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# Seed-Dispersal Ability of the Invasive Perennial Vines *Vincetoxicum nigrum* and *Vincetoxicum rossicum*

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## Abstract

Black swallowwort [*Vincetoxicum nigrum* (L.) Moench] and pale swallowwort [*Vincetoxicum rossicum* (Kleopow) Barb.] are perennial vines of European origin that invade natural areas and perennial cropping systems in the northeastern United States and southeastern Canada. Both species reproduce via wind-dispersed seeds in the form of achenes with comas, but little is known about the extent of dispersal of these seeds. We studied the relationship of seed release height (0.75 m, 2 m), wind speed at the time of release, seed mass, and settling rate on distance traveled. *Vincetoxicum nigrum* and *V. rossicum* seeds traveled up to 72.1 and 79.6 m, respectively. Seeds of both species released from 2 m traveled greater distances than seeds released from 0.75 m, which fell within 20 m of the release point. Release height was the most important factor influencing long-distance dispersal events. Wind speed also strongly interacted with release height for long-distance dispersal of *V. nigrum*. *Vincetoxicum nigrum* seed mass was greater and settling rates faster than for *V. rossicum*. Increasing seed mass generally increased settling rate, which in turn decreased distance traveled, except in *V. rossicum*, for which longer distance–dispersing seeds had a faster settling rate. Our findings suggest that management efforts focus on reducing the presence of these two vines, especially if there is potential for them to climb up taller vegetation such as trees. Seeds released from these greater heights are more likely to travel far from source populations and initiate new populations. Preventing seed production in small, nonclimbing patches will also help suppress the expansion of these two vines, as seeds can still disperse up to 20 m away from parent plants.

## Introduction

Seed dispersal is a critical process for the spread and survival of plant populations (Janzen 1970; Nathan and Muller-Landau 2000; Nathan et al. 2008; Thomson et al. 2017). Fenner and Thompson (2005) highlighted four advantages of seed dispersal in plants: (1) avoidance of specialist predators or pathogens of the parent plant, (2) mitigating the risk that seeds might face in highly heterogeneous or rapidly changing environments or landscapes, (3) minimizing competition with the parents or siblings, and (4) finding “safe sites” for successful germination and seedling establishment. Platt and Weis (1977) suggested that the likelihood of a plant species arriving in a new site depended on the number of dispersing propagules, the dispersal capacity of the propagules, and the distribution of the source plants. Species whose propagules include dispersal structures that facilitate long-distance dispersal by wind (e.g., comas, wings) are able to colonize novel environments even if most seeds often disperse close to the parent plant (Bullock and Clarke 2000; McEvoy and Cox 1987; Neubert and Caswell 2000; Sheldon and Burrows 1973). For instance, Platt and Weis (1977) observed that in a guild of fugitive plant species colonizing badger (*Taxidea taxus* Schreber) mounds in an Iowa prairie, prairie dogbane (*Apocynum sibiricum* Jacq.) and common milkweed (*Asclepias syriaca* L.), which possess comose seeds, were most widespread on the site and had the greatest chance of reaching new mounds and preempting resources relative to species whose seeds had lower dispersal capabilities (e.g., hairy four o'clock, *Mirabilis hirsuta* (Pursh) McMill.; hoary vervain, *Verbena stricta* Vent.).

The distance traveled by seeds with special appendages such as a coma or plumes is in part affected by plant growth form, seed mass, the vertical height at which seeds are released, terminal velocity, and wind direction and speed at the time of seed release (Matlack 1987; Savage et al. 2014; Tammé et al. 2014; Thomson et al. 2011). The rate of propagule descent

### Management Implications

Black swallowwort [*Vincetoxicum nigrum* (L.) Moench] and pale swallowwort [*Vincetoxicum rossicum* (Kleopow) Barb.] are perennial, invasive vines of European origin in the dogbane (formerly milkweed) family. Both species are increasing in abundance in the northeastern United States and southeastern Canada. Prevention of spread is an important control strategy, especially because suppressing existing stands has proved difficult, labor-intensive, and sometimes ineffective. Information about the effects of wind speed, the height of seed release from the mother plant, and various seed-related characteristics can help inform prevention efforts. In our field and laboratory trials, we found that the release height of seeds and wind speed significantly affected dispersal distance in both *Vincetoxicum* species. Seeds of both species released from 2 m traveled greater distances than seeds released from 0.75 m, which fell within 20 m of the release point. The latter seeds would likely be responsible for consolidating already infested areas and expanding the invasion front. *Vincetoxicum nigrum* and *V. rossicum* seeds traveled up to 72 m and 79 m, respectively. These seeds are the most likely to colonize new areas and expand an infestation. To most effectively prevent spread to new areas and habitats, land managers should focus management efforts on plants growing farthest from the ground and where strong wind speeds are common, such as plants growing on the sides of gullies or twining up into trees. While these areas may be difficult to access, even one clipping of these plants before seed set would likely result in substantial reductions in the long-distance dispersal of seeds. Regular monitoring of these areas will be important so that any new populations are detected early enough to manage them effectively. Certainly, given that the vast majority of seeds in our study traveled no more than 20 m from the release point, management efforts should also focus on reducing seed production in established populations.

(i.e., terminal velocity) has often been related to the weight of the propagule and its size; this ratio has been referred to as plume or wing loading (Matlack 1987). Generally, the lower this ratio, the greater the likelihood that propagules will be transported greater distances at a given wind speed than propagules with relatively higher plume-loading ratios (Augsburger 1986; Green 1980; Matlack 1987). The distance traveled is related to terminal velocity or settling rate, because propagules falling slowly are more likely to be exposed to horizontal winds and carried farther from source plants (Matlack 1987). Platt and Weis (1977) found that propagules of *A. syriaca* (terminal velocity = 24.9 cm s<sup>-1</sup>) traveled an average of 13.8 m from source plants in an Iowa prairie at wind speeds of 10 to 15 km h<sup>-1</sup>, whereas propagules of *A. sibiricum* (terminal velocity = 9.9 cm s<sup>-1</sup>) traveled an average of 25.7 m from source plants at the same wind speeds. Matlack (1987) estimated that *A. syriaca* propagules (terminal velocity = 27 cm s<sup>-1</sup>) could travel 18 m from source plants 2-m tall at wind speeds of 10 km h<sup>-1</sup>, whereas hemp dogbane (*Apocynum cannabinum* L.) propagules (terminal velocity = 15 cm s<sup>-1</sup>) could travel 83.3 m at similar wind speeds. Sheldon and Burrows (1973) suggested that the efficiency of propagule wind dispersal was determined to a greater extent by the fine details of plume or pappus geometry than by the ratio of the propagule weight to plume diameter or area. Regardless of the effect of plume geometry, plant species whose propagules have structures facilitating wind dispersal will

likely be able to attain more distant sites and colonize new areas than species whose propagules lack such structures.

Wind-dispersed seeds released from taller plants are likely to travel farther than similar seeds released from shorter plants at the same wind speeds (Marchetto et al. 2010b; Sheldon and Burrows 1973; Soons et al. 2004; Tackenberg et al. 2003a; Thomson et al. 2017; Travis et al. 2010). Herbaceous vines can overcome their lack of support structures and thus attain greater heights and growth by climbing up taller adjacent vegetation such as trees or other inanimate structures (Gianoli 2015). This growth strategy not only allows herbaceous vines to escape competition but also allows their wind-dispersed propagules to travel much greater distances than would otherwise be the case if no tall nearby vegetation or other structures were present. Such a strategy may be especially important for vines that are able to colonize ecotone areas between forest and more open environments such as old fields or pastures. Thus it is not surprising that 55 vines are listed as the world's worst invasive species (Global Invasive Species Database 2013). Of these vines, 29% were introduced into North America from Asia, while only 2% are native to Europe (Sundarapandian et al. 2015). Of the top 10 worst invasive vines listed by Sundarapandian et al. (2015) and occurring in the northeastern United States, only pale swallowwort [*Vincetoxicum rossicum* (Kleopow) Barb.] reproduces primarily by wind-dispersed seeds. Several of the other invasive species listed are woody perennial vines whose propagules are dispersed largely by birds and/or water [e.g., oriental bittersweet, *Celastrus orbiculatus* Thunb.; wintercreeper, *Euonymus fortunei* (Turcz.) Hand.-Mazz.]. All of these vines are aggressive growers and seed producers that can outcompete and displace native flora in invaded areas. Conceivably, all plant species, including herbaceous perennial vines such as *V. rossicum* that are highly dependent on sexual reproduction for range expansion, may benefit from having seeds adapted for long-distance wind dispersal, as this may increase the likelihood of reaching suitable and novel microenvironments (Cohen 1966; Salisbury 1942).

Pale swallowwort [*Vincetoxicum rossicum* (Kleopow) Barb. = *Cynanchum rossicum* (Kleopow) Borhidi] and black swallowwort [*Vincetoxicum nigrum* (L.) Moench. = *Cynanchum louiseae* Kartesz & Gandhi] are herbaceous, perennial invasive vines in the Apocynaceae (dogbane and milkweed) family. Both species are self-compatible and either insect pollinated or self-pollinated (Lumer and Yost 1995; St Denis and Cappuccino 2004). Introduced to the United States from Europe in the 1800s, these species have become increasingly problematic in the eastern United States and Canada (DiTommaso et al. 2005b; Sheely and Raynal 1996). Both *Vincetoxicum* species form dense stands and can dominate plant communities. In addition, *V. rossicum* has been reported as a problem in some perennial cropping systems such as Christmas tree farms, pastures, and no-till cropping systems (DiTommaso et al. 2005b). Both species are capable of establishing in soils of varying pH and texture (Magidow et al. 2013; Sanderson et al. 2015), and *V. rossicum* can readily germinate and establish across a range of temperatures (Sanderson and Antunes 2013).

Management of these *Vincetoxicum* species is difficult once populations have become established. Pulling or clipping of plants is often ineffective, and successful reduction of *Vincetoxicum* biomass usually requires repeated tissue removal or chemical control (Averill et al. 2008; DiTommaso et al. 2013; Milbrath et al. 2016). However, the use of herbicides may be undesirable, especially in natural areas, which are most often invaded. Cutting or mowing plants before seeds mature may reduce the number of seeds dispersed. However,

not all invaded sites are easily accessible or suitable for cutting or mowing operations. Thus, significant research efforts have been made to find effective biological control candidates, with several European insects showing some promise (Milbrath and Biazzo 2016; Weed et al. 2011).

*Vincetoxicum nigrum* and *V. rossicum* reproduce primarily via the production of high quantities of achenes (up to 32,000 m<sup>-2</sup>) that have comas to facilitate wind dispersal (Cappuccino et al. 2002; DiTommaso et al. 2005a, 2005b; Smith et al. 2006). If anecdotal reports of propagules attaching to the fur of white-tailed deer (*Odocoileus virginianus* Zimmerman) are confirmed, this may also aid dispersal. Plants also produce tillers from root crown buds, which allows for localized, short-distance expansion of populations (Averill et al. 2011). Seeds of both *Vincetoxicum* species may be polyembryonic, although this feature is more prevalent in *V. rossicum* (Cappuccino et al. 2002; St Denis and Cappuccino 2004; Smith et al. 2006) despite seeds of *V. nigrum* being generally heavier than those of *V. rossicum* (DiTommaso et al. 2005b). While several studies have characterized *Vincetoxicum* seed dispersal, these have focused largely on the relationship between dispersal distance and seed size and the ability of these seeds to successfully establish (Cappuccino et al. 2002; Ladd and Cappuccino 2005). Clearly, the establishment requirements of a plant species will define which sites are suitable and their availability across the landscape will determine the importance of dispersal ability (Janzen 1970; Platt and Weis 1977). However, seed-dispersal distance is also influenced by height of seed release and horizontal wind speed (Dauer et al. 2006; Greene and Johnson 1989; Tamme et al. 2014; Van Dorp et al. 1996). Given the wide range of habitats in which these two *Vincetoxicum* species occur (e.g., old fields, pastures, ecotones, forest understories), height of seed release and wind speed in addition to other seed traits (i.e., seed mass, settling rate) may be important in determining seed-dispersal distance and overall ability to spread to new environments.

The objective of this study was to determine the importance of seed release height, wind speed, seed mass, and settling rate (i.e., the rate of vertical fall in an undisturbed column of air) on the distance traveled by seeds of these two *Vincetoxicum* species. We hypothesized that increasing wind speed and greater release height will result in increased distance traveled by propagules and that greater plume loading (ratio of seed mass to coma diameter) will increase settling rate, which in turn will reduce the distance traveled. Seeds with slower settling rates are predicted to travel farthest because of increased time for horizontal wind to disperse them. Given that seed mass is generally greater for *V. nigrum* seeds relative to *V. rossicum* seeds and assuming that coma diameter is similar in these two congeners, we predicted that propagules of *V. rossicum* would, on average, travel greater distances than propagules of *V. nigrum*, suggesting that range expansion in *V. rossicum* may be of greater concern. Ultimately, the long-term objective of this research was to accurately determine dispersal distances for propagules of these two invasive vines. In turn, this would allow identification of habitats or regions that may be potentially reached and colonized by these species so that proactive management strategies could be implemented as early as possible.

## Materials and Methods

### Experimental Design

*Vincetoxicum nigrum* seeds were collected from Iona Island in Bear Mountain State Park, Rockland County, NY (41.30°N, 73.98°W)

**Table 1.** Number of seeds released by species per date at each study site.

Site	Date of release	<i>Vincetoxicum nigrum</i>	<i>Vincetoxicum rossicum</i>	All
Game Farm	November 6, 2013	16	18	34
	November 19, 2013	14	9	23
	October 13, 2015	12	12	24
	October 26, 2015	11	6	17
Musgrave Research Farm	November 14, 2013	30	31	61
	November 21, 2013	68	65	133
	October 26, 2015		5	5
	All	151	146	297

in August 2013 and 2015 and *V. rossicum* seeds from the Edwards Lake Cliffs Preserve in Ithaca, NY (42.52°N, 76.52°W) in September 2013 and 2015. Mature follicles (those open and dehiscing seeds or appearing partially dried and soon to open) were collected from a number of different plants, placed in paper bags, and allowed to dry at room temperature for several days. Undamaged seeds were then collected from the dried, open follicles. Seed-dispersal data were collected in two open environments near Ithaca, NY. Seeds of both species were released at both sites on multiple days during autumn 2013 and 2015 to maximize the range of wind speeds occurring during dispersal events (Table 1). Because wind speeds were directly measured, testing for differences between sites or days was not done.

### Seed-Dispersal Distance

A seed-release apparatus was constructed by mounting a wooden clothespin to the top of a PVC pipe of length 0.75 or 2 m, which was then placed vertically over rebar driven into the ground so that the bottom of the pipe rested at ground level. A seed was placed individually in the clothespin, held by the smallest possible section of coma to avoid any damage. A string attached to the clothespin allowed a researcher to crouch down and pull to release the seed from a release height of 0.75 m or 2 m while minimizing wind disturbance near the seed. Seeds were followed until they came to rest, the location marked, and the distance traveled from the release point measured. Wind speed data were collected at the time of each release with a handheld anemometer (Kestrel 2000 Wind Meter, Nielsen-Kellerman, Boothwyn, PA 19061) at approximately 1-m height. A wind-profile power law relating wind speed at one height to wind speed at a second height suggests that wind speed increases less than 1 m s<sup>-1</sup> between 0.75 and 2 m (Justus and Mikhail 1976). Those seeds with intact comas following the dispersal study were collected for use in a subsequent laboratory study to assess their settling velocity (see "Settling Rate" section). In total, 151 *V. nigrum* seeds were released (Table 1), 65 at 0.75-m release height and 86 at 2 m. A total of 146 *V. rossicum* seeds were released (Table 1), 61 at 0.75 m and 85 at 2 m.

### Settling Rate

Settling velocities of all recovered seeds with intact comas were measured following the protocol described by Andersen (1992).

Individual seed–coma units were dropped down a 1.22-m clear plastic tube with 8-cm diameter. Static Guard (Static Guard, B & G Foods, Parsippany, NJ 07054) spray was applied to the inside of the tube to prevent the seeds from clinging to the tube due to static electricity. Air movement inside the tube was presumed to be minimal. Three replicate measurements of falling time were obtained for each seed. Falling time in seconds was converted to mean settling velocities in meters per second. Seeds were then weighed, excluding the coma. The mass of seeds used in the dispersal study that had lost their comas was also determined. Settling-rate data were collected for 89 *V. nigrum* seeds (those retaining intact comas following the dispersal study), 43 from the 0.75-m treatment and 46 from the 2-m treatment. Settling-rate data were collected for 100 *V. rossicum* seeds, 35 from the 0.75-m treatment and 65 from the 2-m treatment. Although, at the time of the seed-dispersal distance and settling-rate studies, we did not measure the diameter (cm) of the coma for each seed, we were able to measure the diameter (cm) of fully expanded comas for 30 randomly selected *V. nigrum* seeds and 30 *V. rossicum* seeds from these same populations that had been carefully stored in open, paper bags at room temperature for 24 mo. Because most of the comas had detached from seeds during this storage period, we were unable to measure coma diameter and the weight of its corresponding seed. Thus, we calculated the plume-loading ratio for each of the species by comparing the average seed weight of the 30 seeds to the average diameter of the 30 comas. Marchetto et al. (2010a) reported that storing musk thistle (*Carduus nutans* L.) capitula in open paper bags for as long as 5 yr did not affect several seed traits (e.g., pappus damage, seed mass) or parameters measured, including terminal velocity. Thus, despite the low number of samples used and possible influence of this extended storage on coma structure, these data allowed us to determine whether there were any broad differences in the plume loading between the two species that could help explain dispersal-distance differences between them.

**Statistical Analyses**

All analyses were completed using R software (R Core Team 2015). Graphs were plotted with ‘ggplot2’ (Wickham 2009). Kernel density curves of seed dispersal were plotted for both species by release height. Various distributions were fit to the observed dispersal distances using the packages ‘SuppDists’ (Wheeler 2013), ‘MASS’ (Venables and Ripley 2013), and ‘fitdistrplus’ (Delignette-Muller and Dutang 2014). A lognormal distribution was found to have the best fit after the Akaike information and Bayesian information were compared (Supplementary Material S1). Data were log<sub>10</sub>-transformed, and a linear model was used to assess the effects of species, release height, wind speed, and all interaction terms on seed-dispersal distances. The linear model was subjected to an ANOVA with the ‘Car’ package (Fox and Weisberg 2011).

Quantile regressions were performed for both species separately to investigate the effect of wind speed and height on seed dispersal of each quantile (also called tau) of distance with the ‘quantreg’ package (Koenker 2013). In ecology, quantile regression has been proposed and used as a way to determine more useful predictive relationships between variables in cases in which there is no relationship or only a weak relationship between the means of such variables (Cade and Noon 2003). For example, mean seed dispersal, that is, the 0.50 quantile, is less relevant to the aim of this study than the 5% of seeds that dispersed the farthest, that is, the 0.95 quantile. Quantile regressions were

implemented for tau from 0.05 to 0.95, by 0.05 increments, as distance = height + wind speed.

Differences in settling rates and seed mass by species were tested by *t*-tests. The relationships between seed mass and settling rates were depicted with smooth lines and a 95% confidence interval with ‘ggplot2’ for three categories of seed-dispersal distances: short, the 25% lowest values (1st quartile); long, 25% highest values (4th quartile); and mid, intermediate distances from 2nd to 3rd quartile.

Interactions between wind speed, representing horizontal movement, and settling rates, representing vertical wind-free movement, were investigated for their effects on seed-dispersal distance for both species with contour plots based on the linear model log<sub>10</sub>(distance) = settling rate + wind speed + settling rate × wind speed. Contour plots were generated with the contour function of the ‘rsm’ package (Lenth 2009).

**Results and Discussion**

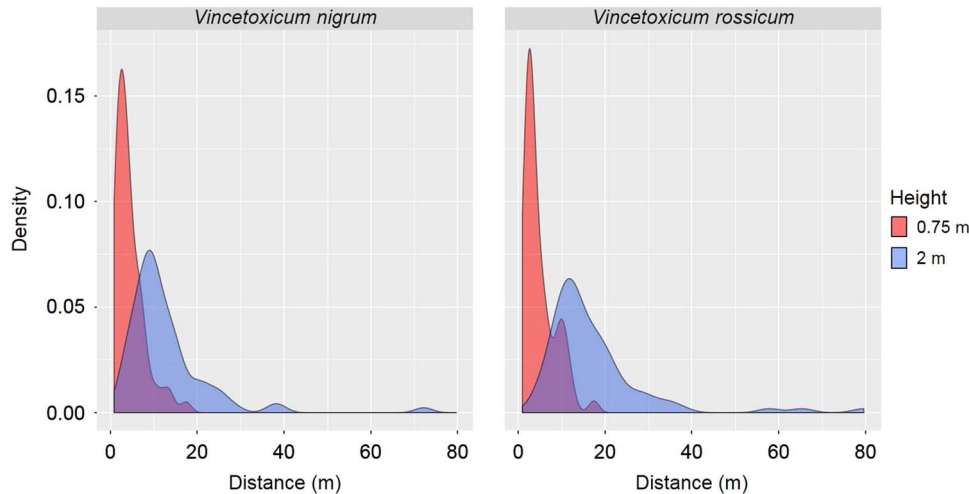
**Seed-Dispersal Distance**

**Main Explanatory Factors**

Species, release height, wind speed, and the interaction between release height and wind speed had a significant effect on dispersal distances (Table 2). Overall, *V. nigrum* seeds landed closer to the release point than *V. rossicum* seeds, and seeds of both species released from 0.75 m were more likely to land closer to the release point (*V. nigrum*: 4.4 ± 3.3 m, *V. rossicum*: 4.7 ± 3.5 m; reported as mean ± standard deviation) than seeds released from a 2-m height (*V. nigrum*: 12.6 ± 9.6 m, *V. rossicum*: 17.1 ± 12.1 m; Figure 1). The probability of a seed released from 0.75 m falling within 20 m of the mother plant was 100%, whereas 80.7% of seeds released from 2 m would do the same (Figure 1). Long-distance dispersal events (>20 m) only occurred for seeds released from 2 m (Figure 1)—the maximum distance measured in this study was 72.1 m for *V. nigrum* and 79.6 m for *V. rossicum*. These findings are comparable to results from an experiment using *A. syriaca*, the closest relative for which data are available, in which seeds traveled farther when released from higher points (Morse and Schmitt 1985), and with the general trend that seeds produced by tall plants disperse greater distances than seeds from short plants (Thomson et al. 2017). Matlack (1987) estimated that propagules of *A. syriaca* and *A. cannabinum* released from a height of 2 m could travel 18.1 and 83.3 m, respectively when subjected to winds of 10 km h<sup>-1</sup>. Platt and Weis (1977) measured the distance traveled by 200 propagules each of

**Table 2.** Effects of species (*Vincetoxicum nigrum* and *Vincetoxicum rossicum*), seed release height (0.75 m and 2 m), and wind speed (km h<sup>-1</sup>) on the seed dispersal (distance in m, log<sub>10</sub>-transformed) assessed by linear model.

Factor	X <sup>2</sup>	df	F	P
Species	0.560	1	8.38	0.004
Height	16.750	1	247.63	<0.001
Wind speed	1.920	1	28.49	<0.001
Species × height	0.150	1	2.28	0.13
Species × wind speed	0.003	1	0.05	0.81
Height × wind speed	0.460	1	6.85	0.009
Species × height × wind speed	0.200	1	2.98	0.08



**Figure 1.** Kernel density curves of the seed dispersal of *Vincetoxicum nigrum* and *Vincetoxicum rossicum* according to release height (0.75 m or 2 m). The area under the curve of a density function represents the probability of finding a seed dropped from a particular height at a particular distance from the mother plant.

*A. syriaca* and *A. sibiricum* in a Iowa prairie at wind speeds of 10 to 15 km h<sup>-1</sup> and reported mean distances traveled of 13.8 and 25.7 m, respectively. These workers did not specify the height from which propagules were released, except to state that they released seeds at the height they occurred on parent plants. However, *A. syriaca* plants can attain heights of 0.6 to 1.5 m (Bhowmik and Bandeen 1976) and *A. sibiricum* plants can grow as tall as 1.2 m, but are often 0.6- to 0.9-m tall (Minnesota Wildflowers 2018).

While all the 297 seeds tracked in this study were followed until they came to rest, several seeds released from the 2-m height in preliminary trials were lost. These seeds either traveled faster than researchers could track them or were carried high enough that they were lost from sight, usually at distances greater than 100 m from the release point. Cappuccino et al. (2002) also reported losing sight of a *V. rossicum* seed released from a height of 1.5 m. Thus, for both species, rare events of very long-distance dispersal can occur under windy conditions, especially when seeds are released from heights of 1.5 m or greater.

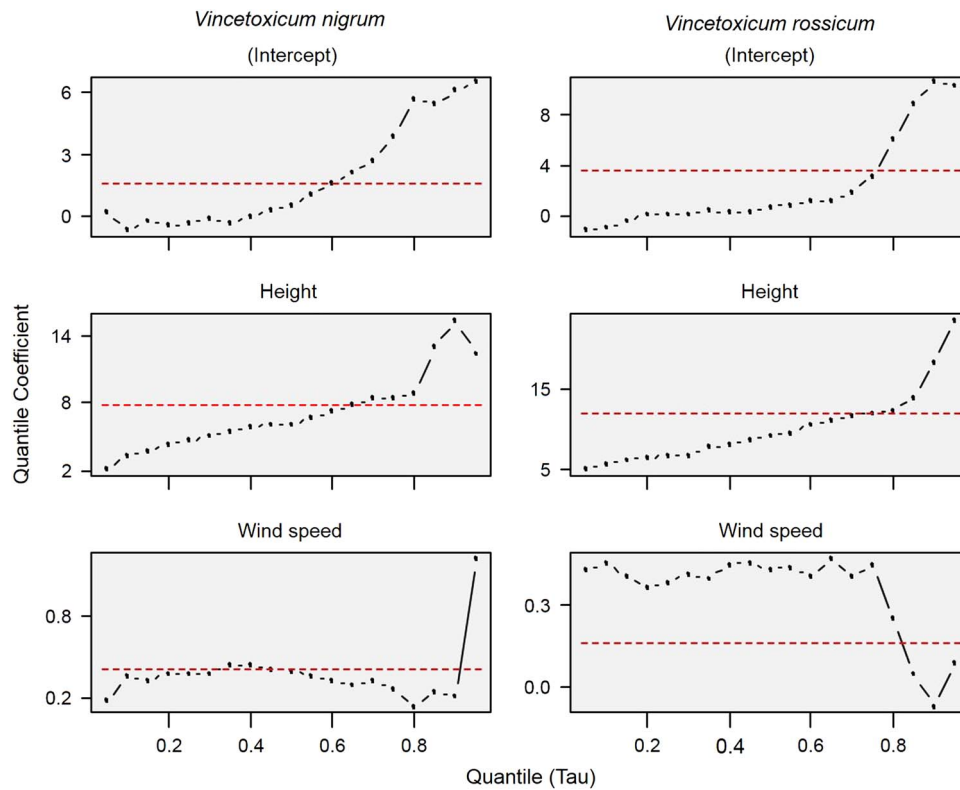
#### Wind Speed versus Release Height for Short and Long Dispersal Distance

Because of the highly significant interaction between wind speed and release height (Table 2), quantile regressions were used to explore these two factors. Quantile coefficients estimated by quantile regression (Figure 2) show that release height was only important in explaining dispersal distances for both *V. nigrum* and *V. rossicum* for quantiles above 0.80; that is, release height was highly influential in promoting long-distance dispersal of *Vincetoxicum* seeds. Wind speed had little effect on dispersal of *V. nigrum* seeds until the 0.95 quantile (the longest distances recorded), where wind speed became highly predictive of dispersal distances. In contrast, wind speed was useful for predicting *V. rossicum* dispersal distances for the lower 85% of distances measured in our data set but was not predictive for the longest distances (Figure 2). Thus, for long-distance dispersal, both seed release height and wind speed were very important factors for *V. nigrum*, whereas only height appeared to matter for *V. rossicum*. A possible explanation for these findings is that for the generally heavier seeds of *V. nigrum* (see “Settling Rates and Relationship with Seed Traits” section), both higher seed release points and stronger winds

were required for long-distance dispersal, whereas for the lighter *V. rossicum* seeds, long-distance dispersal could be achieved as long as they were at sufficient height to perhaps be caught up in updrafts and be transported in the atmospheric boundary layer (Savage et al. 2014; Shields et al. 2006; Skarpaas et al. 2006). That height may be especially important for long-distance dispersal of *V. rossicum* seeds is also consistent with our finding that mean plume-loading ratio (i.e., seed weight:coma diameter) was greater for *V. nigrum* (2.6) than *V. rossicum* (1.8), thus possibly limiting long-distance dispersal of *V. nigrum* in the absence of strong winds even at relatively high propagule release heights (e.g., 2 m).

The effect of wind speed on seed-dispersal distances for each species and release height was further examined with quantile regressions by selected quantiles (Figure 3). At 0.75-m height, the effect of wind speed on seed dispersal was primarily positive for both species, but differed among quantiles. Dispersal distance of *V. nigrum* seeds increased weakly with increasing wind speed but sharply increased at the 0.95 quantile, promoting rare long-distance dispersal (Figure 3A). For *V. rossicum*, dispersal distance increased significantly with increasing wind speed beginning at short distances, but this relationship was not evident for quantiles greater than 0.90 (Figure 3B). Neither *V. rossicum* nor *V. nigrum* dispersal distance was much affected by wind speed at the 2-m height, except for a weak effect on *V. nigrum* at the 0.95 quantile (Figure 3C and D). Wind speed was therefore more influential for seed dispersal when seeds were released at lower heights (0.75 m).

The limitations of measuring wind in the field must be noted. Wind-speed measurements reflected the conditions at the moment of propagule release, but it was not possible to measure all forces exerted on any propagule for the duration of its dispersal. While higher wind speeds were generally found to positively affect dispersal distance, making it more likely that a propagule would travel horizontally while it fell to the ground, wind is rarely a direct and steady horizontal force. Modeling studies have found that updrafts are an important factor affecting dispersal distances in dandelion (*Taraxacum officinale* G. H. Weber ex Wiggers) (Tackenberg et al. 2003b) and that turbulence is an important factor in long-distance dispersal (Nathan et al. 2002; Savage et al. 2014; Soons et al. 2004). It is probable that updraft and turbulence sometimes influence *Vincetoxicum* seed dispersal, but this is difficult to quantify in the field, and



**Figure 2.** Quantile coefficients estimated by quantile regression (distance ~ height + wind speed) for each quantile (tau) of distance varying from 0.05 to 0.95. Red lines are the least-squares estimates. Dots are the value of the quantile coefficients (y-axis) for the particular tau value (x-axis).

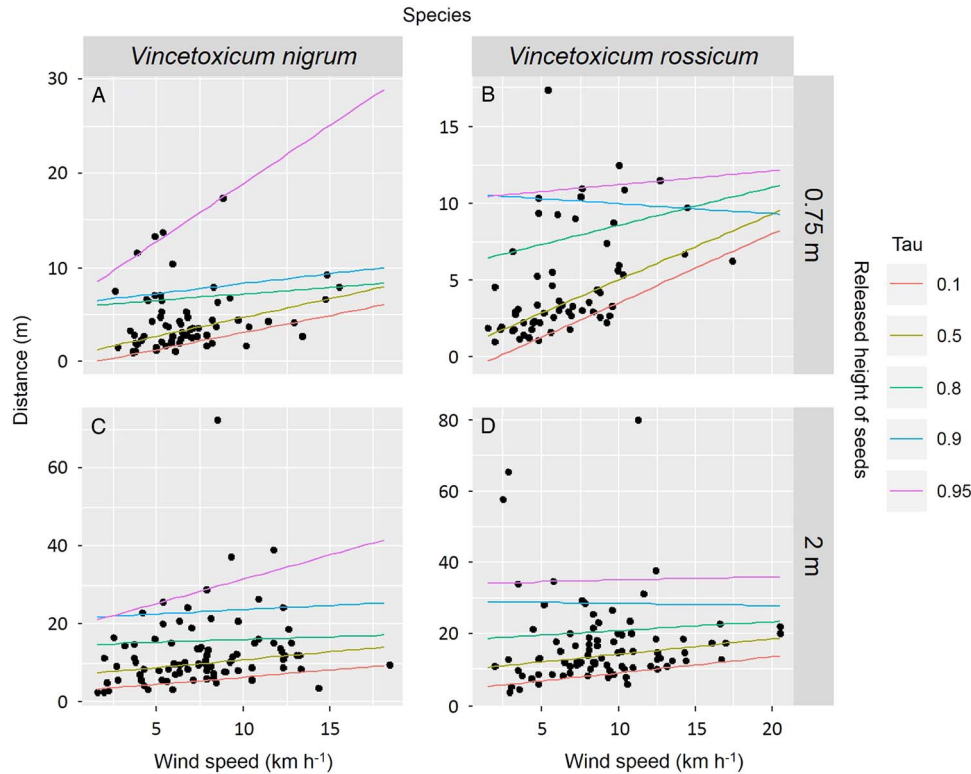
frequency of updraft events could vary according to the surrounding landscape. The few *Vincetoxicum* seeds previously mentioned that were lost in preliminary studies did appear to be caught by updrafts (CAS, personal observation).

### Settling Rates and Relationship with Seed Traits

Mean settling rate was  $0.59 \pm 0.23 \text{ m s}^{-1}$  for *V. nigrum* and  $0.43 \pm 0.11 \text{ m s}^{-1}$  for *V. rossicum*, a significant difference by species (Figure 4A). *Vincetoxicum nigrum* showed a higher range of settling rates (from 0.23 to  $1.43 \text{ m s}^{-1}$ ) compared with *V. rossicum* (from 0.19 to  $0.74 \text{ m s}^{-1}$ ; Figure 4A). The faster settling rates of *V. nigrum* likely resulted in less time for potential effects of horizontal wind to occur, producing the shorter dispersal distances discussed earlier. Seed mass was also significantly higher for *V. nigrum* ( $0.013 \pm 0.008 \text{ g seed}^{-1}$ ) compared with *V. rossicum* ( $0.008 \pm 0.004 \text{ g seed}^{-1}$ ; Figure 4B) as was plume-loading ratio, as discussed earlier. Linear regression indicated that settling rate (SR) increased with increasing seed mass (SM) for *V. rossicum* ( $\text{SR} = 42.3 \text{ SM} + 0.13$ ;  $P < 0.001$ ;  $R^2 = 0.44$ ) and *V. nigrum* ( $\text{SR} = 35.1 \text{ SM} + 0.14$ ;  $P < 0.001$ ;  $R^2 = 0.20$ ). This relationship is what would logically be expected, as heavier seeds would likely fall faster, assuming comas of similar diameter (i.e., increasing plume-loading ratios). However, a further division of seeds into long- (25% highest values), moderate- (middle 50% values), and short-dispersing (25% lowest values) seeds did not always show the same seed mass by settling-rate relationships (Figure 5). In *V. rossicum*, as expected, settling rate increased in all three seed-dispersal divisions as seed mass increased. Cappuccino et al. (2002) also predicted that heavier *V. rossicum* seeds would travel shorter distances from the source plants. In our

study, the settling rate did not vary with seed mass for *V. nigrum* seeds that dispersed short distances, whereas for seeds that dispersed long and middle distances, settling rates increased with increasing seed mass and then reached a plateau. Because both small and high-mass seeds fell near the release point, the plume area of the coma may be more variable in short-dispersing *V. nigrum* seeds (Greene and Johnson 1990). Although we did not correlate coma diameter of *V. nigrum* seeds to the distance traveled, coma diameter in this species was much more variable (4.0 to 5.8 cm; mean = 5.2 cm) in the 30 samples we measured compared with coma diameter for *V. rossicum* (4.3 to 4.7 cm; mean = 4.5 cm).

Regarding *V. rossicum*, two previous studies found that increasing seed mass resulted in shorter dispersal distances and greater germination and seedling survival (Cappuccino et al. 2002; Ladd and Cappuccino 2005), although the authors noted that the relationship between mass and distance was weak. Ladd and Cappuccino (2005) suggested that if smaller seeds do indeed have decreased germinability and survival, coupled with a higher probability of long-distance dispersal, then long-distance dispersal in *Vincetoxicum* may not contribute as much to population spread as expected. However, in a 2-yr field study at two locations in central New York State, Averill et al. (2010) found that in the better-drained site, seeds of *V. rossicum* were able to germinate and seedlings to successfully establish in plots subjected to a range of disturbances. Disturbance regimes ranged from intact resident vegetation (controls) to highly disturbed plots in which the resident vegetation was killed using an herbicide followed by a tillage operation. Although establishment rates in their study were relatively low ( $15\% \pm 1\%$ ), these data nonetheless suggest that seeds of *V. rossicum* that may be dispersed long distances are



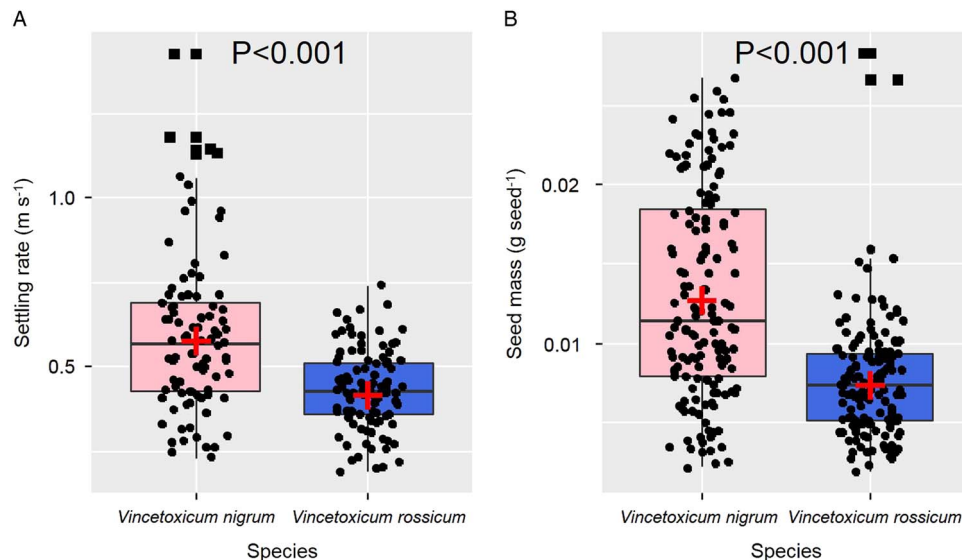
**Figure 3.** Quantile regressions for some selected quantiles (taus) predicting seed dispersal according to wind speed, by species (A and C, *Vincetoxicum nigrum*; B and D, *Vincetoxicum rossicum*) and release height. Dots are measured data. Lines are regression lines for each quantile (tau).

capable of germinating and establishing seedlings in a wide range of heterogeneous microenvironments.

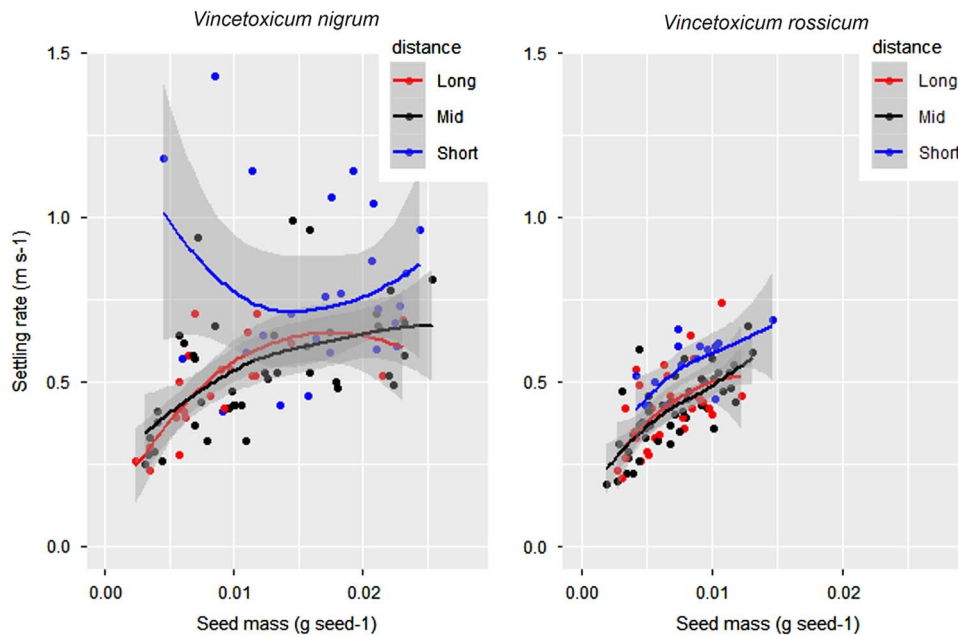
#### Trade-Off between Horizontal and Vertical Dispersal Speed

When seed-dispersal distances were estimated using a linear model including settling rate and wind speed, *V. nigrum* seeds were predicted to travel farthest when settling rate was low or wind speeds were high (Figure 6). In combination, lower vertical

seed speeds (settling rate) and higher horizontal wind speed led to high seed dispersal. However, seeds with settling rates less than  $0.3 \text{ m s}^{-1}$  were predicted to disperse more than 10 m regardless of wind speed, and at wind speeds greater than  $13 \text{ km h}^{-1}$ , predicted seed dispersal was 10 m or more regardless of the settling rate. *Vincetoxicum rossicum* showed similar trends, except when wind speeds were between 10 and  $15 \text{ km h}^{-1}$  and settling rates were lower than  $0.3 \text{ m s}^{-1}$  (Figure 6). Also, when wind speed exceeded  $15 \text{ km h}^{-1}$ , seeds of any settling rate were predicted to disperse



**Figure 4.** Settling rates (A) and seed mass (B) by species. Red crosses indicate averages. Black dots and squares are measured values; squares are values greater than  $1.5 \times$  the box height (outliers). *t*-Tests for significant differences between species (P-value).

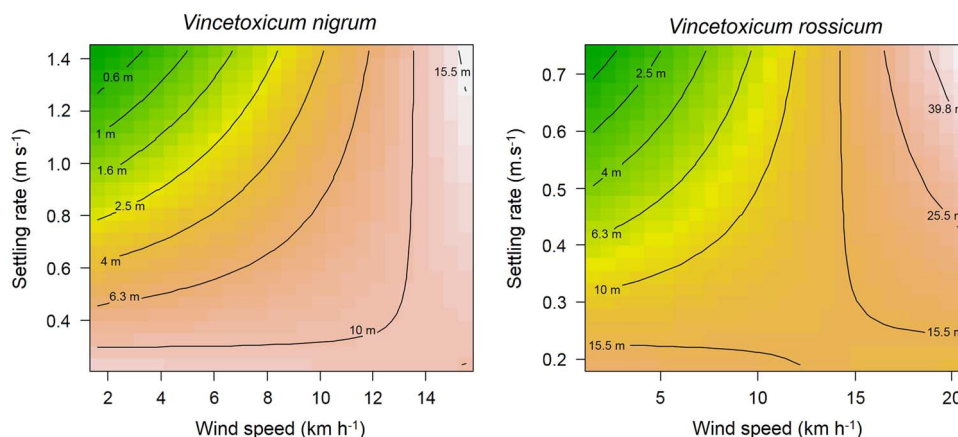


**Figure 5.** Relationship between seed mass and settling rate for seeds found at the shortest (Short: 25% lowest values, 1st quartile), longest (Long: 25% highest values, 4th quartile), and intermediate distances (Mid: from 1st to 4th quartile).

very far, particularly those with high settling rates (Figure 6). The response of *V. nigrum* is what would be expected: the slower a propagule falls, the more opportunity there is for wind to move the propagule horizontally before it comes to rest on the ground. The response of *V. rossicum* was also largely what was expected, except for the increased distance traveled at high wind speeds and high settling rate. It may be that these propagules have smaller coma diameters, which we did not measure, resulting in a higher plume-loading ratio and hence settling rate (Greene and Johnson 1990). Further experiments could examine the relationship of coma size or plume area and distance traveled, coupled with the other variables included here.

Long-distance dispersal events of any plant are of great interest when considering possible establishment of new populations and spread of the species (Nathan 2006). Seeds landing very near the mother plant may bolster and slowly expand an existing population, but long-distance dispersal events have the potential to

result in comparatively rapid colonization of a new area by a plant species. The potential for long-distance dispersal of propagules also reduces the likelihood that established seedlings in the new environment are negatively affected by specialist diseases or predators of the parent plants (Fenner and Thompson 2005; Janzen 1970). Because both *Vincetoxicum* species are self-compatible and either insect pollinated or self-pollinated (Lumer and Yost 1995; St Denis and Cappuccino 2004), there is reduced risk that plants establishing far from source populations would be isolated from nonvectored pollen sources. This understanding of spread, coupled with the information that prevention is usually the most time- and cost-effective management strategy, suggests that preventing long-distance dispersal events is important in slowing population spread of invasive plants. Because both *V. nigrum* and *V. rossicum* are vines with stems reaching 2-m lengths or more (DiTommaso et al. 2005b), it is conceivable that large numbers of seeds abscise from follicles at heights of 1 to 2 m



**Figure 6.** Contour plot representing seed dispersal (numbered lines are distances, back-transformed from log<sub>10</sub>), estimated according to the horizontal wind speed and the vertical falling speed without wind (settling rate) by linear model as: log<sub>10</sub>(distance) ~ settling rate + wind speed + settling rate × wind speed.



from vines climbing up trees. In upstate New York, *V. rossicum* can often be found growing in gullies or on outcrops, where even greater release heights could be obtained. If the greater height of these seeds means a higher likelihood of increased dispersal distance, land managers might focus their efforts on plants growing in high, exposed areas or climbing up into trees, other vegetation, or structures. Because high wind speeds also have a major effect on longer-distance dispersal of *V. nigrum*, managers could target sites that experience the highest wind speeds or gusts for management efforts. While long-distance dispersal events may not contribute as much to population growth of *Vincetoxicum* spp. due to poor germination and survival of the seeds (Ladd and Cappuccino 2005), the ability of a few seedlings to successfully establish in a new area following long-distance dispersal is likely to provide an opportunity for these species to substantially expand their range (Averill et al. 2010). Where prevention or reduction of spread is a priority, land managers should focus their management efforts on plants growing farthest from the ground and where higher wind is expected (Marchetto et al. 2010b). The findings reported in this study also provide important information for developing species-specific dispersal-kernel models that will aid in better targeting management efforts across the landscape and help prioritize the optimal traits of potential biological control agents to be used for managing these highly aggressive perennial vines (e.g., Shea 2004; Skarpaas and Shea 2007).

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**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2018.8>

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