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Short communication

Heterosis in invasive F_1 cattail hybrids (*Typha* × *glauca*)

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ABSTRACT

Rapid evolution following interspecific hybridization can facilitate biological invasions. Around the Great Lakes in North America, the hybrid cattail *Typha* × *glauca* is dominating wetlands and displacing both parental species. We measured water depth and height of *T.* × *glauca* and its parental species (*Typha angustifolia* and *Typha latifolia*) throughout the growing season at a site near Lake Ontario that harbors both parental species plus hybrids. We found no evidence of niche partitioning by water depth, nor was there evidence that water depth was influencing plant height. At the beginning of the growing season, *T. latifolia* comprised the tallest plants, but this potential advantage was short-lived, and for most of the growing season, F_1 hybrids were taller than all or most other taxa (*T. angustifolia*, *T. latifolia*, and advanced-generation/backcrossed hybrids). Heterosis, inferred from height, is therefore evident in F_1 hybrids, but not in advanced-generation/backcrossed hybrids. *Typha* stands often achieve high densities, and the competitive advantage of superior height is likely contributing to the invasive success of *T.* × *glauca* F_1 hybrids in the Great Lakes region.

1. Introduction

Biological invasions occur when species that are introduced outside their native range subsequently establish and spread, thereby presenting major environmental and economic threats (Pimentel et al., 2005). In the past decade, the potential role of rapid evolution in successful bioinvasions has been increasingly highlighted, and it has become apparent that hybridization, an important driver of speciation and evolutionary novelty in flowering plants (Arnold, 1997), also provides a mechanism that can promote biological invasions through rapid evolutionary change (reviewed in Prentis et al., 2008). Following hybridization, recombination and heterosis can result in elevated fitness of hybrids relative to parental species (Prentis et al., 2008). The beneficial effects of heterosis should be strongest in the F_1 generation, which may be larger and have greater yield than the parentals (Hochholdinger and Hoecker, 2007), but heterosis often diminishes in later generations, following a decrease in heterozygosity (Rhode and Cruzan, 2005). As a result of the transient nature of heterosis, recombination may be a more important driver in the evolution of invasive species; however, exceptions to this can be found in invasive species that reproduce clonally, and in which heterosis may therefore persist (Prentis et al., 2008).

One example of a successful clonal hybrid invader is the cattail *Typha* × *glauca*, which is the hybrid of the broad-leafed cattail, *Typha latifolia*, considered native to North America (Grace and Harrison, 1986), and the narrow-leafed cattail, *Typha angustifolia*, which was most likely introduced to North America from Europe (Ciotir et al., 2013). *Typha* hybrids now greatly outnumber, and are displacing, both parental species in areas around the Great Lakes and the St. Lawrence Seaway of eastern North America (Freeland et al., 2013; Kirk et al., 2011; Travis et al., 2010). Although advanced-generation and backcrossed hybrids are widespread, they typically persist at lower frequencies than F_1 hybrids (Travis et al., 2010; Freeland et al., 2013), and little is known about their relative vigor (hereafter we will refer to these collectively as advance-generation hybrids because of difficulties reliably distinguishing F_2s from back crosses or more complex combinations; see Freeland et al., 2013). Plant height provides one potential measure of vigour, because invasiveness of non-native species is associated with performance-related traits affecting characters that include growth rate and growth size (Goodwin et al., 1999; van Kleunen et al., 2010). Light competition is critical for survival, growth and reproduction of plants in dense stands, where taller plants intercept more light while shading their shorter competitors, thereby obtaining a potential competitive advantage (Anten and Hirose, 1998). In *Typha*, greater ramet height could help hybrids outcompete their parental species by limiting the parental species' access to light; indeed, shoot height has previously been identified as one reason why *T. angustifolia* is able to outcompete *T. latifolia* (Tanaka et al., 2004; Weisner, 1993). More recently, a common-garden experi-

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ment determined that *T.* × *glauca* generated significantly greater above-ground, but not below-ground, biomass compared to its parent species (Bunbury-Blanchette et al., in press). In this study we compared the heights of parental species and hybrids throughout the growing season in a natural setting in which they co-exist. We tested the hypothesis that F_1 hybrids may have a competitive advantage over parental species and advanced-generation hybrids because of an earlier start to their growing season, and greater height throughout the growing season.

2. Methods

In the Great Lakes region, the domination of cattail stands by *T.* × *glauca* and the local paucity of one or the other parental species (Freeland et al., 2013; Travis et al., 2010) make it challenging to find sites in which *T. latifolia*, *T. angustifolia*, and hybrids co-exist. We therefore limited our study to Cedargrove Park in Peterborough, Ontario (44°18′N, 78°19′W), which was previously identified as harboring both of the parental species plus hybrids (previously genotyped plants from that site revealed approximately16% hybrids, 47% *T. latifolia*, and 37% *T. angustifolia;* Ball and Freeland, 2013). This is an urban park that includes a stormwater management pond under the jurisdiction of the City of Peterborough, and at the time of construction (2003) was planted with a number of species including *T. angustifolia* and *T. latifolia* (XCG Consultants Ltd., 2009). There is no record of *T.* × *glauca* at this site, which suggests that the hybrids arose naturally after 2003. We visited this site 14 times throughout the summer, with visits separated by periods of 6–17 days (mean sampling interval = 10.5 days) between April 12th, 2012 (Day 1) and August 29th, 2012 (Day 138). At each visit we sampled between 31 and 61 plants (Table 1) that at the time of sampling were marked with indelible marker to avoid re-sampling. We also measured the water depth of sampled plants. Plants were initially sampled based on visibility and spacing, i.e., during the first visit we sampled all visible plants that were separated by at least 1 m. Repeated site visits and the avoidance of previously sampled plants precluded the establishment of fixed transects, and as more plants emerged, additional ramets were therefore sampled and measured on a roughly ad hoc basis, but with the goals of (1) maximizing distances between sampled ramets which was done by ensuring that sampling was distributed as evenly as possible around the pond, (2) sampling ramets across transects that ran from the periphery of the stand to the waterbody (to ensure that plants were sampled from the maximum possible range of water depths), and (3) sampling plants with a wide range of leaf widths in order to maximize the likelihood that we were sampling from parent species and hybrids. Differentiating between hybrids and parental species based on morphology is challenging, because morphological characters overlap between hybrids and parental species (Olson et al., 2009), and this should have minimized biases in sampling hybrids versus parental species. From each measured plant a leaf sample was collected for DNA extraction and genotyped or the purposes of taxonomic identification, following the method of Ball and Freeland (2013).

Before comparing plant heights, we had to investigate the potential influence of water depth on shoot height. We conducted intraspecific linear regressions of height versus water depth using StatPlus Professional v2009 (AnalystSoft Inc.). We then used general linear models to compare shoot heights across taxa, for each sampled time period, in which shoot height was identified as the dependent variable, and water depth and taxon were identified as independent variables, again using StatPlus Professional. Neither of these analyses identified a relationship between shoot height and water depth, and so we subsequently ignored water depth and used ANOVAs in StatPlus Professional to compare shoot heights among taxa for each time period. We also used ANOVAs to compare water depths among taxa at each time period, to determine whether there was evidence of niche partitioning by water depth.

3. Results and discussion

We genotyped a total of 673 plants, of which approximately 41% were *T. latifolia*, 36% were *T. angustifolia*, 13% were F_1 hybrids, and 10% were advanced-generation hybrids. We found no difference between the water depths at which the taxa were growing except for day 48 when the measured *T. angustifolia* were growing in deeper water than the measured F_1s (Appendix A). Multiple previous studies have suggested that *Typha* spp. partition habitat, with *T. latifolia* growing in shallower water than *T. angustifolia* (Grace and Wetzel, 1981; Travis et al., 2010), and *T.* × *glauca* favoring low or fluctuating water levels (Lishawa et al., 2010). There has also been some contradiction within studies, for example Travis et al. (2010) found that water depth influenced height at all of their sites, although the effects were inconsistent: at some sites, ramet height increased with water depth, and at other sites it decreased. Furthermore, Waters and Shay (1990) found that there was a relationship between water depth and ramet height in vegetative but not in flowering shoots of *T.* × *glauca*. However, consistent with the results of this study, Sharma et al. (2008) found no difference in the ramet height of *T. angustifolia* growing at different depths, and McKenzie-Gopsill et al. (2012) found no evidence of niche segregation by taxon within *Typha* stands that were located in the same geographic region as this study. We do note, however, that our site was fairly shallow overall (average measured water depth was only 2.41 cm), and we cannot rule out the possibility of obtaining different results with respect to niche partitioning at sites with larger and deeper water bodies. Regardless, our data do not suggest that at Cedargrove Park hybrids are establishing themselves after capitalizing on under-utilized niches,a conclusion that is consistent with a study that, as noted earlier, found no evidence of niche partitioning among *Typha* taxa (McKenzie-Gopsill et al., 2012).

In addition to finding no difference in water depths, we also found no evidence that water depth affects shoot height. None of the intraspecific regressions of shoot height versus water depth revealed a significant result; nor did any of the intraspecific comparisons of shoot height among taxa based on linear generalized models identify water depth as a significant influence on shoot height. As noted in the Methods, earlier studies of the effects of water depth on ramet heights have yielded mixed results. There are at least two possible explanations for these contradictions in the literature (including this study). First, it is possible that an effect of water depth on ramet height is manifest only in sites with relatively large bodies of water; we may have seen an effect if our samples had spanned a greater range of water depths. Second, it is possible that plant height is influenced by a more complicated range of factors than simply water depth, for example a combination of depth, interspecific competition, and nutrients may be relevant (Tanaka et al., 2004). The latter could explain the varying relationships between water depth and ramet height that Travis et al. (2010) found. Regardless, our analyses show that water depth is not the explanation for differences in plant heights in our study.

The four taxonomic groups (*T. latifolia*, *T. angustifolia*, F_1 hybrids, and advanced-generation hybrids) each showed roughly the same growth pattern, with a plateau reached by around day 99 (July 22nd) (Fig. 1). The flowering period spanned days 58–75 and, as has been previously documented (Ball and Freeland, 2013), there was overlap in the flowering time among all taxa. Data from the earliest visits suggest that *T. latifolia* is the first to emerge. This is consistent with the fact that *T. latifolia* has broader, shorter leaves than *T. angustifolia*, and is therefore thought to photosynthesize more efficiently at the start of the growing season (Grace and Wetzel, 1981). However, the height advantage in *T. latifolia* was short-lived: