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Hybrid *Typha* × *glauca* outperforms native *T. latifolia* under contrasting water depths in a common garden

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Abstract

Hybridization can result in the formation of highly competitive lineages that displace their progenitor species and other native organisms. In eastern North America, hybridization between native *Typha latifolia* and introduced *Typha angustifolia* yields the vigorous hybrid species *T.* × *glauca*. The hybrid has become increasingly prevalent over the past century in eastern North America, where there are indications it displaces native plants. Moreover, it has been suggested that water depth influences the growth performance of hybrid vs. native cattails but there have been no comparisons of plant performance under contrasting water depths. Using a common-garden experiment with two levels of a water-depth treatment we compared the above- and below-ground growth performance of *T. latifolia* vs. hybrid cattails collected from 12 sites in southern Ontario. We found that hybrids outperformed all other plants in terms of total and above-ground biomass production and, depending on the method of species assignment used, in terms of the number of ramets produced. However, there was no difference in the mass of rhizomes produced between species. Consistent with a previous study of natural populations from the same region, growth performance of the different species was similar across the different water depths used in the experiment. Collectively, our results indicate that enhanced hybrid performance was driven by the production of larger and more numerous ramets and not via increased investment in rhizomes.

Zusammenfassung

Hybridisierung kann zur Bildung von konkurrenzstarken Verwandtschaftslinien führen, die ihre Ausgangsarten und andere einheimische Organismen verdrängen. Im östlichen Nordamerika ergibt die Hybridisierung der einheimischen *Typha latifolia* und der eingeführten *Typha angustifolia* die wuchsstarke Hybride *T.* × *glauca*. Die Hybride ist im vergangenen Jahrhundert im östlichen Nordamerika zunehmend vorherrschend geworden, und es gibt Anzeichen, dass sie einheimische Arten verdrängt. Außerdem gab es Meinungen, dass die Wassertiefe die Wuchsleistungen der hybriden und einheimischen Rohrkolben unterschiedlich beeinflusst, aber es hat keine Untersuchungen zur Leistung der Pflanzen bei unterschiedlichen Wassertiefen gegeben. In einem common-garden-Experiment mit zwei Wassertiefen verglichen wir die ober- und unterirdische Wuchsleistungen von *T. latifolia* und der Hybride, die aus zwölf Vorkommen im südlichen Ontario stammten. Wir fanden, dass die Hybriden alle anderen Pflanzen hinsichtlich gesamten und der oberirdischen Biomasseproduktion übertrafen und – in Abhängigkeit von der zur taxonomischen Zuordnung eingesetzten Methodik – auch hinsichtlich der Anzahl produzierter Ramets. Indessen gab es keinen Unterschied hinsichtlich der Biomasse der produzierten Rhizome. In Übereinstimmung mit einer früheren Untersuchung an

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Freilandpopulationen in der gleichen Region war die Wuchsleistung der verschiedenen Arten bei unterschiedlichen Wasserständen gleich. Insgesamt zeigen unsere Ergebnisse, dass die verstärkte Wuchsleistung der Hybride durch die Produktion von größeren und zahlreicheren Ramets bedingt war und nicht durch gesteigerte Investitionen in Rhizome.

Keywords: Common-garden experiment; Hybridization; Invasive species; Mixed-effects models; *Typha* × *glauca*; SSR markers

Introduction

Opportunities for hybridization and the formation of new, potentially invasive lineages are created when non-native organisms are introduced to regions containing closely related species (Schierenbeck & Ellstrand 2009; Ward, Gaskin, & Wilson, 2008). If these hybrids are competitively dominant, displacement of native lineages can occur. For example, hybridization has been linked to the displacement of native *Spartina foliosa* from San Francisco Bay (Sloop, Ayres & Strong 2010; Ayres, Zaremba, & Strong 2004) and the displacement of *Typha latifolia* and *Typha angustifolia* from sites in the Great Lakes region of North America (Shih & Finkelstein 2008; Travis, Marburger, Windels, & Kubátová, 2010; Freeland, Ciotir, & Kirk 2013). In the case of *Typha*, three species co-occur in eastern North America: *T. latifolia*, thought to be native (Grace & Harrison 1986); *T. angustifolia*, which dispersed relatively recently between North America and Europe, and most likely originated in Europe, possibly with early European settlers (Ciotir, Kirk, Row, & Freeland, 2013), and their hybrid, *T.* × *glauca* (Galatowitsch, Anderson, & Ascher, 1999). In the Great Lakes region, the hybrid predominates and is associated with the occurrence of hybrid swarms via backcrossing (Travis et al., 2010; Kirk, Connolly & Freeland 2011; Freeland et al. 2013).

The dominance of *Typha* hybrids in wetlands is deleterious to biodiversity: hybrids are taller (Galatowitsch et al. 1999) and more productive than *T. latifolia*, contributing large amounts of slowly decaying litter that cover the soil surface, altering temperature and soil nutrients, excluding light, and ultimately leading to the reduction of native plant diversity (Angeloni, Jankowski, Tuchman, & Kelly, 2006; Boers, Veltman, & Zedler, 2007; Farrer & Goldberg 2009; Tuchman et al., 2009; Travis et al., 2010; Mitchell et al., 2011; Larkin, Freyman, Lishawa, Geddes, & Tuchman, 2012). Ecological dominance of hybrids might arise via the segregation of novel recombinant genotypes that are better adapted than parental genotypes (Hochholdinger & Hoecker, 2007; Donovan, Rosenthal, Sanchez-Velenosi, Rieseberg, & Ludwig, 2010), and/or the masking of deleterious recessive alleles (Prentis, Wilson, Dormontt, Richardson, & Lowe, 2008). Examples of hybrid vigour across multiple taxa demonstrate that parental species can be outcompeted across a wide range of environments (Vilà & D'Antonio, 1998; Ayres et al. 2004; Johnston, Donovan & Arnold 2004). A similar process might be driving range expansion and increased domination of wetlands by *Typha* × *glauca* in some North American regions where *T. latifolia* and *T. angustifolia* occur sympatrically (Sullivan, Wildová, Goldberg, & Vogel, 2010; Lishawa et al. 2013) and at lower frequencies than hybrid cattails (Freeland et al. 2013).

One way in which hybrids can expand their range is through the occupation of under-utilized niches (Seehausen 2004). Water depth is a key factor regulating patterns of habitat occupancy in aquatic plants (Warwick & Brock 2003; van der Valk, 2005; Lacoul & Freedman 2006), but there is mixed evidence from natural populations that it affects the distribution of *Typha* spp. within stands. For example, *T. latifolia* has been observed to occupy significantly shallower water depths than other cattails (Grace & Wetzel 1982; Travis et al., 2010). Similarly, cattail invasion of Lake Ontario wetlands following lake-level regulation involved *T. angustifolia* occupying deeper water and *T.* × *glauca* occupying higher elevations (Wilcox, Kowalski, Hoare, Carlson, & Morgan 2008). However, a study designed to evaluate whether cattails occupy different water depths in mixed stands failed to detect any differences between species (McKenzie-Gopsill, Kirk, Van Drunen, Freeland, & Dorken, 2012). Smith (1967) and Lishawa, Albert, and Tuchman (2010) further concluded that *T.* × *glauca* favours fluctuating and low water levels, respectively but studies exclusively of *Typha* hybrids indicated that they perform well in a range of water depths (Waters & Shay 1990, 1992). Together, these results suggest that water depth might affect the performance of cattail species but that controlled experiments are needed to evaluate the effect of water depth on the performance of parental vs. hybrid cattails.

We used the production of biomass to contrast the performance of *T. latifolia* and *T.* × *glauca* under two levels of a water-depth treatment. Above-ground biomass has been shown to affect competitive success in cattails (Weiner 1993; Weihe & Neely 1997; Farrer & Goldberg 2009; Larkin et al., 2012; see also Sullivan et al., 2010), and so should provide insights into the structuring of mixed stands of cattails and competitive exclusion by cattail species that outperform congeners under specific environmental conditions. Below-ground biomass should also contribute to overall plant performance: cattails are clonal and vegetative propagation occurs via rhizomes (Tanaka, Asaeda, Hasegawa, & Tanimoto, 2004). We predicted that hybrid *T.* × *glauca* would have greater above- and below-ground biomass production than parental species but that the difference in performance