

Adaptive Strategies of Common Reed *Phragmites australis*

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Introduction

Phragmites australis, common reed, is a tall (1.5-4.0 m) coarse perennial grass found primarily in brackish and freshwater wetlands, growing at or above mean high water. It has a worldwide distribution (Tucker 1990) and is endemic to North America (Niering & Warren 1977). Along the Atlantic coast of the United States it is common in tidal and nontidal wetlands, in moist open uplands and wet areas behind the dune systems of the barrier islands (Gleason & Conquist 1963; Brown & Brown 1984).

In wetlands, *P. australis* (henceforth *Phragmites*) is generally a nuisance species because it is an efficient colonizer of the disturbed soils and acts as a climax species thereby forming extensive monocultures that reduce plant and animal biodiversity. Although specific studies quantifying patterns of change in *Phragmites* populations in North America are rare, reports from the United States (Hauber et al. 1991; Fell et al. 1998), South America (Weisser & Parsons 1981) and anecdotal evidence from numerous wetlands managers along the Atlantic and Gulf coast and the Chesapeake Bay wetlands suggest that populations are rapidly increasing in many areas. These increases appear to correlate well with human population growth and active wetland management. In these same areas, formal programs designed to reduce *Phragmites* populations have been developed (Ailstock et al. 1999). Most recently through the passage of Executive Order 13112 Invasive Species signed February 3, 1999, control of *Phragmites* on Federal land is encouraged.

In the United States, *Phragmites* classification in the National List of Plant Species That Occur in Wetlands (Reed 1988) as a facultative, wetland perennial, emergent grass and its frequent appearance in mid-Atlantic jurisdictional wetlands make efforts to control *Phragmites* subject to review by numerous local, state, and federal regulatory agencies. In an effort to accommodate the concerns of these groups, several methods for controlling *Phragmites* have been examined. These include biological control through insect introduction (Tscharntke 1989), hydrological control through flooding (Hellings & Gallagher 1992), mechanical control by cutting or burning (Lee 1990; Cowie et al. 1992), excavation (Ailstock 1991), and chemical control with non-specific herbicides (Cross & Fleming 1989). Non-chemical controls have proven ineffective for control and often interfere with the specific management objectives associated with control efforts. None of the control techniques are completely effective as a single treatment and some are restricted by constraints of property ownership, topography and site and off site land use. Much of the difficulty in devising control efforts can be attributed to the superior adaptive strategies of *Phragmites* for colonizing disturbed wetland soils and to positive ecological contributions of the species.

Adaptive Strategies

Reproduction

The aggressive nature of *Phragmites* is a direct reflection of the adaptive features of its life cycle. *Phragmites* is an efficient colonizer of disturbed environments because it seeds profusely and spreads vegetatively by a vigorous system of rhizomes and stolons (Best et al. 1981; Hara et al. 1993; Marks et al. 1994). Although some *Phragmites* colonies in the northeastern United States have been reported to produce mostly non-viable seeds (Tucker 1990) inflorescences exposed to overwintering conditions that allow for after ripening of the embryo produce abundant viable seeds (M. S. Ailstock, unpublished data). Seeds are dispersed primarily by wind during the winter months, but may also be distributed by birds such as Redwinged Blackbirds (Haslam 1969) and through transport of seed contaminated soil. Rhizome segments containing at least one axillary bud are also an effective propagule for plant establishment. Such segments are distributed in nature by water currents from areas prone to erosion and by feeding, den and nest building activities of large aquatic birds and mammals. Viable rhizome segments are also efficiently dispersed by machinery, especially track vehicles commonly used to transverse wetland terrain. It is noteworthy that successful establishment of new *Phragmites* from the small seeds or rhizome segments is highly favored by their placement on bare wetland soils such as those created by erosion, feeding activity of snow geese, ditch and pond building and maintenance construction projects in and around wetlands and by marsh burning.

Apical Dominance

When *Phragmites* becomes established, whether by seeds or rhizome segments, colony expansion occurs primarily by rhizomes in wet organic soils and rhizomes and stolons in sandy soils. Under optimal conditions, growth in excess of 10 meters is common within a single growing season. Such rapid growth is possible because the horizontal stems of *Phragmites* exhibit strong apical dominance. Growth is channeled to the extension of these stems rather than the production of new aerial stems from subtending nodes. When the rhizomes and stolons extend to an unfavorable environment where growth of the apical bud is inhibited or the apical bud is damaged, axillary buds along the rhizome axis are released and new photosynthetic stems are produced. This phenomenon common in the aerial stems of many terrestrial plants accounts for the frequent observation of explosive growth of a colony within a single season after one or more seasons of apparent stability or slow expansion.

Gas Exchange

In addition to apical dominance *Phragmites* has two other physiological adaptations that contribute to its ability to rapidly colonize diverse wetland habitats. Oxygen as an essential nutrient for all living plant parts is one of the primary limiting factors restricting plant growth in most wetland habitats. Many aquatic plants have evolved on internal ventilation systems that direct oxygen absorbed from the air and that generates as a by-product of photosynthesis to their subterranean parts to compensate for the lack of oxygen in the subsurface environment. The tissue responsible for internal gas exchange, aerenchyma, is abundant in the stems, rhizomes, and roots of *Phragmites*. For example, the aerenchyma volume of *Phragmites* stem and rhizomes is 49.67 and 32.77 percent respectively for the cross sectional stem volume while *Spartina*

alterniflora, a plant frequently displaced by *Phragmites*, has an aerenchyma stem volume of only 45.96 and rhizome volume of 21.33 percent. The diameter of *Phragmites* stems and rhizomes are also 2-5 times greater than those of *S. alterniflora*. Thus, *Phragmites* has a much more efficient pathway for providing oxygen to its underground structures than other emergent marsh vegetation. This efficiency is reflected in the rapid growth of its subterranean parts. A second feature that contributes to improved gas exchange is the size, distribution, and density of stomata on both upper and lower leaf surfaces. Moreover, the stomatal densities are extremely high. *Phragmites* has an average of 406 stomates/mm² on its adaxial leaf surfaces and 633/mm² on the abaxial surface. In comparison, *S. alterniflora* has none on the adaxial surface and only 18.3/mm² on the lower surface (Ailstock et al. In press). Interestingly *Typha latifolia*, cattail, an aquatic plant also considered by some to be invasive, has stomata on both leaf surfaces at densities comparable but significantly lower than those of *Phragmites*. (See Table1.)

Table 1. Stomatal distribution patterns among some common wetland plant species.

	Leaf Stomatal Density mm ²		Leaf Stomatal Size (um)	
	Upper Surface	Lower Surface	Upper Surface	Lower Surface
<i>Phragmites australis</i>	406.1	622	16.4	14.5
<i>Typha latifolia</i>	303.5	296.8	19.5	19.2
<i>Spartina alterniflora</i>	0.1	18.3	N/A	26.8
<i>Acer rubrum</i>	0.1	223.8	N/A	13.3

The value of high stomatal densities is efficient gas exchange between the plant and air; oxygen availability provides the necessary reactant for aerobic respiration throughout the bipolar plant axis, carbon dioxide the essential substrate for photosynthesis. In aquatic environments where water by definition is seldom a limiting factor stomates can remain open to effect gas exchange virtually all of the time. The length of time for which *Phragmites* can remain open over most of its range provides a third selective advantage. *Phragmites* transpires large quantities of water. Since nutrient transport from the soil follows the same pathway as water, nutrients for aerial plant growth are efficiently transported by bulk flow. Moreover, the water removal from soils by transpiration favors increased concentration of oxygen in the soil in all *Phragmites* habitats not saturated with water. Taken collectively, the double presence of aerenchyma, stomatal size, and patterns of stomatal distribution on *Phragmites* leaves makes *Phragmites* more efficient at acquiring O₂ for aerobic respiration in all plant structures, carbon dioxide for photosynthesis, and mineral nutrients for growth and development than any other emergent wetlands plant.

Mechanical Adaptations

The adaptive features of *Phragmites* responsible for its ability to colonize and dominate wetland plant communities extend beyond those that dictate its reproductive potential, growth regulation, and its ability to efficiently assimilate essential plant nutrients from wet soil habitats. *Phragmites* also possesses three adaptations that inhibit the growth of other species of wetland

vegetation. First, the quantity and arrangement of mechanical tissues allows *Phragmites* to attain greater heights than other herbaceous wetland vegetation. Light attenuation by the elevated *Phragmites* leaf canopy imparts increasing stress to shorter understory wetland plant species that are normally dependent upon full sunlight exposure to achieve optimal growth. Second, the stem densities observed in monotypic colonies is high. Secondary rhizomes produce much shorter internodes than the primary rhizomes produced to colonize new areas. As new aerial stems emerge from these secondary rhizomes, stem densities in the oldest areas of the clonal population can exceed 30 living stems/m². Total erect stems which include both living and dead stems often exceed 160 stems/m² (Ailstock et al. 1989). The combination of mechanical tissue and high stem densities result in a third adaptive strategy that makes use of dead aerial stems. These stems tend to persist but when they break, they generally do so at the first or second node above the soil surface. As a consequence, *Phragmites* colonies tend to form a dense thatch that is elevated above the soil. Without soil contact, decay is slow. Thatch layers which can exceed 30 cm in well-established colonies in concert with the dense combination of living and dead aerial stems virtually block all sunlight from reaching the soil surface. When this occurs, the population is protected from competition from other plants that might be present in the soil seed bank. At this point *Phragmites* assumes its position as the climax species in the habitat.

Summary

The adaptive features of *Phragmites* that account for its general perception as a nuisance species have direct implications on the recommendations in place for development of control and eradication programs. Some of these relationships are summarized in Table 2 (Ailstock et al. 1999). However, if *Phragmites* is viewed within the context of the ecological value of wetlands, a different perception can emerge. In many ecosystems *Phragmites* serves as an excellent stabilizer of soil and acts as an efficient nutrient sink through its accumulation of large quantities of persistent biomass. Moreover, it is the most efficient herbaceous aquatic plant for transpiring large volumes of water and it does provide outstanding habitat for many species of aquatic and semi-aquatic fauna. Given these values, the most important aspect of *Phragmites* management is the development of project specific objectives. The objectives must provide for the establishment of a plant community whose combined ecological value exceeds that of the *Phragmites* dominated system being replaced. The adaptive features of *Phragmites* makes meeting these objectives a significant challenge.

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Table 2. Adaptation vs Management Efforts

Plant Adaptation	Management Action
• Wetland plant	<ul style="list-style-type: none"> ◇ Requires permits to control ◇ Specialized site access ◇ Limited application options
• Abundant seeds	<ul style="list-style-type: none"> ◇ Avoid soil disturbance ◇ Cover bare soil ◇ Monitor fill dirt
• Large rhizomes	<ul style="list-style-type: none"> ◇ Clean equipment ◇ Monitor fill dirt ◇ Treat excavated soils ◇ Avoid repeat harvesting for control
• Apical dominance	<ul style="list-style-type: none"> ◇ Requires project planning to prioritize sites
• Efficient ventilation	<ul style="list-style-type: none"> ◇ Avoid excavation as a control ◇ Avoid flooding as a control
• Numerous stomates	<ul style="list-style-type: none"> ◇ Prioritize invasive plant control efforts to include <i>Phragmites</i>
• Mechanical strength	<ul style="list-style-type: none"> ◇ Negates enhancing competition with other species as a viable control option
• Self mulching	<ul style="list-style-type: none"> ◇ Apply herbicide followed by burning to hasten recovery of site biodiversity
• Extended growth	<ul style="list-style-type: none"> ◇ Time application of herbicide to achieve selectivity ◇ Assume control requires multiple years of treatment

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