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Influence of Neighboring Vegetation Height on Seed Dispersal: Implications for Invasive Plant Management

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Controlling invasive plant infestations is very costly and often unsuccessful. Preventing invasions is more cost-effective than controlling invasive plants after they are established. Because prevention guidelines do not suggest any tools or methods to limit wind dispersal of invasive plant seeds, we investigated the influence of neighboring vegetation height on seed dispersal of a wind-dispersed (yellow salsify) and nonwind-dispersed (medusahead) species. To examine the influence of neighboring vegetation height on dispersal, seeds of both species were released in front of an artificial stand of desert wheatgrass in a modified wind tunnel. Treatments were a complete factorial design with two species, four vegetation heights (10, 30, 40, and 60 cm), three wind speeds (3, 5.5, and 10 km h^{-1}), and three release distances from the neighboring vegetation (0, 15, and 30 cm). The ability of medusahead and yellow salsify seeds to disperse was influenced by the height of neighboring vegetation. Increasing height of neighboring vegetation decreased the number of yellow salsify seeds dispersing across neighboring vegetation. The greatest percentage of medusahead seeds dispersed across the neighboring vegetation was at the shortest height. Based on these results, we suggest that maintaining or promoting tall vegetation neighboring invasive plant infestations may reduce wind dispersal of seeds. More research is needed to investigate the influence of varying heights, densities, structural attributes, and composition of vegetation neighboring infestations and the dispersal of invasive plants.

Nomenclature: Medusahead, *Taeniatherum caput-medusae* (L.) Nevski; yellow salsify, *Tragopogon dubius* Scop.; desert wheatgrass, *Agropyron desertorum* Fisch. Ex Link J.A. Schultes.
Key words: Weed prevention, invasion, weed management, containment.

Invasive plant species are displacing desirable species, altering ecological processes, degrading wildlife habitat, destabilizing systems, and reducing productivity across rangelands throughout the world (DiTomaso 2000; Masters and Sheley 2001). Because resources are typically allocated to control measures instead of prevention efforts, invasive plants are rapidly increasing the amount of land infested (Westbrooks 1998). However, prevention is being recognized as an important component of a successful invasive-plant management program and is often the most cost-effective option (DiTomaso 2000; Sheley et al. 1996). A proactive approach with a focus on preventing and eradicating new infestations would be more effective than the current reactive approach (Peterson and Vieglais 2001; Simberloff 2003; Smith et al. 1999; Zavaleta 2000). On average, every dollar spent on prevention and control of new invasive-plant infestation saves $17 in later expenses (Office of Technology Assessment 1993).

Prevention could be even more effective as new tools and methods are developed to reduce invasive-plant spread, especially those strategies that reduce wind dispersal of seeds. The dispersal of invasive plants by wind is important to their spread and should be included in invasive-plant management plans (Ghersa and Roush 1993; Jordan 1992; Maxwell and Ghersa 1992). However, methods and tools to prevent wind dispersal of invasive plants are lacking. General prevention guidelines provide methods to reduce animal, human, vehicle, and water dispersal of invasive plants (Clark 2003; Sheley et al. 1999) but do not provide any tools to prevent or limit wind dispersal. Furthermore, these guidelines do not suggest possible strategies to prevent wind dispersal. In contrast, Davies and Sheley (2007) hypothesized that maintaining or promoting tall vegetation around invasive plant infestations may be a possible mechanism to reduce wind dispersal. However, this hypothesis was not tested. The literature does not provide methods for limiting wind dispersal of invasive plants.

Invasive plants with seeds that are traditionally considered wind-dispersed have seed appendages that increase the surface-to-weight ratio (Augspurger and Franson 1987; Burrows 1986). However, even seeds that are primarily dispersed by mechanisms other than wind can be dispersed, at least relatively short distances, by wind. High wind speeds have the potential to disperse relatively heavy seeds that have no adaptations for wind dispersal (Augspurger and Franson 1987; Katul et al. 2005). Thus, methods to limit wind dispersal are important for the management of most invasive plant species.

The purpose of this study was to determine the potential influence of neighboring vegetation height on seed dispersal. We also wanted to determine how the influence of vegetation height varied by species with wind-dispersed, compared with nonwind-dispersed, seeds. Yellow salsify and medusahead were selected for the experiment because they had the desired seed traits to represent wind-dispersed and nonwind-dispersed species, respectively. Yellow salsify seeds have large plumes, and medusahead seed is heavy with a long awn (Figure 1). Plumes on seeds are adaptations for wind dispersal (Sorensen 1986), whereas awns facilitate animal dispersal (Burrows 1986). We hypothesized that (1) increasing neighboring vegetation height would decrease the number of seeds dispersing across the neighboring vegetation, and dispersal distances would be shorter; (2) as the distance between the release location and neighboring vegetation increased, the number of seeds dispersing beyond neighboring vegetation and dispersal distances would decrease; (3) yellow salsify seeds would disperse past the neighboring vegetation more and to greater distances than medusahead seeds; and (4) increasing wind speeds would increase dispersal beyond the neighboring vegetation and dispersal distances.

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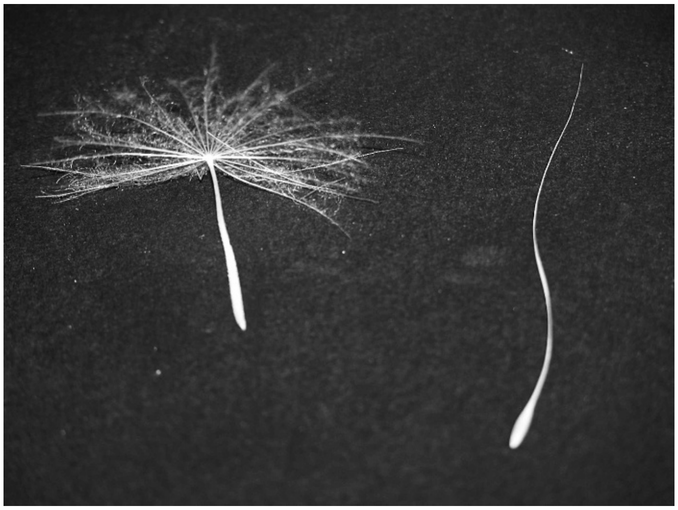

Figure 1. Photograph of a yellow salsify (left) and a medusahead (right) seed.

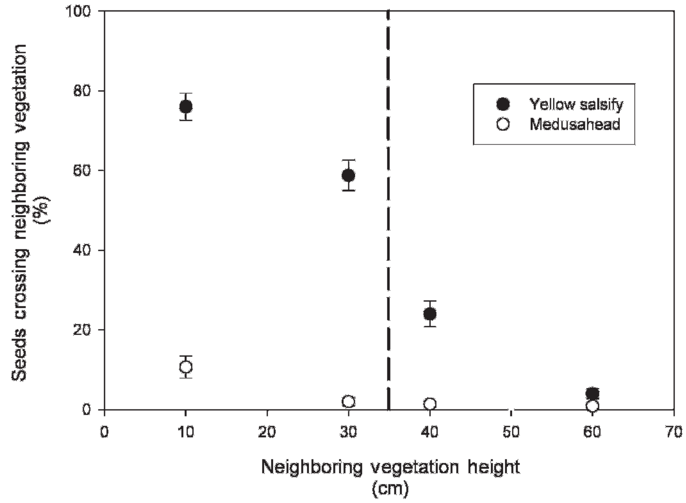

Figure 2. Percentage of yellow salsify and medusahead seeds (mean ± SE) dispersing across different neighboring vegetation heights. The vertical dashed line indicates the height (35 cm) at which seeds were released for dispersal.

Materials and Methods

Experimental Design. A randomized design was used to evaluate the effects of neighboring vegetation height, wind speed, distance from neighboring vegetation, and released species on dispersal distance and percentage of seeds transported beyond the neighboring vegetation. The study was conducted in mid-July of 2006. Treatments were a complete factorial design with two released species, four neighboring vegetation heights, three wind speeds, and three release distances from the neighboring vegetation. The two species used were yellow salsify and medusahead. The three wind speeds were 3, 5.5, and 10 km h^{-1} at the edge of the neighboring vegetation. Neighboring vegetation heights were 10, 30, 40, and 60 cm. Different vegetation heights were obtained by defoliating (clipping) the desert wheatgrass to the desired height. Release distances from neighboring vegetation were 0, 15, and 30 cm. Each treatment was replicated five times, and five seeds were released for each treatment replicate. Each seed was released only once and then discarded.

Percentage of seeds that traveled across the neighboring vegetation was measured for each treatment replicate. The distance that seeds traveled before ground contact was measured to the nearest centimeter. Seeds were release by one individual while another individual, standing on a platform overlooking the wind tunnel, marked where seeds first made ground contact.

Procedure. To examine the influence of neighboring vegetation height on seed dispersal, a modified wind tunnel was constructed inside an enclosed warehouse. A 0.5-m-diam, variable-speed fan, centered at a 35-cm height, was used to produce the different wind speeds. Simulated neighboring vegetation was created by placing a stand of desert wheatgrass in front of the fan. Mature desert wheatgrass plants were placed into a 15 by 150 cm pot in the floor of the modified wind tunnel. The upper edge of the 15 by 150 cm pot was flush with the floor of the modified wind tunnel. The desert wheatgrass stand was 15 cm deep and 1.5 m wide. Basal crowns were 15 by 15 cm and placed 5 cm from one another. Soil was used to fill in the space between desert wheatgrass plants in the 15 by 150 cm pot. Basal crowns of the wheatgrass plants were flush with the floor of the modified wind tunnel. The long edge of the desert wheatgrass stand was perpendicular to the wind direction. In the field, the density of neighboring vegetation will vary by site conditions and plant species. This simulated neighboring vegetation width and density is not representative of a specific site but broadly elucidates the potential influence of neighboring vegetation on wind dispersal of seeds. Walls (2 m high) were placed on each side of the simulated neighboring vegetation. The walls paralleled the wind direction and were 4 m long, 1 m before and 3 m after the desert wheatgrass stand. The walls were constructed of plywood framed on the outside with wood boards (5 by 10 cm). This structure created a modified wind tunnel 1.5 m wide, 2 m tall, and 4 m long with a 15 cm deep desert wheatgrass stand across its entire width 1 m into the tunnel. Seeds of yellow salsify and medusahead were released at 35 cm height by placing them on a 35 cm tall smooth wood block with forceps while the fan was running.

Statistical Analysis. ANOVA was used to determine the influence of neighboring vegetation height, species, distance from the neighboring vegetation, wind speed, and their interactions on the number of seeds that dispersed beyond the neighboring vegetation and the distance traveled by seeds.[1] Species were also analyzed individually because the species-by–neighboring vegetation height and species-by–wind speed interactions were important for determining the number of seeds that dispersed beyond the neighboring vegetation and the dispersal distance ($P < 0.01$). Analyzing species individually also simplified presentation and better illustrated the treatment effects on response variables of individual species. Data were not transformed because assumptions of normality were met. Differences were considered significant if $P < 0.05$ ($\alpha = 0.05$).

Results

Both Species. Yellow salsify seeds dispersed beyond neighboring vegetation in greater numbers than medusahead seeds ($P < 0.\ 01$), with differences up to 2.7-fold higher (Figure 2). However, as neighboring vegetation height increased, the

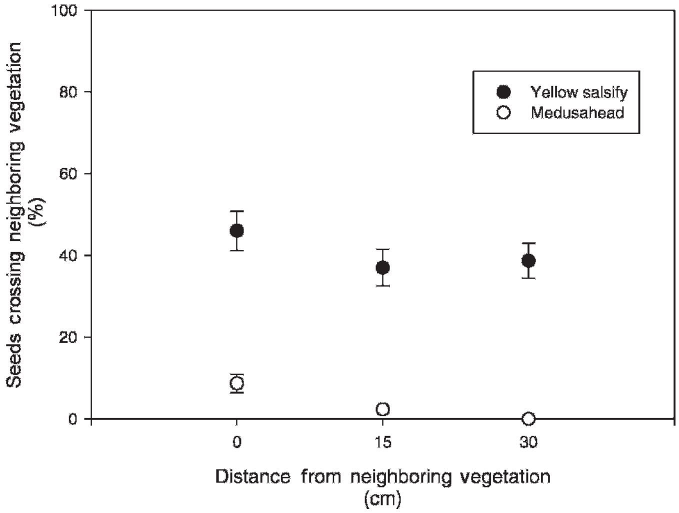

Figure 3. Percentage of yellow salsify and medusahead seeds (mean ± SE) dispersing across the neighboring vegetation at different distances between the release location and neighboring vegetation.

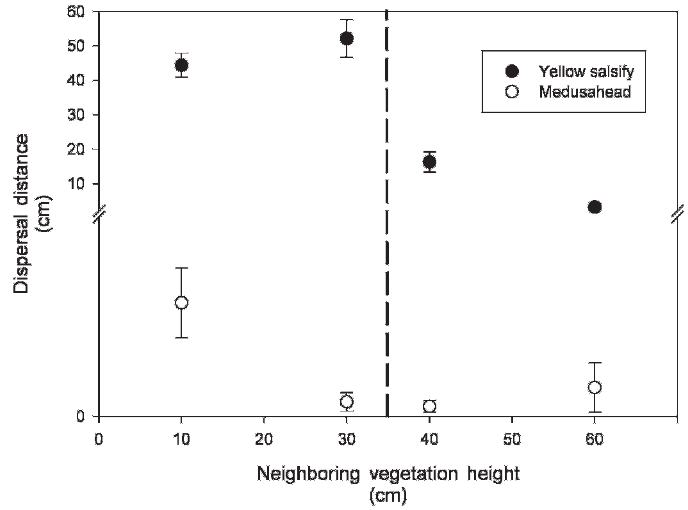

Figure 5. Dispersal distances of yellow salsify and medusahead seeds (mean ± SE) at different neighboring vegetation heights. The vertical dashed line indicates the height (35 cm) at which seeds were released for dispersal.

difference between the percentage of medusahead and yellow salsify seeds dispersing past the neighboring vegetation decreased ($P < 0.01$). Percentage of seeds dispersing beyond the neighboring vegetation varied by distance between the release location and neighboring vegetation ($P < 0.01$) (Figure 3). In general, as distance between the seed release location and neighboring vegetation increased, the percentage of seeds dispersing across the neighboring vegetation decreased. Increasing wind speeds increased the number of yellow salsify seeds more than the number of medusahead seeds dispersing across neighboring vegetation ($P < 0.01$) (Figure 4). There were no interactions between neighboring vegetation height and wind speed, neighboring vegetation height and distance (between release location and neighboring vegetation), and wind speed and distance, or among neighboring vegetation height, wind speed, and distance influencing the percentage of seeds dispersal across neighboring vegetation ($P > 0.05$).

Yellow salsify seeds dispersed farther than medusahead seeds ($P < 0.01$), with distances up to 40-fold greater (Figure 5). Influence of neighboring vegetation height on dispersal distances varied by species ($P < 0.01$). Distance between the release location and neighboring vegetation did not influence dispersal distances ($P = 0.83$) (Figure 6). Dispersal distances varied with wind speed ($P < 0.01$); however, the influence of wind speed on dispersal distance varied by species ($P < 0.01$) (Figure 7). There were no interactions between neighboring vegetation height and wind speed, between neighboring vegetation height and distance (release location and neighboring vegetation), between wind speed and distance, or among neighboring vegetation height, wind speed, and distance influencing seed dispersal distances ($P > 0.05$).

Yellow Salsify. As neighboring vegetation height increased, fewer yellow salsify seeds dispersed across neighboring vegetation ($P < 0.01$) (Figure 2). Distance between the release location and neighboring vegetation influenced the percentage of seeds dispersing beyond neighboring vegetation ($P = 0.04$) (Figure 3). Percentage of seeds dispersing across

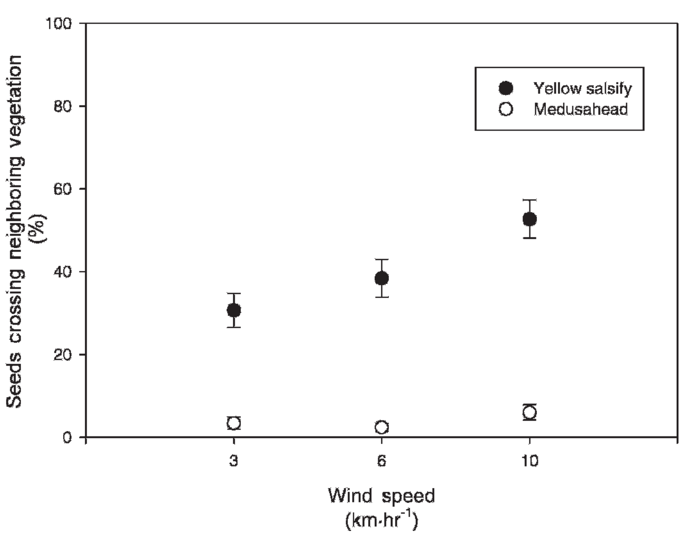

Figure 4. Percentage of yellow salsify and medusahead seeds (mean ± SE) dispersing across the neighboring vegetation at different wind speeds.

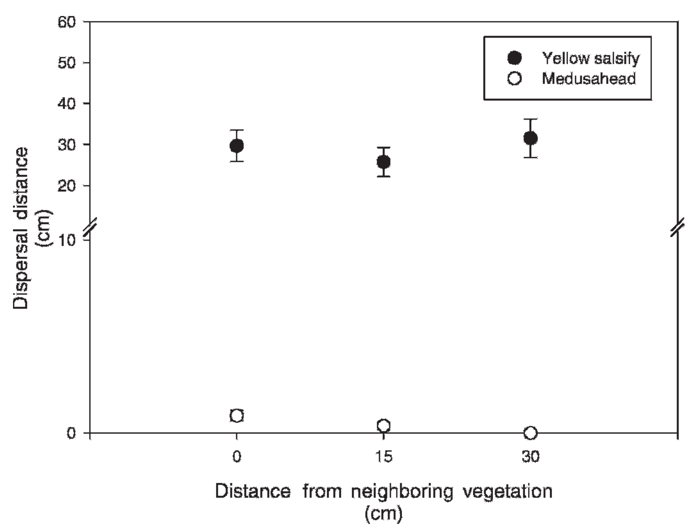

Figure 6. Dispersal distances of yellow salsify and medusahead seeds (mean ± SE) at different distances between the release location and neighboring vegetation.

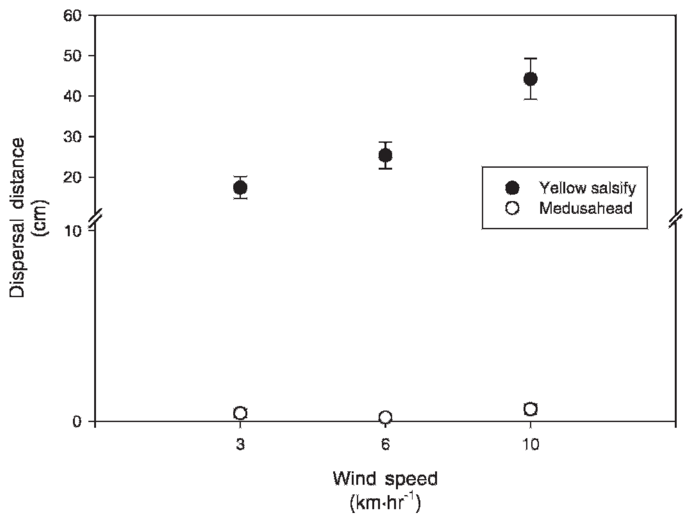

Figure 7. Dispersal distances of yellow salsify and medusahead seeds (mean ± SE) at different wind speeds.

the neighboring vegetation generally decreased as distance increased between the release location and neighboring vegetation. However, there was not a decrease in the percentage of seeds dispersing across the neighboring vegetation when the distance was increased from 15 to 30 cm. Increasing wind speed increased the percentage of seeds crossing the neighboring vegetation ($P < 0.01$) (Figure 4).

Neighboring vegetation height influenced the dispersal distance of yellow salsify seeds ($P < 0.01$) (Figure 5). When neighboring vegetation was taller than the release location, yellow salsify seeds dispersal distances were reduced. Increased wind speed increased the dispersal distance ($P < 0.01$) (Figure 7). The distance between the seed release location and neighboring vegetation did not influence dispersal distances ($P = 0.68$) (Figure 6). The percentage of yellow salsify seeds dispersing across neighboring vegetation and the distance they dispersed were not influenced by interactions among the explanatory variables ($P > 0.05$).

Medusahead. Percentage of medusahead seeds dispersing across neighboring vegetation varied by neighboring vegetation height ($P < 0.01$) (Figure 2). The greatest percentage of seeds that dispersed beyond neighboring vegetation occurred at the shortest neighboring vegetation height. Increasing distance between the release location and neighboring vegetation decreased the percentage of seeds dispersing across the neighboring vegetation ($P < 0.01$) (Figure 3). Wind speed did not influence the ability of medusahead seeds to cross neighboring vegetation ($P = 0.20$) (Figure 4).

Dispersal distance also varied by neighboring vegetation height ($P < 0.01$) (Figure 5). Medusahead seeds dispersed the farthest when the neighboring vegetation was only 10 cm tall. Dispersal distance of medusahead seeds also varied with the distance between the release location and neighboring vegetation ($P < 0.01$) (Figure 6). In general, as the distance between the release location and neighboring vegetation increased, dispersal distances decreased. Increasing wind speeds did not influence dispersal distances ($P = 0.24$) (Figure 7). Interactions among explanatory variables did not influence the distance medusahead seeds dispersed or the percentage of seeds dispersing across neighboring vegetation ($P > 0.05$).

Discussion

The height of vegetation neighboring invasive-plant infestations can significantly affect the spread of the infestation. The general trend of increasing neighboring vegetation height decreasing the percentage of seeds dispersing past neighboring vegetation and the distance seeds dispersed supports our first hypothesis. Yellow salsify seeds that did not disperse beyond the neighboring vegetation were physically intercepted. Medusahead seeds that did not disperse across neighboring vegetation were intercepted by neighboring vegetation or made contact with the ground before neighboring vegetation (especially at long release distances).

Based upon the difference between yellow salsify and medusahead seed dispersal as neighboring vegetation increased above the release height, we suggest that, for wind-dispersed invasive plants, the largest gain in preventing dispersal per unit increase in neighboring vegetation height is achieved as neighboring vegetation becomes taller than the invasive plants. However, nonwind-dispersed seeds appear to achieve this point somewhere before neighboring vegetation exceeds release height. Thus, we suggest that neighboring vegetation taller than the invasive plants without adaptations for wind dispersal may not be as critical for limiting seed dispersal as it is for wind-dispersed species. Also, neighboring vegetation that is just shorter than nonwind-dispersed invasive-plant species will probably limit seed dispersal almost as effectively as neighboring vegetation slightly taller than the invasive plant species. A more thorough investigation of other wind-dispersed and nonwind-dispersed species is needed to verify that this can be applied beyond the species examined.

Our hypothesis that as the distance between the release location and neighboring vegetation increased, the number of seeds dispersing beyond the neighboring vegetation and dispersal distances would decrease was not supported by our data. The lack of influence of the distance between the release location and neighboring vegetation on yellow salsify seeds dispersal distances may be the result of updrafts. When yellow salsify was released farther from the neighboring vegetation, it may have been able to use updrafts created by the wind deflecting off the ground to increase dispersal distances. Tackenberg et al. (2003) reported that updrafts were an important determinant in the distance dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers) seeds dispersed. When yellow salsify was released close to the neighboring vegetation, it may have become intercepted by the neighboring vegetation and could not take advantage of updrafts.

Differences in wind speeds tested in this study may not have been large enough to result in measurable increases in medusahead dispersal. Medusahead seeds are not adapted to wind dispersal; they have awns that are more likely to facilitate dispersal by animals (Monaco et al. 2005). Awned seeds are commonly dispersed by adhesion to animals (Sorensen 1986). Thus, we cannot conclude that medusahead seed dispersal is not influenced by wind speed even though our results demonstrated increasing wind speeds did not influence medusahead dispersal. In contrast to medusahead, yellow salsify seeds have large plumes that enhance their ability to be wind dispersed, and thus, they responded more noticeably to small increases in wind speed. Plumed appendages on seeds facilitate wind dispersal (Burrows 1986). The hypothesis that increasing wind speed would increase dispersal was supported by yellow salsify response to wind speeds but remains unclear for medusahead.

Though natural settings potentially have more variable wind speeds with multiple and extreme wind events than tested here, we suggest that increasing the height of relatively short vegetation around invasive plant infestations will reduce seed dispersal beyond the neighboring vegetation regardless of the distance from neighboring vegetation and wind speed. Maintaining or promoting tall vegetation around invasive plant infestations may be an effective prevention method to limit wind dispersal of seeds and should be investigated further. Land managers may need to minimize or exclude grazing around wind-dispersed invasive plant infestations or remove grazing early to allow adequate time for regrowth of neighboring vegetation before seed shatter. In areas where existing vegetation height is relatively short compared with the invasive plant species, establishing a barrier of taller vegetation around the infestation may help limit seed dispersal by wind. Research could improve the ability of management to limit wind dispersal of invasive plant species by investigating optimum neighboring vegetation barrier widths, evaluating the effectiveness of different plant species or combinations of species as vegetation barriers, and determining the influence of plant structural differences on limiting dispersal. Research investigating invasive-plant spread and how management actions influence spread can be combined with current management to develop effective invasive-plant prevention practices (Thill and Mallory-Smith 1997).

Source of Materials

[1] S-PLUS computer program, Version 7.0; Microsoft, One Microsoft Way Redmond, WA 98052-6399.

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