes of decline in *A. vesiculosa* (Jennings & Rohr 2011), with suitable habitat becoming increasingly scarce and exacerbating the heavily disjunct nature of the species' distribution. Though *A. vesiculosa* appears to demonstrate a rather unprecedented genetic uniformity, with molecular studies presenting extremely low levels of variation between individuals from populations isolated by many thousands of kilometers (Elansary *et al.* 2010; Hoshi *et al.* 2006; Maldonado San Martín *et al.* 2003; Adamec & Tichy 1997), recent data supports a distinction between European and non-European accessions (Elansary *et al.* 2010; Maldonado San Martín *et al.* 2003). Research to further elucidate genetic variation in the species is ongoing, however such limited polymorphism strongly suggests that *A. vesiculosa* possesses an extraordinary adaptive capacity and broad ecological tolerance, rather than a number of discretely adapted populations.

Two morphological characters have traditionally been used to differentiate between the two inferred genetic clades: pigmentation (the presence or absence of an anthocyanin expression in plant tissues), and the production of turions (Maldonado San Martín *et al.* 2003; Breckpot 1997). Plants originating from central and southern Africa, Australia, and western Hungary display the

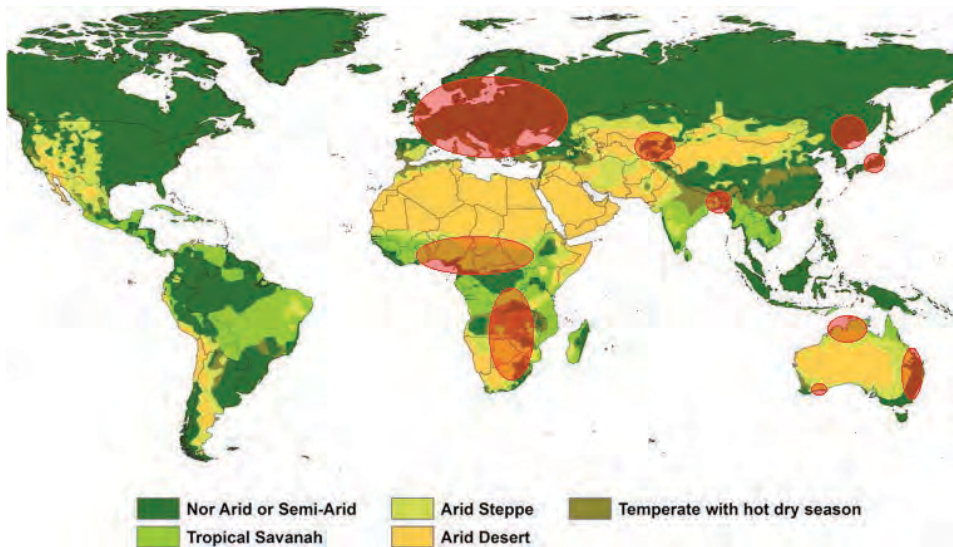


Figure 1: Map indicating Köppen climatic zones grouped by precipitation (from Achten *et al.* 2012) overlaid with ellipses showing the generalized historic population loci for *Aldrovanda vesiculosa*.

characteristic reddening associated with anthocyanin production (*A. vesiculosa* var. *rubescens*; Cross 2012b), while all other known extant populations lack this pigmentation (*A. vesiculosa* var. *vesiculosa*). Herbarium specimens from East Timor and northern equatorial Africa suggest that these populations may also have possessed anthocyanin; however the coloration of Hungarian plants is an exception to the European/non-European population distinction. As anthocyanin production is regulated by at least five associated enzymatic processes, the disruption of even a single pathway through environmental pressures resulting in the loss of pigmentation (Gould *et al.* 2008; Andersen & Markham 2006), it seems unlikely that coloration explains the inferred genetic difference (Back Cover). The sympatric occurrence of pigmented and non-pigmented populations within a relatively small geographic area in Eastern Europe also suggests that gene flow may be even lower than expected between *A. vesiculosa* populations.

The differentiation of populations based on the production of turions remains a matter of some debate. Some growers and researchers believe that populations of *A. vesiculosa* var. *rubescens* are not capable of producing overwintering structures, based on the observation that plants tend to slow or halt growth during the colder months. This may be perpetuated by suggestions that only non-pigmented Eurasian populations are capable of producing fully dormant hibernacula (Adamec 2005; Breckpot 1997), despite published evidence to the contrary (*e.g.* Adamec 1999a). Adamec (2005) notes that plants originating from the Okavango Delta in Botswana and from Lake Balata-to in Hungary, both pigmented, readily form dormant turions. Lájér (2006) confirms the production of winter buds by plants from Hungary. Zaman *et al.* (2011) also note the presence of turions on plants collected from Bangladesh. During an analysis of *A. vesiculosa* herbarium records from around the world by the author, turions were observed on specimens from France, Germany, Austria, Switzerland, Russia, Poland, Lithuania, Romania, Italy, and Japan (*A. vesiculosa* var. *vesiculosa*). These records are supported by numerous recent studies, with turion formation in various populations observed either at field sites or in cultivation (*e.g.* Adamec 2005, 2003, 1999b; Vilkonis 2004; Komiya 1989;



Figure 2: Turions forming in early winter (June) on *A. vesiculosa* individuals from Esperance, southwest Western Australia, cultivated at Kings Park and Botanic Garden (Perth, Western Australia).

Kamiński 1987a,b). Darnowski (2002) mentions the development of hibernacula on plants from the Northern Territory of Australia (*A. vesiculosa* var. *rubescens*), as does Adamec (1999a). Turions have been found in the sediment of high altitude *A. vesiculosa* var. *rubescens* habitat in Armidale, New South Wales (D. Bell, pers. comm.), and observed on cultivated plants from other coastal areas of eastern Australia (Adamec 2003a). Recently, turions have also been observed by the author to form readily on pigmented Australian plants originating from Esperance (southwest Western Australia; Fig. 2), Darwin (Northern Territory), Broulee (southeast New South Wales), and the Kimberley (northern Western Australia; Cross, unpubl.). The only regions remaining for which no record of turion production exist are those from East Asia (Kazakhstan, China, North and South Korea), Southeast Asia (East Timor), and equatorial Africa north of Botswana. *Aldrovanda vesiculosa* is poorly represented in herbarium records from all three regions, and there is little or no information available on the persistence of any of these populations in the last few decades.

It may be concluded therefore that every *A. vesiculosa* population, irrespective of geographical location or coloration, possesses the intrinsic potential to produce turions in response to unfavourable conditions. Failure to do so indicates that plants in any given region may not be experiencing the climatic cues to which they have become locally adapted in their location of origin, or that conditions never become adverse enough to require turion development (see Sculthorpe 1967). This variable response may result in the varying depths of dormancy presented in detail by Adamec (2003b), who notes that populations of tropical affinity produced only weakly dormant buds (termed imposed dormancy, in contrast to the innate dormancy described for populations experiencing regular and pronounced adverse winter conditions). This does not necessarily imply that populations from dif-

ferent climates are ecologically discrete, more that they are likely to possess complex and deeply ingrained autoecological mechanisms that may take several seasons to adapt to new conditions. While the depth of dormancy may be seen to vary temporally or spatially, the ability to produce overwintering structures remains an innate ecological feature.

For example, plants of several Australian (originating from Esperance, Darwin, Broulee, and the Kimberley) and one east Polish population are cultivated at Kings Park and Botanic Garden, Perth, Western Australia (experiencing a Mediterranean climate with warm, dry summers and cool, wet winters). During the relatively mild winter of 2011, where temperatures rarely fell below 8–10°C, turion formation was observed only on Polish individuals (~60%). These remained dormant on the substrate of the cultivation tank until mid-spring, contrasting with the vigorous growth of Australian plants in early spring when water temperatures rose to around 25°C. However, after several weeks of uncharacteristically cool weather in the winter of 2012 (minimum 2–6°C), widespread turion development was observed in all populations. The buds detached, sank, and remained dormant on the substrate uniformly until mid-late spring, when all of the populations began new season growth.

The evidence suggests that neither pigmentation nor turion production are likely to represent significant differentiating factors in *A. vesiculosa* population genetics, and highlights the necessity for genetic studies utilizing both high resolution and highly reproducible techniques. Perhaps as these studies progress we may find some answers to long-held questions regarding population structure, gene flow, and the origin of the species. However, in the face of its continuing decline, the ecological plasticity and apparent adaptive capacity of *A. vesiculosa* suggests a very heartening possibility: if the loss and degradation of the species' habitat is alleviated, remaining populations, however rare they may be, may well possess a significant capacity to slowly adapt to a changing environment if carefully safeguarded and preserved.

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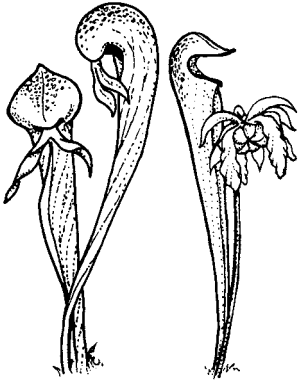


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Front Cover: *Pinguicula x gresivaudanica* growing in the French Alps. Photo by Aymeric Roccia. Article on page 36.

Back Cover: *Aldrovanda vesiculosa* var. *rubescens* (A. Cross & L. Adamec) from southwest Western Australia, displaying a gradient of coloration due to variable sun exposure. All individuals originate from the same maternal plant, but have been independently grown from left to right in full sun, 50%, 70%, and 90% shade. Photo by Adam Cross. Article on page 57.

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