Vernal Rock Pools
Pedersen, Ole; Pulido Pérez, Cristina; Nicol, Dion; Winkel, Anders; Tuckett, Renee

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Vernal rock pools host some of the smallest and prettiest aquatic plants. These rock pools may contain as little as 40 l (11 gal.) of water and yet host up to five or more species of aquatic plants. The plants typically have to complete their entire life cycles in four months as the pools dry out and turn into a desert until the winter rain fills them again. These vernal pools also host a unique fauna that need similar adaptations to periods of complete desiccation (drying out) and high temperatures. Here we show examples of submerged plants from pools on granite outcrops in Western Australia, some of which display the most stunning aquascapes.

The physical environment

Rivers and lakes are usually connected to the regional groundwater reservoir. Percolating rainwater fills these reservoirs eventually resulting in runoff via streams, rivers and sometimes lakes. However, some vernal pools found directly on the bedrock rely solely on rainfall to fill. The aquatic habitats found here fit Keeley and Zedler’s (1998) definition of the vernal pool habitat as “precipitation-filled seasonal wetlands inundated during periods when precipitation exceeds evaporation. In Western Australia, this typically happens from May to August. The long term average annual rainfall in the area around Mukinbudin (300 km north east of Perth) is about 286 mm (12”), though this is highly variable. This will fill the vernal pools found on the granite outcrops. For a few months, these pools flourish and maintain a unique aquatic habitat with flora and fauna not found elsewhere in the world. These vernal pools are shallow, often less than 10 cm deep, and experience dramatic diurnal changes water temperature, pH and CO₂ (Keeley & Zedler 1998).

The granite rock pools are nature’s nano aquaria. Some pools are less than 1 meter in diameter and perhaps only 5 cm deep and yet, such pools may host 2 – 3 species of aquatic plants along with highly specialized invertebrates that keep the aquascape almost free from algae. Other pools are much larger, up to 20 m in diameter, but on the granite outcrops the depth rarely exceeds 10 cm.

The small volume of water relative to the high plant biomass also results in huge diurnal fluctuations in pH and CO₂. At night, when respiration processes produce large amounts of CO₂, pH decreases and dissolved CO₂ builds up in the water column. In Californian vernal pools, pH decreased to 7 while CO₂ rose to 200 µmol/L (9 mg/L). In contrast, the plants consume all CO₂ during the day so that the CO₂ concentration drops to almost zero while pH may rise to 10 (Keeley & Zedler, 1998). The dramatic changes in pH is caused primarily by CO₂ that acts as a weak acid but since the water consists of poorly buffered rainwater, the change in pH is enormous. When we visited the vernal pools around Mukinbudin in August 2009, the pools had experienced frost the previous night but the late afternoon temperature of the shallow water was nevertheless 25°C (77°F). Consequently, the aquatic plants found in this extreme physical environment display a suite of special adaptations to cope with the physical challenges.

The plants of vernal rock pools

Vernal rock pools in Western Australia host a diverse array of aquatic plants with submerged, floating-leaved and emergent species all being represented in the flora. The flora is comprised of no less than 22 specialist species growing in no other form of temporary wetland (such as peat-lands and sump-lands) in Western Australia, along with many cosmopolitan species. Examples of the cosmopolitan flora include species from *Aponogeton*, *Isoëtes*, *Marsilea*, *Myriophyllum*, *Pilularia* and non-native *Calitrichie* and *Cras-
Endemic species include members of the dicots such as *Glossostigma* and *Hydrocotyle*, and the monocots such as *Amphibromus*, *Ottelia*, *Schoenus*, *Trithuria* and *Wurmbea*.

For the aquatic vegetation, perhaps the most important challenge is the short duration of complete inundation. In late fall, it starts raining and the dry substrate quells and promotes the germination of many seeds and spores. Other seeds and spores do not germinate until they are waterlogged or completely submerged. They are all annual plants and able to complete their entire life cycle within the few months of inundation. There is one exception; *Amphibromus nervosus*, a perennial grass, lives in some of the pools and resprouts every winter.

During the period of complete inundation, the submerged plants face other challenges such as how to get CO₂ for underwater photosynthesis. Basically, there are three sources of inorganic carbon that aquatic plants can tap into: i) CO₂ dissolved in the water column, which is then taken up by the submerged leaves; ii) CO₂ from the atmosphere taken up by floating leaves or aerial leaves possessing stomata; or iii) sediment-derived CO₂ taken up by the roots followed by molecular diffusion up into the leaves. All plants in the vernal rock pools probably use dissolved CO₂ from the water column to some extent but because of the huge biomass relative to the shallow water column, this source of CO₂ only lasts for a limited time early in the morning, after which CO₂ drops to almost zero (Keeley & Zedler 1998). On the other hand, the high biomass also produce respiratory CO₂ during the night that dissolves in the water column so there is definitely a source of inorganic carbon to tap into during the early morning hours. But what happens when this pool of inorganic carbon has been used?

Perhaps the most conspicuous adaptation to low CO₂ availability during the day is the evolution of CAM photosynthesis in some of the submerged plants occupying the vernal rock pools. CAM was first described in the family of *Crassulaceae* and since it involves organic acids as storage for CO₂ it was...
termed Crassulacean Acid Metabolism or CAM. Terrestrial CAM plants often inhabit dry habitats where lack of water severely limits plants growth. However, CAM plants open their stomata primarily during the night when the temperature is lower and the relative humidity higher. CO₂ can then be taken up from the atmosphere without causing much water loss. But since it is dark, photosynthesis cannot fix CO₂ into sugars and CO₂ must be temporarily stored in organic acids for use during the day. Malate is the most abundant organic acid in CAM plants (diurnal fluctuations in malate is used an indicator of CAM photosynthesis). But submerged plants in vernal rock pools do not suffer from lack of water and here, the evolution of CAM photosynthesis is not considered an adaption to conserving water but rather an adaption to take up CO₂ when it is present in high concentrations during the night.

We found at least two species in the vernal rock pools that are known to exhibit CAM photosynthesis. One, *Crassula natans*, even belongs to the Crassulaceae whereas the other, *Isoëtes australis*, is an aquatic fern. *Crassula natans* is not native to Western Australia but was brought in from South Africa. The *Crassula* genus is also represented in the well-studied Californian vernal pools by *Crassula aquatica*. Apart from CAM photosynthesis, *Crassula natans* also forms floating leaves. The floating leaves enable the plant to tap into the rich CO₂ pool of the atmosphere and it also presents a nice support of the aerial flower, which is formed on the floating rosette.

In contrast, *Isoëtes australis* is only found in vernal pools in Australia. It exhibits CAM photosynthesis (Keeley 1983) and is annual. Species of *Isoëtes* are also known to use sediment-derived CO₂ for photosynthesis but whether *Isoëtes australis* also relies on sediment-derived CO₂ in addition to CAM photosynthesis remains to be tested. However, its morphology and anatomy do not suggest that sediment-derived CO₂ should not play an important role and this makes *Isoëtes australis* one of the most specialized aquatic plants we have ever come across. The next four months of research here at the University of Western Australia will show if we are right in this assumption.

A final challenge that the aquatic vegetation has to cope with is the nutrient-poor environment. To the best of our knowledge, no one has studied nutrient availability in the vernal rock pools of Western Australia. Since the pools are precipitation-fed, the water does not carry high amounts of nutrients. Consequently, the sediment must provide almost all nutrients to the plants but the sediment primarily consists of coarse gravel produced by weathering processes in the granite. In this kind of nutrient-poor environment mycorrhiza fungi could potentially play an important role in nutrient uptake. Mycorrhiza are symbiotic associations between fungi and plants, where the plant provide organic carbon (sugars and amino acids) for the fungus while the fungus via its hyphae explores large volumes of soil, taking up inorganic phosphorus, which is then given to the plant in return for the organic carbon. We hypothesize that mycorrhiza plays an important role in the nutrient uptake in these super nutrient-poor environments and thus, we are going to screen species of *Isoëtes*, Glossostigma and *Crassula* for mycorrhizal symbiosis.

Western Australian vernal pools are host to a number of rare and threatened species including *Myriophyllum lapidicola* recorded on just a few rocks in the northern wheatbelt of Western Australia. This particular species is morphologically very different to the typical *Myriophyllum* with round floating leaves compared to the dissected filamentous seen in most common *Myriophyllum* species. Further, this particular species is restricted to a specific rare type of vernal rock pool. While most pools are flat and shallow *M. lapidicola* only occurs deeper pools that form on the steep slopes of granite inselburgs (an isolated rock hill, knob, ridge, or small mountain that rises abruptly from a gently sloping or virtually level plain; also called a monadnock). These particular pools are inundated for longer periods of the year (up to 10 months in 2008) and have deeper soils that may be some of the physical properties restricting this species to such few locations, although no study has yet confirmed this.

**Invertebrates of vernal rock pools**

Aquatic animals occupying vernal pools are met with the same major challenges as the plants: the short duration of inundation after which follows a long period of desiccation (Bayly 1997). Probably one of the best adapted animals to cope with this challenge is the seed shrimp (*Ostracoda*). Seed shrimps are laterally flattened crustaceans protected by a two valves hinged on the back of the animal. They are among the first animals to appear when setting up a new aquarium and their eggs are extremely desiccation tolerant and present almost everywhere. In vernal pools, giant species of seed shrimps sometimes appear as there are no fish or other predators to prey on them. The vernal rock pools of Mukinbudin are no...
and they grow in shallow nutrient-poor substrates. However, their natural habitat is a high-light habitat with direct sunlight in a really shallow water column that does not dampen light very much and so, they are all adapted to high light levels. Whether they also require high light to grow is not really known but they certainly do not mind direct sunlight.

In terms of providing a completely different architecture, *Isoëtes australis* is perhaps the plant with the greatest potential for planted tanks. The genus *Isoëtes* has many species that thrive under very modest light conditions—almost as modest as some of the aquatic mosses. For example, *Isoëtes lacustris* grows primarily in the deeper water of lobelia lakes found in the northern hemisphere; not because it does not like high light but merely because it is such a weak competitor so it is restricted to depths of low light where no other plants are able to compete. *Isoëtes australis*, however, is found in direct sunlight in shallow water so it may have intrinsic high light requirement. On the other hand, it often forms monocultures in the vernal pools so competition with other plants is absent. Time will tell if this unique little plant finds its way into the planted aquarium hobby.

_Glossostigma elatinoides_, which also comes from Australia, is already being used in planted aquaria but it is known as a difficult plant. It requires high to very high light and onlythrives in soft water (www.tropica.com). The pools we visited were also characterized by having extremely soft water (from 10 – 90
This 8 cm deep pool reveals a spectacular aquascape showing natural bubble formation on species of mosses and *Crassula natans* following intense photosynthesis.

μS/cm) since they are 100% rain-fed and sit on granite with no alkalinity at all. But we do not know if the species found here are as demanding as *Glossostigma elatinoides*.

Finally, *Crassula natans* is a pretty little stem plant that also forms beautiful gas bubbles during periods of intensive photosynthesis. Even under high light, *Crassula natans* possesses relatively long internodes making it somewhat less attractive as an ornamental plant but in combination with low carpet-forming plants such as species of *Glossostigma* it should make a nice morphological contrast in the tank.

Being so small and inconspicuous as most of the plants in the vernal rock pools, one could possibly come to the wrong conclusion that these plants are competitively inferior and do not present much danger as invasive species. However, *Glossostigma cleistanthum* (previously thought to be *Glossostigma diandrum*) has been shown to spread and overgrow natural vegetation in North American pristine waters (Les et al. 2006); one of the few known examples where an invasive species require oligotrophic conditions in order to present any danger to the native vegetation. So, as always one should be cautious upon disposal of these plants in non-native environments.

In conclusion, the vernal rock pools of Western Australia support stunning aquascapes formed by plants that have adapted well to the physical challenges of the changing environment. Some of the plants described here may hold a potential for use in nano aquaria and planted tanks although they are expected to have high light requirement as judged from their natural habitats.

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**Literature cited**


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"Fishkeeping & Aquascaping" continued from page 33.

TetrasAndBarbs.com.) Most obvious is appearance: like plants, fish vary in color, size and shape. But fish contribute what plants and hardscape cannot—behavior. The common perception recites that these fishes are "mid-water schooling" fishes. That perception is overly simplistic and generic. Variations of behavior can be grouped three ways:

- fish-to-fish (schooling, pack, shoaling, loaners, territorial, predators)
- as a social catalyst within the community (dither, target)
- niches (strata, proximity to various aquascaping elements, water current, nocturnal and contributing to biotope/habitats themes)

Ultimately, the weight of both appearance and behavior can classify fish into *compositional* roles (showcase specimens, background fish, accent/contrasting and novelty). As a quick example, let’s look at the five-banded barb (*Barbus pentazona*). It contributes patches of fairly intense red, distinct vertical marks; a preference for actively swimming in the open but near the refuge of plants; and “pack” behavior (a group of fish that drift about the tank as a pack with ongoing interaction that is fairly intense—in contrast to the unison of tight schooling). Its bold markings contrast both with horizontally-lined species (such as *Rasbora borapetensis*) and the green plants behind them. This species also contributes as a natural addition to a soft-water habitat and to the Malaysian biotope, should either of these be a theme of the composition. The contribution of these roles should be evaluated when composing for theme, variation, contrast and balance. Much more easily said than done.

Aquariums are about the satisfaction that its keeper gets from keeping it. That satisfaction may come from plants or it may come from fish. As a result, the practices of aquarists can range from high-tech aquascaping to breeding fish in bare tanks. Aquariums are also about the visual beauty of the whole. If this truly is the goal of an aquarist, he or she should leverage both plants and fish.