

Biological control of invasive *Phragmites australis* will be detrimental to native *P. australis*

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European *Phragmites australis* is widespread as a nonnative genotype in North America, abundant in many places, and often considered a pest. There is also a much less common North American native genotype of *P. australis*, and a “Gulf Coast” genotype (Saltonstall et al. 2004). The genetics of *Phragmites* are complex, and in North America there are hybrids between *P. australis* and other species of *Phragmites*

as well as between the European and North American native genotypes of *P. australis* (Paul et al. 2010; Lambertini et al. 2012; Meyerson et al. 2012). *P. australis* is one of the best-studied plants globally (Hulme et al. 2013).

European *P. australis* can become highly dominant in marshes, with effects on plant communities, birds, fishes, insects, and other organisms, as well as ecosystem processes (Meyerson et al. 2000a, b; Kiviat 2013). Some of these effects are considered negative and others positive, depending upon a stakeholder’s interests or management goals. Besides habitat functions, *P. australis* provides a number of non-habitat ecosystem services in both its native and introduced ranges related to its high above and belowground biomass and productivity. Among these services are formation and stabilization of tidal wetland soils for protection against sea level rise, carbon sequestration, wave attenuation, evapotranspirational cooling of the microclimate, and removal of macronutrients and trace metals from surface waters (Meyerson 2000; Meyerson et al. 1999, 2000a, b; Hershner and Havens 2008; Kiviat 2013).

A group of researchers has been developing classical biological control for European *P. australis* in North America (Schwarzländer and Häfliger 2000; Tewksbury et al. 2002; Häfliger et al. 2005, 2006; Blossey 2014). Currently, at least two species of European noctuid moths are being tested as potential biological control agents. The proposed biological control is intended to affect only the European *P.*

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Phragmites invasion.

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australis (Haplotype M or “invasive” *P. australis*), and not the native *P. australis* (Häfliger et al. 2005; Hinz et al. 2014). A recent request for proposals released by the New York Department of Transportation (<http://files.ctctcdn.com/08b78404201/13a45c32-5814-4869-8bb4-f2cee531dcab.pdf>) is soliciting proposals for monitoring and release of potential bio-control agents against invasive *P. australis* in New York State.

As longtime researchers on the ecology and genetics of *P. australis* in the United States, we raise important concerns about the potential outcomes and effects of classical biological control for *P. australis* in North America. Here we address several points that have attracted little discussion in the literature during the development of *P. australis* biological control agents.

1. Successful biological control of an invasive plant genotype, variety or subspecies that is sympatric with a native genotype, variety or subspecies of the same species would require an unprecedented degree of specificity of the biological control agent. There has never been a case of successful biological control at the subspecific level. Although the literature is replete with examples of differences in preference and performance between genotypes of the same plant species (e.g., Horner and Abrahamson 1992; Underwood and Rausher 2000; Kleine and Müller 2011), these differences are rarely absolute. Even if such a case existed, the evolution of increased diet breadth is a real possibility—for example, Graves and Shapiro (2003) found that 34 % of California butterflies had adopted exotic host plant species into their diets (see also Jahner et al. 2011). Adopting a novel genotype of the same species into an herbivore’s diet should be even more likely (Pemberton 2000). Host shifts could result in enemy-free space for the biological control agent that may enhance its impact on the novel host plant; i.e., the native *P. australis* genotypes (Holt and Lawton 1993).

For *P. australis*, the preponderance of evidence suggests that North American native and introduced herbivores perform better on, and do more damage to, native *P. australis* than European *P. australis*. According to Tewksbury et al. (2002), at least 21 species of *P. australis* herbivores have been accidentally introduced into North America, most all of which now feed on native *P. australis*. Three species of herbivores reportedly have been restricted to a single

P. australis genotype in a mixed-genotype marsh in New York (Blossey 2003; Saltonstall et al. 2014)—for example, *Lasioptera hungarica* was found only on European *P. australis* whereas the gall midge *Calamomyia phragmitis* was only found on native *P. australis*. As a cautionary tale, the stem galler *Lipara pullitarsis* was previously reported to occur only on European *P. australis* (Blossey 2003) but later found on both genotypes (Allen et al. 2015). Moreover, *L. hungarica* attacked native-invasive hybrids suggesting that a host shift to the native genotypes may be possible through these intermediate hybrids (i.e., the hybrid bridge hypothesis; Floate and Whitham 1993). In both field surveys and common-garden studies in North America, introduced mealy plum aphids (*Hyalopterus pruni*) and specialist gall flies (*Lipara* sp.) are more prevalent on native than invasive *P. australis* (Lambert and Casagrande 2007; Lambert et al. 2007; Park and Blossey 2008; Cronin et al. 2015; Allen et al. 2015). Tissue damage from the entire guild of chewing herbivores was also greater on the native genotypes (Cronin et al. 2015). Finally, experimental studies with the aphid and a generalist chewing herbivore (fall armyworm, *Spodoptera frugiperda*) revealed that these patterns of damage or abundance are the result of differences in performance on native and invasive *P. australis* genotypes (Bhattarai et al. in review). Complete specificity, both in the short term and long term, to invasive *P. australis* is exceedingly unlikely.

2. Spillover effects, associational susceptibility and apparent competition will likely occur and negatively impact native *P. australis*. Even if strong preferences exist for invasive *P. australis*, herbivore spillover onto native *P. australis* stands will occur, particularly at high herbivore densities. Consider that many native *P. australis* stands are typically quite small and are often found in close proximity to expansive monocultures formed by invasive *P. australis*. The susceptibility of the native *P. australis* genotypes to these herbivores may increase simply because they are proximal to a large reservoir of herbivores (i.e., associational susceptibility), or because as the quality of the invasive genotypes deteriorates (owing to extensive herbivore damage), the relative quality of the native genotypes improves (Barbosa et al. 2009). Spillover can also lead to apparent competition (i.e., indirect negative interactions between two species mediated through their shared herbivores; e.g. Holt and Lawton 1993). In an

experimental study conducted in mixed-genotype marshes, Bhattarai (2015) found that native *P. australis* suffered increased herbivory in the presence of invasive *P. australis*, an indication that apparent competition occurs between native and invasive *P. australis*. Unless specificity is absolute, spillover of the biological control agent is almost certainly going to have negative consequences for the native *P. australis*.

3. Biogeographical considerations are important and necessary because of the broad North American distribution of native and invasive *P. australis*. Field surveys along a 19° latitudinal transect indicated that damage and abundance of herbivores from several feeding guilds vary with latitude for native *P. australis*, suggesting that resistance to herbivores also varies with latitude (Cronin et al. 2015). Common-garden experiments further demonstrated that latitudinal variation in herbivore resistance in both native and invasive genotypes is genetically based and phenotypically plastic (Bhattarai 2015; Bhattarai et al. in review). What this means is that herbivore preference for and/or performance on invasive *P. australis* is likely to depend on the latitude of origin of the invasive plants and the environment within which the herbivores are released. For example, preference for invasive relative to native *P. australis* may be high if the release is conducted in the north but be low if it is conducted in the south. Consequently, spillover effects, associational susceptibility, and apparent competition may also vary with latitude (see Bhattarai 2015). These kinds of biogeographical considerations are rare for invasive plant management programs (Cronin et al. 2015). However, in the process of testing biological control agents, particularly for continent-wide invaders, pest managers should not ignore the possibility of geographic variation in the relative susceptibility of native plants to attack by that biological control agent.

Concerns about *P. australis* biological control were published as early as 2000 (Rooth and Windham 2000) and also addressed by Meyerson et al. (2009) and Cronin et al. (2015). *Phragmites australis* biological control is intended to address a major invasion in North America and is likely to change the ecology of vast areas of coastal and inland wetlands. However, the real risks to the native North American genotypes of *P. australis* (as indicated by recent research summarized above) may not have been fully considered, particularly the extirpation of native populations or the eventual

extinction of the native North American lineage altogether. The concerns we raise need to be considered in the process of developing and approving the release of biological control agents and the entire approval process would benefit from greater transparency and wider input from *Phragmites* researchers globally.

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