

Wind speed thresholds for *Typha* cattail seed release and local reduction of wind speed by mixed cattail/*Phragmites* stands

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Introduction

The growth of large, monoculture stands of cattail *Typha* species and the common reed, *Phragmites australis*, has earned them the status of highly productive invaders in various parts of eastern North America, particularly in wetland habitats disturbed by man (Mitich, 2000; Derr, 2008; Farnsworth and Meyerson, 2003). Comparative ecophysiological studies indicate various traits that increase the competitive success of these species, such as their ability to efficiently convert CO₂ and nutrients into aboveground biomass in both freshwater and brackish habitats and their longer growing season relative to other vegetation owing to the emergence of leaves combined with long leaf longevity (Farnsworth and Meyerson, 2003). While both *Phragmites* and *Typha* can reproduce vegetatively to form large colonies via rhizomes, studies of genetic diversity in wetlands suggest that *Phragmites* spreads mostly by airborne seeds, not through invasion via a few seeds arriving and subsequently propagating (Belzile et al., 2009). Rapid growth of colonies to heights over to 4 m by either species (Mitich, 2000; Farnsworth and Meyerson, 2003) may quickly form a physical blockade limiting air circulation in the wetland. *Phragmites* in particular is known to reduce wind velocity in its dense canopy (Brix, 1994). The impacts in marshes and shorelines dominated by tall grasses and sedges, where at times 47 species (28% of the community) have wind dispersal mechanisms (Soons, 2006), have not been fully explored.

Combining small, lightweight seeds with high release height is a strategy for long distance dispersal in plants. Sexual reproduction and dispersal in *Typha* is by achenes, seeds born on the wind by silky threads (Mitich, 2000). Cattail seeds are small (0.05 mg) and after studying falling distances in still air, Matlack (1987) estimated travel distances of 154 feet in 10 km/h winds. Low achene terminal velocities are also reported (<0.15 m/s for *Typha* spp., <0.25 m/s for *Phragmites*), permitting seeds to be carried several kilometers in updrafts and stormy conditions (Soons and Bullock, 2008).

The timing of seed release related to wind speed can also have significant impacts on dispersal distance and migration rate (Schippers and Jongejans, 2005; Soons and Bullock, 2008). The drag of wind on plant seeds creates the force necessary to detach them from the plant from the main body of the plant. The tension required to remove seeds from the plant should provide an indirect measure of the wind speed needed to produce enough force via drag to remove seeds. If plants exercise some form of control over the process of abscission, the separation of a plant part such as a flower or fruit, until wind conditions are ideal, they will have an advantage in long distance dispersal.

This study is exploratory in nature and seeks to determine the wind speed threshold for seed detachment in *Typha angustifolia* cattail spikes. A field survey will describe patterns of wind speed loss at varying heights and then determine whether wind speeds sufficient to spread seeds are reached at the border between patches of *Phragmites* and *Typha* in wetlands. Wind speed is expected to fall with decreasing height as vegetation blocks the flow of air. Further, it is hypothesized that the number of seeds released will be inversely proportional to the tension required to remove achenes from the spadix. At low tensions, less energy is required to pull off seeds, and consequently more will be released. The threshold wind speed (the wind speed of the first observed seed release) is likewise anticipated to be low.

Methods

Field survey of wind speeds

The ± 0.75 ha Villanova University constructed stormwater wetland, located at Villanova, Pennsylvania, 19085 USA was created nine years prior to this study to capture and treat runoff from a 41 acre suburban site (Map 1). A program to control the invasion of *Phragmites* by spraying glyphosate herbicide during the spring and summer growing season followed by winter cutting has not been successful and the majority of the wetland is dominated by the reed.

Five 1 m² plots, sites A-E (Map 1), were selected to span the boundary between *Phragmites* and *Typha* stands. Wind speed within each plot was measured using a Dwyer Instruments Mark II wind speed indicator scale. Wind direction was not noted but was observed to vary greatly. Readings were taken at five height categories: the average and maximum stalk height of *Typha* in the individual plot, the average stalk height and maximum stalk height of the *Phragmites* in the plot, and 0.5 m above the tallest plant in the plot. Thus, the wind speed measurements taken for the category “maximum *Phragmites* height” at site A were not

necessarily taken at the same absolute height above the wetland floor as those measures taken for the maximum *Phragmites* height category at site B, C, D, or E, and so on. Measurements were repeated on ten days in November between 1030 and 1500h.

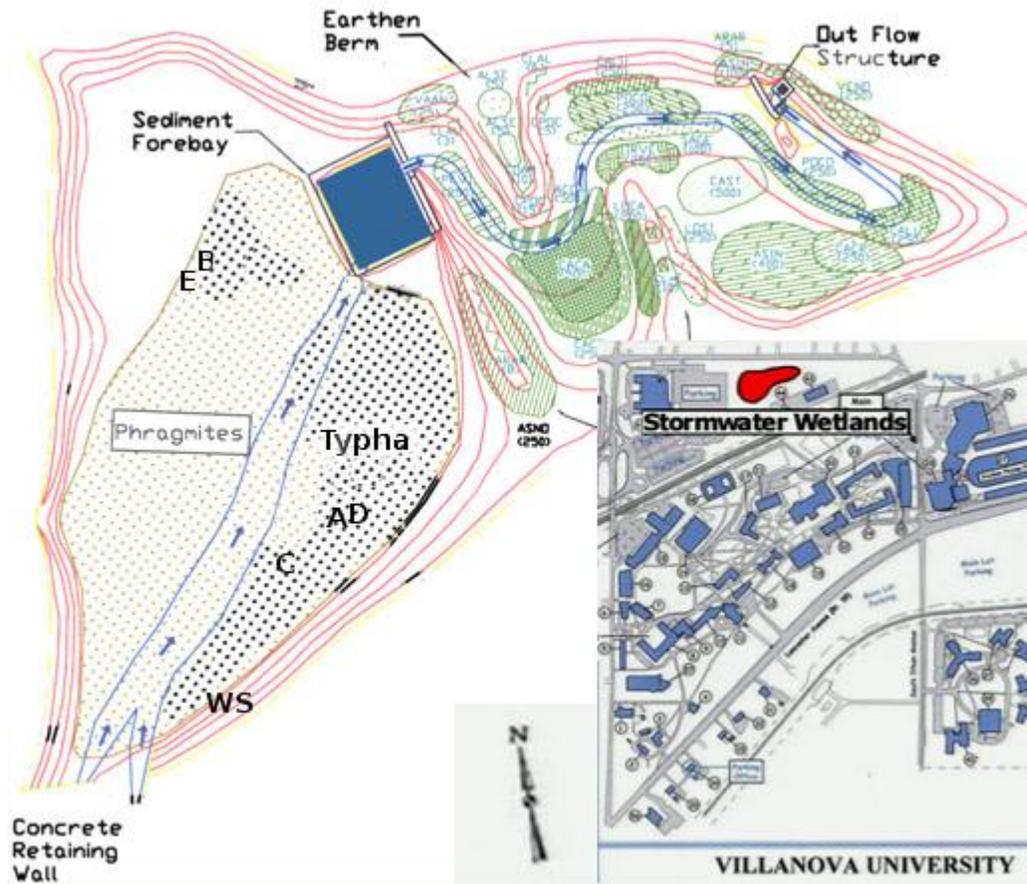
As a control representing the absolute wind speed above the wetland without interruption from vegetation, data from a weather station (WS) on a bank directly above the wetland were utilized (Map 1). The weather station continually measures wind speed and records averages every minute. The weather station's minute-by-minute data were later averaged for the hours spent in the field each day of data collection (between 45 min and 1.5 hrs).

Lab experiments to determine wind speed threshold needed to detach Typha achenes

Before taking the above-discussed wind speed measurements, the seed-bearing spadix “spikes” of the cattails (n=47) were harvested from each wetland site. 14 days after collection, these spadices were experimentally subjected to wind to observe the threshold wind speed. Following Soons and Bullock (2008), the threshold wind speed was defined as the speed at which the first achene is observed to detach from the spadix. A gradual increase in air movement was achieved by attaching a floor fan to a rheostat. Individual sample spadices were placed whole 10 cm in front of the fan, centered vertically in the flow of air. Wind speed at this location was increased from still air to a maximum of 6.71 m/sec by hand adjustment of the rheostat over the course of ± 20 seconds, after which the fan was held at top speed for an additional 5 seconds. All experiments took place inside a closed green house to minimize air circulation and turbulence.

A 35 x 35 cm square of overlapping strips of duct tape was hung 1 m downstream of the fan (90 cm downstream of the sample). Achenes became trapped on its surface allowing for a representative quantification of the number of seeds released by each spadix. The tape trap was replaced between each test run that released seeds.

After collecting threshold wind speed data and seed counts, 15 x 2 mm areas of achenes were pulled by hand from spadices by grasping with a small metal binding clipped padded with a slip of craft foam and lined with metal slats for even grip. Readings of the force being applied at the moment the sections of seeds tore free from the spadices were taken on a 3 N spring tensometer attached to the clip. Tension measurements were repeated three times, once near the top of the spadix, once near the middle, and once near the bottom.



Map 1. Schematic of the Villanova University constructed stormwater wetland. Study sites A-E are indicated by letters. WS = weather station. Dark and light stippling represents the estimated range within the wetland of *Typha angustifolia* and *Phragmites australis*, respectively. Flow of water proceeds from the bottom left toward the reconstructed area with native tree and shrub plantings in the upper right. **Inset** are a compass rose and map of the university campus, indicating the location of the wetland in a suburban environment. Image modified from Villanova Urban Stormwater Patternship resources, available from <http://www3.villanova.edu/VUSP/>.

Results

Between-site variation: plant heights

Water quality, measured using a LaMotte Water Monitoring Kit, did not vary greatly between sites (1-2ppm phosphates, 0 ppm nitrates, pH 7±0.5). Sites were dominated by *Phragmites australis* and *Typha angustifolia*. The tallest plant at every site was *Phragmites*. Plants below 1 m in height were not measured and were observed to be few and nonflowering. While average heights were similar, the heights of *Phragmites* were more varied (standard deviation=48.01) than those of *Typha* (SD=25.24).

The number of *Phragmites* to *Typha* plants per square meter site varied, with the ratio of *Phragmites* to *Typha* population size from 0.636 to 1.429 (Table 1). Linear regression showed no significant correlation between plant average or maximum height and this ratio or overall plant density (all $R^2 < 0.2$; figures not reported here). ANOVA analysis shows *Phragmites* heights did not differ significantly by site ($F=1.693$, $p=0.17$). Despite site C having significantly shorter cattails (one-way ANOVA, $F= 18.03$, $p<0.0001$) than the other sites (Fig. 1), wind speed measurements at this site followed the pattern observed across other sites (Fig. 2).

Table 1. Height categories and summary statistics for variation in flora among sites. The tallest plant at every site was *Phragmites*. Asterisk (*) indicates statistically significant difference from other sites ($p<0.0001$).

	<i>Phragmites</i> maximum height (cm)	<i>Phragmites</i> average height (cm)	<i>Typha</i> maximum height (cm)	<i>Typha</i> average height (cm)	Number <i>Phragmites</i> : <i>Typha</i>	Maximum height +0.5 m
Site A	264	223	234	186.7	9:10 (0.9)	314
Site B	248	180.64	230	203.13	11:8 (1.375)	298
Site C	215	168.75	181	157.64*	8:11 (0.727)	265
Site D	296	198.29	212	197.09	7:11 (0.636)	346
Site E	269	190.8	238	218.57	11:10 (1.429)	319
Overall average	258.4	192.29	219	192.62	1.01	308.4

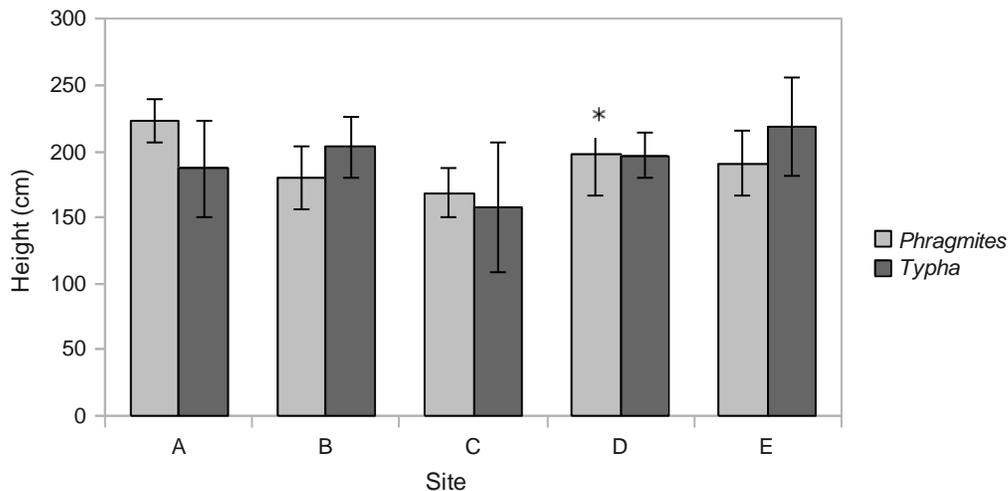


Figure 1. Plant heights by site. Sample size varies by site: a) *Phragmites* n=9, *Typha* n=10; b) *Phragmites* n=11, *Typha* n=8; c) *Phragmites* n=8, *Typha* n=11; d) *Phragmites* n=7, *Typha* n=11; e) *Phragmites* n=11, *Typha* n=7. Vertical error bars represent the standard deviations for the means. One-way ANOVA shows *Typha* height differs significantly only at site C ($F= 18.03$, $p<0.0001$), indicated by an asterisk (*). *Phragmites* heights do not differ significantly between sites.

Wind speeds in the field

Wind speed at the maximum *Phragmites* and *Typha* heights and 0.5 m above the tallest plant did not differ significantly from the average speed measured by the weather station at any site (Fig. 2). At the lowest heights (site average *Phragmites* and *Typha* heights), wind was significantly lower than the weather station data for sites C, D, and E. Site B wind speeds at the average *Typha* height (203 cm) were significantly lower than above the wetland as reported by the weather station but did not differ significantly at the average *Phragmites* height (180 cm). Wind at site A did not differ significantly from weather station data at any height (Fig. 2).

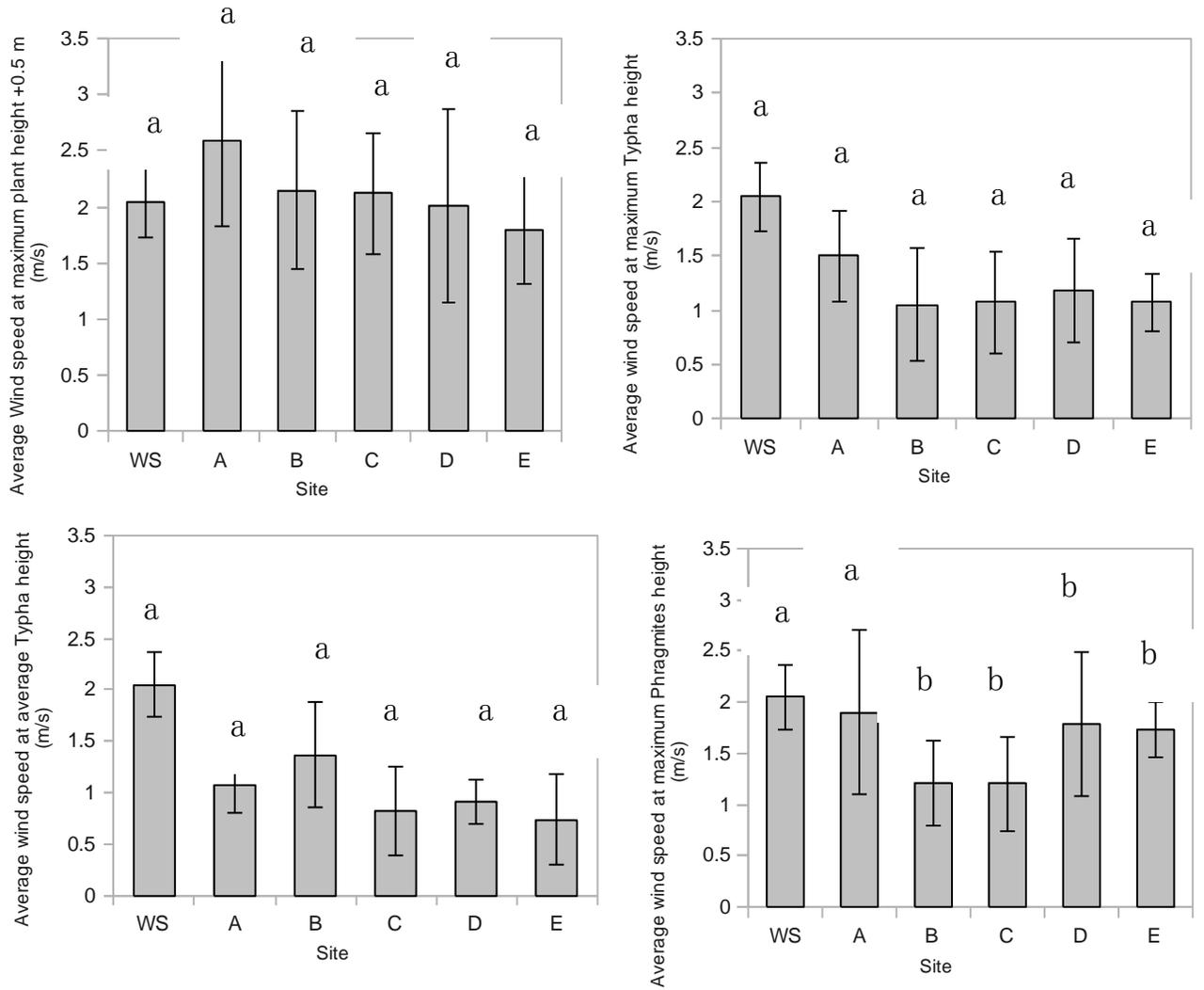
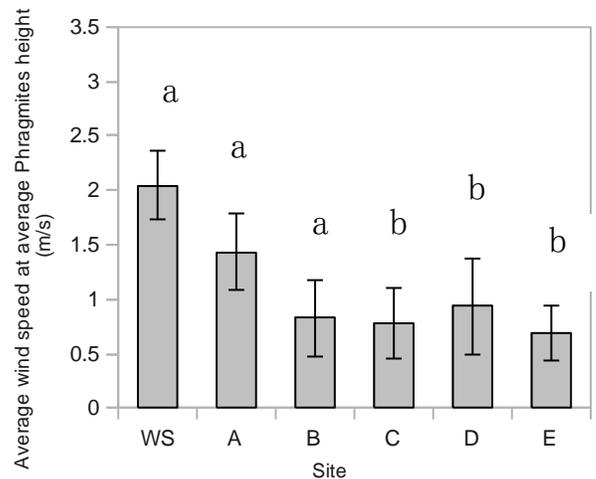


Figure 2. Average wind speed at five wetland sites and as measured by a weather station anemometer. Instantaneous wind speed data collected on 10 days. Site WS = weather station on embankment above wetland. Sample sizes for plant heights vary by site: a) Phragmites n=9, Typha n=10; b) Phragmites n=11, Typha n=8; c) Phragmites n=8, Typha n=11; d) Phragmites n=7, Typha n=11; e) Phragmites n=11, Typha n=7. Vertical error bars represent the standard deviations for the means. One-way ANOVA shows wind speed differs significantly only at the level of the Phragmites average height per plot and Typha average height per plot ($p < 0.05$). Letters above bars indicate wind speeds that differ significantly.



Because of low between-site variation, wind speed measurements were pooled from all sites to create a wind speed profile at continuous heights above the wetland floor (Fig. 3). Linear regression of this direct relationship yields the equation: wind speed = (0.01 * height) – 0.7. When the ten wind speed measurements at each height are converted into percentages of the weather station measurements, averaged, and plotted against height, a similar relationship is found (Fig. 4). Linear regression shows the percentage of the wind speed at any given height = (height * 0.44) – 35.71. Percentages over 100 were observed at both the maximum plant height +0.5 m and maximum *Phragmites* height levels. Maximum observed wind speed sometimes exceeded weather station values (Table 2). Zero wind speed was recorded at least once at all sites and in all height categories.

Table 2. Wind speeds by height category. Data averaged across five sites. Wind speeds were greatest above maximum plant height and decreased with decreasing height above the wetland floor. Percentages above 100 likely due to the comparison of instantaneous data to weather station (WS) averages by minute (see Discussion).

	Average height (cm)	Average wind speed (m/s)	Maximum wind speed (m/s)	Average % of WS wind speed
+0.5 m	308.4	2.13	6.04	105.58
Max <i>Phrag</i>	258.4	1.57	5.81	76.29
Avg <i>Phrag</i>	192.29	0.93	2.68	45.59
Max <i>Typha</i>	219	1.18	3.13	59.49
Avg <i>Typha</i>	192.62	0.98	3.58	48.38

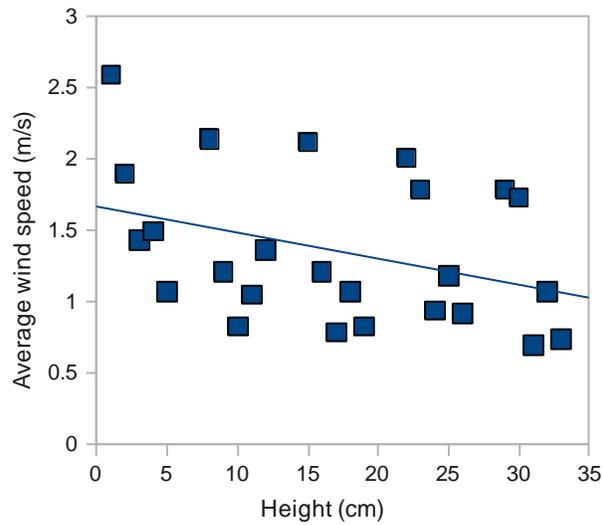


Figure 3. Scatterplot of relationship between height above wetland floor and average wind speed. Instantaneous wind speed data collected at five sites on 10 days. A linear regression shows there is a positive association between height and average wind speed ($R^2=0.74$).

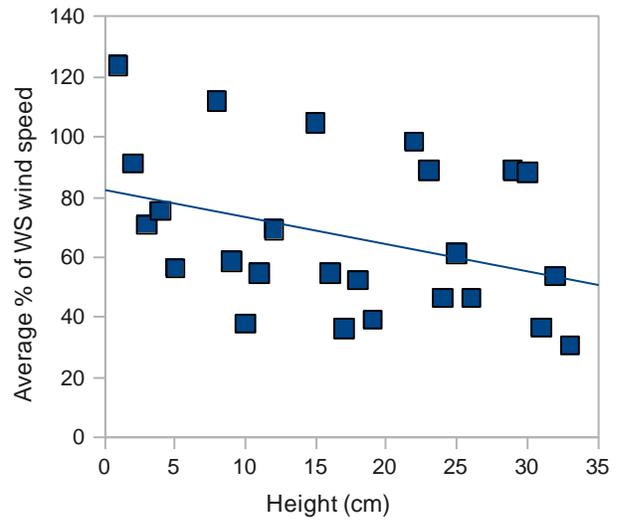


Figure 4. Scatterplot of relationship between height above wetland floor and average percent of wind speed as measured at a weather station (WS) above the wetland. Instantaneous wind speed data collected at five sites on 10 days. Weather station is an average of continuous data for the time period during which readings were taken in the wetland. Percentages above 100 possibly due to the comparison of instantaneous data to averages (see Discussion). A linear regression shows there is a positive association between height and average percent of wind speed above the wetland ($R^2=0.73$).

Wind speed thresholds for release of seeds in Typha

Spadices were collected from a total of 47 Typha and stored in a cool, dry location for 14 days before wind speed tests. When subjected to steadily increasing wind speeds, the vast majority of spadices (n=29) released no seeds, even after five seconds at top speed (6.71 m/s). Two samples released over 300 seeds beginning at relatively low wind speed thresholds (~3 m/s), and one sample released 127 seeds beginning at 3.58 m/s. Fewer than 15 seeds were trapped from each of the remaining releasing samples (n=15). Three broad groups of readiness to release seeds are discernible (Table 3; Fig. 5). Analyses of tension near the top, middle and bottom of the spadix and of the average of these three tensions all yielded no significant correlation with number of seeds caught by tape traps (all linear regression $R^2 < 0.09$, $p > 0.5$, Fig. 6) or with threshold wind speed (Fig 7).

Threshold wind (Table 3) are far below the average wind speed observed in the field study at all heights (Table 2), but this may be an artifact of the inability to downregulate the fan's speed sufficiently in this experimental setup. Maximum field wind speeds fall within the range of seed detachment thresholds but in all height categories except the range of the tallest Phragmites, some thresholds were not met by measured field wind conditions (Table 2). The peak minute-long average wind speed recorded by the weather station was well above threshold values (7.51 m/s).

Table 3. Three groups of seed-releasing spadices may be observed: Dark gray shading indicates samples (n=2) that readily released many seeds (300+) at very low threshold wind speeds and had low tension. Middle gray indicates sample (n=1) that released

Average Tension (N)	Threshold wind speed (m/s)	# seeds caught in tape	many seeds (127) at a low threshold wind speed
0.67	3.04	338	and had middling tension.
0.27	3.04	364	Light gray indicates the
2.15	3.24	6	largest group (n=15),
1.17	3.58	127	whose member spadices
0.65	3.58	8	released fewer than 15
0.47	3.73	2	seeds each across a
0.42	3.8	4	spectrum of wind speeds.
0.38	3.84	12	The majority of spadices
0.97	3.86	2	did not readily release
1.07	4.57	6	seeds at the wind speeds
0.32	5.29	5	they were subject to in
1.38	5.84	3	this study.
1.22	5.84	14	
0.28	6.19	4	
0.45	6.49	6	
0.48	6.49	3	

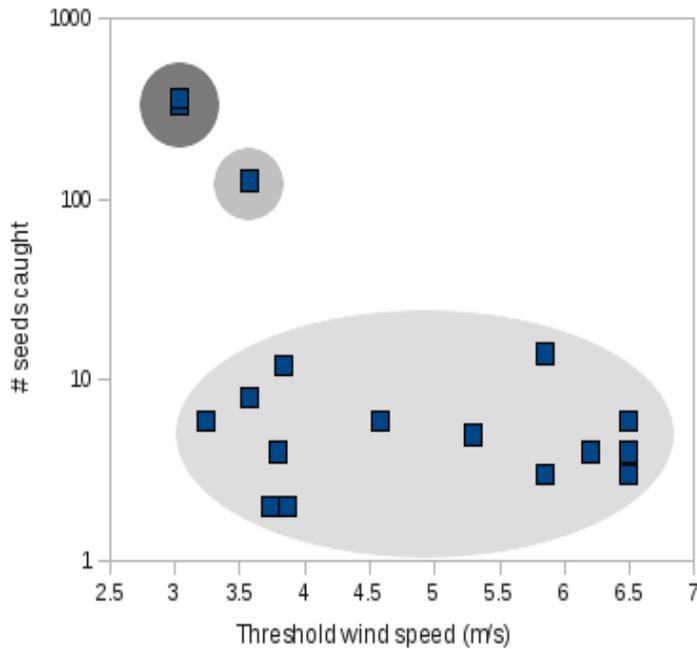


Figure 5. Scatterplot of relationship between threshold wind speed and the number of seeds caught in sticky seed trap downwind. While regressions show no significant correlation between the threshold wind speed and number of seeds caught, three distinct groups are notable. Dark gray shading indicates samples (n=2) that released many seeds (300+) at very low wind speeds. Middle gray indicates sample (n=1) that released many seeds (127) at low wind speed. Light gray indicates the largest group (n=15), whose member spadices released fewer than 15 seeds each across a variety of wind speeds. Note logarithmic scale on the Y-axis.

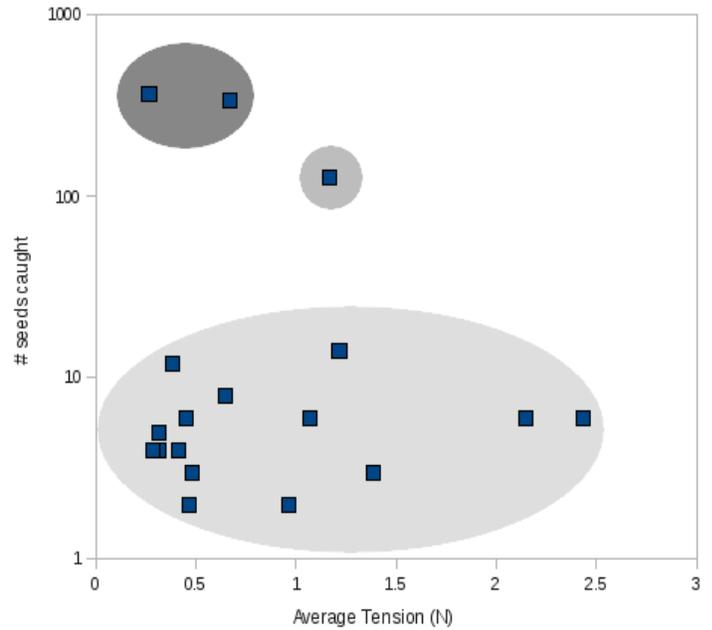


Figure 6. Scatterplot of relationship between average tension required to remove a 15 x 2 mm strip of *Typha* achenes by hand (n=3) and the number of seeds caught in sticky seed trap downwind. While regressions show no significant correlation between average tension and number of seeds caught, three distinct groups are notable. Dark gray shading indicates samples (n=2) that released many seeds (300+) and had low tension. Middle gray indicates sample (n=1) that released many seeds (127) and had middling tension. Light gray indicates the largest group (n=15), whose member spadices released fewer than 15 seeds each. Note logarithmic scale on the Y-axis.

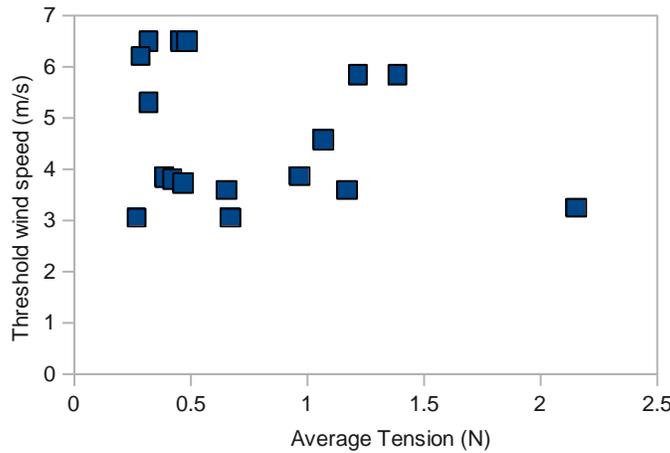


Figure 7. Scatterplot of relationship between average tension required to remove a 15 x 2 mm strip of *Typha* achenes by hand (n=3) and threshold wind speed for release of the first achene. Removal of the possible outlying data point at tension=2.2N does not change the lack of significance of linear regressions (all $R^2 < 0.04$).

Discussion

The finding at maximum plant height and at 0.5 m above plant height wind speeds greater than those well above the wetland as measured by the weather station was initially troubling but may be explained by discrepancies in methods of data collection. Specifically, wind speed among the plants at each height category was measured instantaneously, while the weather station recorded average wind speeds every minute. Thus, measurements at various heights were susceptible to the influence of gusts of wind, while the weather station only recorded sustained breezes; strong blasts would tend to be evened out over the course of 60 seconds. However, the maximum one-minute average wind speed recorded for a one-month period was 5.17 m/s at 1100h, indicating that wind velocity at the Villanova stormwater wetland site does at least occasionally reach high levels for sustained bursts around the hours of day relevant to this study. Future studies should perhaps employ a digital anemometer for simultaneous wind speed measurements to prevent similar occurrences of this misalignment of data types.

Because wind speed directionality was not recorded, it is difficult to discern whether reduced wind speeds at lower heights above the wetland floor are due to blocking by *Phragmites*, *Typha*, or simply the presence of any physical resistance to air flow at all. Comparing site C to other sites showed that despite significantly shorter *Typha* overall similar levels of wind blockage occur at low heights. This is evidence in favor of the argument that *Phragmites* are blocking the significant portion of the wind, but more controlled replicate studies are need to know with any surety.

It can be stated that while *Typha* does not on average grow to height beyond where wind speed is significantly reduced, wind speed levels in this zone is not

consistently below threshold values for seed release as measured in the experimental portion of this study and as such the impact of reduced wind speed on the ability of *Typha* to get seeds airborne may be minimal. However, the terminal velocity of the seeds is very low, allowing seeds to travel long distances in weak, turbulent thermal updrafts (Soons, 2006).

Visually, *Typha* are seen to shift from a tight, compact spadix structure to a light, fluffy, or airy texture that corresponds with mass seed abscission. This mechanism is key to cattail migration and understanding the stimuli that trigger the change to senescence and seed release will inform efforts to curb invasions. Although the sample size of spadices that released seeds was low and, statistically, tension does not appear to be a reliable method of measuring the wind speed at which a spadix will begin to release seeds to the wind or the number of seeds that will be released, I was able to classify three differing degrees of spadix readiness to undergo at least partial seed abscission (the color groups in figures 5 and 6 and in table 3) based number of seeds released and seed release threshold wind speeds. However, a single spadix contains tens of thousands of seeds and no sample released even a modest fraction of this overall amount when subjected to wind in this study.

A likely explanation for the lack relationship between tension and threshold wind speed and the staggered grouping of seed release readiness is the existence of an additional, intervening mechanism at the interface between the two. Thigmotropic responses are a likely example. Plants are known to react to physical pressure, including from wind. Responses include cell differentiation, regulation of chemical pathways, localized growth both toward and away from stimuli, the deployment of defensive stinging cells and the physical projection of seeds for dispersal (Jaffe, et al., 2002).

In the case of seed abscission, physical pressure may come directly through contact when spadices impact one another as they sway in the wind, knocking open the tightly-packed seed head. This may explain the low variation in *Typha* height when compared to *Phragmites*; differences in fruiting body structure (club-like spadix versus feathery plume) may mean that seeds have different likelihoods of being knocked off the plant due to physical contact and therefor may benefit more or less from growing more densely along the vertical gradient.

There is also evidence for indirect thigmotropic control of seed abscission. Recently, a theoretical modeling framework illustrates that non-random abscission of seeds can greatly impact the likelihood of long distance seed dispersal by altering the shape of the curve of seed shadows which model seed release and dispersal distance (Schippers and Jongejans, 2005; Soons and Bullock, 2008) . Related wind tunnel and seed trapping experiments with heath plants suggest plants selectively release seeds during strong gusts of wind, principally at the

beginning of the gust and during turbulent air flow (Soons and Bullock, 2008) .

Typha seeds are small and lightweight and have great potential to disperse over many kilometers once airborne (Soons, 2006). Though the act of seed abscission is small-scale, because established wetland communities act as seed sources for an expanding front of dispersal, the dynamics of wind speed within the structure of existing plant communities therefor bear heavily on implications for patterns of invasion across the landscape.

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References

- Belzile, F., J. Labbe, M. LeBlanc, and C. Lavoie . 2009. Seeds contribute strongly to the spread of the invasive genotype of the common reed (*Phragmites australis*) . *Biol Invasions* . 12: online edition.
- Brix, H. 1994. Functions of Macrophytes in constructed wetlands. *Water Science Technology* 29: 71-78.
- Derr, J.R. 2008 . Common Reed (*Phragmites australis*) Response to Postemergence Herbicides. *Invasive Plant Sci & Management* 1:153-157.
- Farnsworth, E.J. and L.A. Meyerson. 2003. Comparative ecophysiology of four wetland plant species along a continuum of invasiveness. *Wetlands* 23: 750–762.
- Matlack, G. R. 1987. Diaspore Size, Shape, and Fall Behavior in Wind-Dispersed Plant Species. *American Journal of Botany* 74 **8** :1150-1160.
- Mitich, L.M. 2000. Common Cattail, *Typha latifolia* L. *Weed Technology* 14: 446-

450.

Mordecai J. Jaffe, M.J., A.C. Leopold, and R.C. Staples. 2002. Thigmo responses in plants and fungi. *Amer J Botany*. 89:375-382.

Schippers, P. and E. Jongejans. 2005. Release thresholds strongly determine the range of seed dispersal by wind. *Ecological Modelling*. 185: 93-103.

Soons, M.B. 2006. Wind dispersal in freshwater wetlands: knowledge for conservation and restoration. *Appl Veg Sci* 9: 271-278.

Soons, M.B. and J.M. Bullock. 2008. Non-random seed abscission, long-distance wind dispersal and plant migration rates . *J Eco*. 96: 581-590.