



Morphological variations in southern African populations of *Myriophyllum spicatum*: Phenotypic plasticity or local adaptation?



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ABSTRACT

Variability in aquatic plant morphology is usually driven by phenotypic plasticity and local adaptations to environmental conditions experienced. This study aimed to elucidate which of these drivers is responsible for the morphological variation exhibited by three populations of *Myriophyllum spicatum* L. (Haloragaceae), a submerged aquatic plant whose status as native or exotic within southern Africa is uncertain. Individuals from three populations on the Vaal River (Northern Cape), Klipplaat River (Eastern Cape) and Lake Sibaya (KwaZulu-Natal) were grown under two nutrient treatments (high: 30 mg N/kg sediment and low: sediment only), while all other variables were kept the same. Morphological characteristics were measured at the start of the experiment to obtain a baseline morphology, and again eight weeks later. By the end of the experiment, the individuals from each population had responded to the different growing conditions. In most cases, the individuals from each population were significantly larger under the high nutrient treatment (Stem diameter: $F_{(5,86)} = 18.435$, $P < 0.001$, Internode length: $F_{(5,86)} = 5.0747$, $P < 0.001$, Leaf length: $F_{(5,86)} = 19.692$, $P < 0.001$). Despite these differences in nutrient treatments, the growth pattern of each population remained true to the original starting point indicated by the lack of overlap between populations in the PCA groupings. This suggests that local adaptations are responsible for the differences in morphology between populations of *M. spicatum*, but shows that phenotypic plasticity does play a role as evidenced by individual responses to the different nutrient conditions. The development of these local adaptations within southern Africa suggests that the populations have had a long evolutionary history in the region and are relatively isolated with little reproductive mixing.

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1. Introduction

It is widely accepted that aquatic plants are plastic in their responses to environmental variables, and their morphology can be extremely variable between populations and/or between seasons (Barko and Smart, 1981; Barko and Smart, 1986; Koch and Seeliger, 1988; Barrett et al., 1993; Idestam-Almquist and Kautsky, 1995; Santamaria, 2002). Changes in plant morphology and physiology between populations of the same species are often linked to both physiological stresses, such as limited resources (De Kroon and Hutchings, 1995; Hutchings and John, 2004), and to physical/mechanical stresses such as wave action or current (Strand and Weisner, 2001; Boeger and Poulsan, 2003; Arshid and Wani, 2013). These species responses are usually driven by adaptive mechanisms, such as phenotypic plasticity (Grace, 1993; Barrett et al., 1993; Hofstra et al., 1995) or local adaptations (Sultan, 2000; Kawecki and Ebert, 2004; Ward et al., 2008) that allow them to

adapt to the different climatic and environmental stresses to which they are exposed.

Local adaptation is a genetic change, primarily driven by natural selection on a local scale, where specific characters of a plant that enhance its fitness are selected for in a novel environment (Kawecki and Ebert, 2004), while phenotypic plasticity is the ability of a single genotype to respond with changes in phenotypic characters that will better suit the population to the prevailing habitat conditions (Bradshaw, 1965). The wide distributional range of many aquatic species is often coupled with relatively low genetic variation of individuals within populations, but high variation between populations, probably linked to clonal or vegetative reproduction (Grace, 1993; Barrett et al., 1993). In many cases, aquatic plants are thought to have a “general purpose genotype” usually characterised by low levels of genetic variability but capable of adapting to a diverse range of environmental conditions through phenotypic plasticity (Baker, 1965; Barrett et al., 1993). There are two forms of phenotypic plasticity that can be classed as either physiological plasticity, where the responses have a physiological end point, such as changes in photosynthetic capabilities; or as morphological plasticity where the responses are manifested as a change in

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morphology (Bradshaw, 1965). These plastic responses, both physiological and morphological, are important for the survival of a species in a multitude of different environments over the wide geographical ranges in which they are found (Bradshaw, 1965; Barrett et al., 1993).

Understanding the mechanisms that drive changes in the phenotype of aquatic plants can prove useful in gaining insights into the genetic diversity and evolutionary history of the species in a region. Morphological differences in introduced populations of aquatic plants are thought to be primarily driven by phenotypic plasticity because of the relatively low levels of genetic diversity and short time spent in the region (Riis et al., 2010). In a study of three invasive submerged macrophytes in New Zealand, Riis et al. (2010) concluded that the primary adaptive strategy of all three species was phenotypic plasticity due to the low levels of genetic diversity, coupled with the relatively short time period since the first introduction of any of the species. The oldest introduction was *Elodea canadensis* Mitch. (Hydrocharitaceae), and at just over 100 years, is considered too young for the development of local adaptations, especially given the lack of genetic diversity within and between populations in New Zealand (Riis et al., 2010). Local adaptations are driven by the process of natural selection, which result in different genotypes adapted to local conditions and are likely to express differences in morphological characters over much longer time scales (Kawecki and Ebert, 2004). A prerequisite for local adaptations to take place between populations is a relatively diverse gene pool within populations for natural selection to act upon (Ward et al., 2008). In the case of introduced species, this can be achieved through multiple introductions from different source populations, and local adaptation can be considered an important adaptive mechanism for the successful invasion of a species (Parker et al., 2003).

Myriophyllum spicatum L. (Haloragaceae) is considered an invasive species in southern Africa (Weyl and Coetzee, 2014), however, there are questions as to how long this species has been present in the region. Understanding the drivers of the morphological differences between populations can infer how long this species has been here. There are three distinct varieties or growth forms of *M. spicatum* which are found in different regions that have very different climatic conditions (Jacout Guillarmod, 1979). The differences in the morphology are so great that it was initially thought that there were at least two species of *Myriophyllum* in southern Africa, however, pollen analysis confirmed a single species (Jacout Guillarmod, 1979). The first variety is characterised as large and robust with large leaves and relatively thick stems (Fig. 1A and D) and is found in the Vaal River, Northern Cape, South Africa. This is the only population to be recorded as problematic in South Africa. The second variety is characterised as delicate small plants, with small leaves and highly branched, thin stems (Fig. 1B and E). It is found growing in the subtropical environment in Lake Sibaya, KwaZulu-Natal, South Africa. The third variety is large plants, and similar to the first variety in growth form, but the internode length is very short so the leaves become tightly packed leading to a bottlebrush type appearance (Fig. 1C and F), and is found in the high altitude regions, including the Amathola Mountains, Eastern Cape and the KwaZulu-Natal Midlands, South Africa. These varieties in southern Africa can be identified in the earliest herbarium specimens from the regions where they originate, for example, the Vaal River variety was first collected in 1897, the Lake Sibaya variety in 1966 and the high altitude variety collected in the Mooi River in 1894 (Fig. 1). These morphological characteristics are still present in the populations found in these biogeographic regions today (Fig. 1).

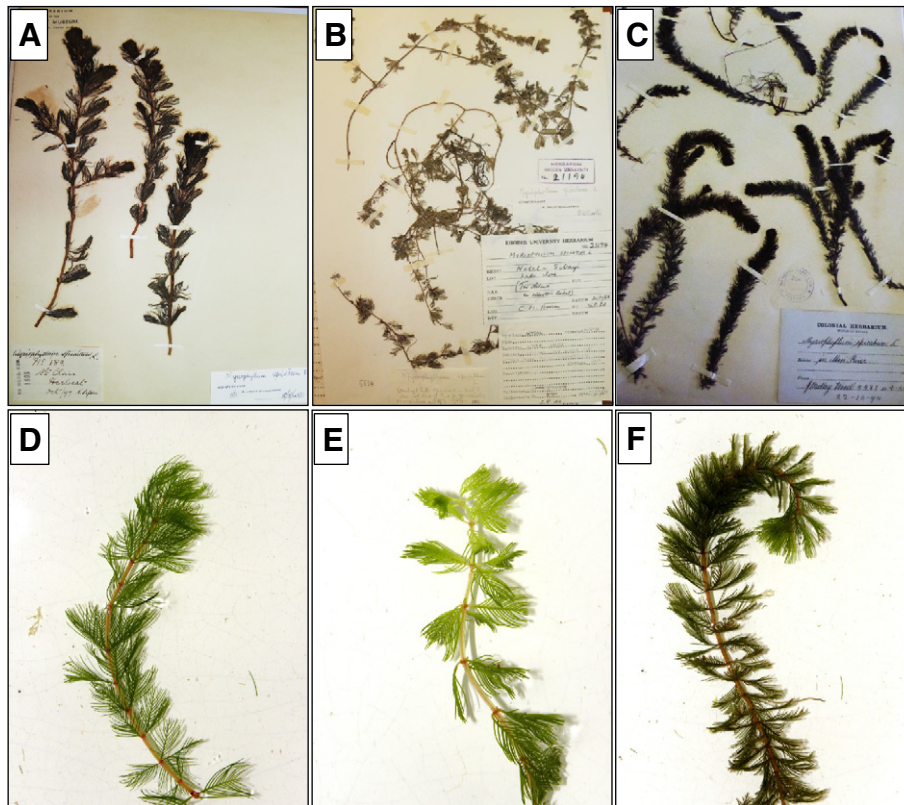


Fig. 1. The three morphological variations of *Myriophyllum spicatum* found in southern Africa as recorded by herbarium specimens (A–C) and present day photographic representations of living specimens (D–F). The first A & D: robust large leaf form collected from the Vaal River, Northern Cape, the second B & E: delicate branched form collected in Lake Sibaya, KwaZulu-Natal and the third C & F: the large growth form with very short internode lengths giving it a bottlebrush appearance, the herbarium specimen collected in the Mooi River, KwaZulu-Natal Midlands and the living specimen collected in Hogsback, Eastern Cape.

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