

DISSERTATION

DISPERSAL OF AN INVASIVE TUMBLEWEED

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

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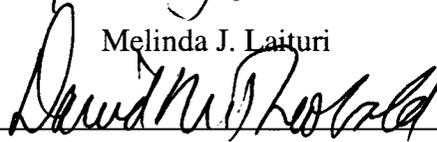
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ABSTRACT OF DISSERTATION

DISPERSAL OF AN INVASIVE TUMBLEWEED

Dispersal is of critical importance for species conservation and reducing the spread of invasive species. I investigated the dispersal of the invasive tumbleweed, *Centaurea diffusa*. Tumbleweed dispersal is composed of three components; the plant stem must break free; wind must be sufficient to move plants; and seed must be retained in the plant with time and distance. Dispersal peaks were variable in space and time. Dispersal events correlated with wind gusts and variability in temperature. However, 18 and 78% of plants tumbled over 2 years at sites near Larkspur and Superior, CO, respectively. Weather did not fully explain the differences in dispersal magnitude. Raising plants from the sites in common garden revealed that Larkspur plants required 57% greater force to break than plants from the Superior site. In addition, plants under dry post-senescence soil conditions required four to six times greater force to break compared to plants under moderate to high soil moisture. Based on wind tunnel measurements, wind velocities necessary to break *C. diffusa* stems ranged from 16 to 37 m/s. I developed a GIS-based model for the movement patterns of this plant based on topography, vegetation and wind patterns. Such modeling could provide information to help reduce the spread of this important invasive weed. However, model accuracy needs to be improved before it will be applicable to management. I conducted field and wind tunnel experiments to estimate seed dispersal with time and distance. The 95 percentile confidence limits for the half-life of seed retention in non-dispersed plants were 3 and 14 weeks suggesting that even late-dispersing plants have strong potential for longer distance dispersal of seeds. Seeds

were commonly retained in plants for distances of 200 to 400 m and one still had seed in it after traveling over 1 km. Seed dispersal with distance seems linear, though exponential decay may better represent extreme dispersal events. Both models substantially overpredicted dispersal distances for field data collected during a drought year in the presence of biocontrol insects. This research has substantially increased knowledge of the dispersal of this plant and has highlighted future research needs.

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Dedicated to my parents

- Van and Sheila Baker -

for

Inspiration,

Support,

Friendship

and

for allowing me to draft them for field work on numerous occasions.

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Note: The body chapters (2 through 5) as well as the appendices were written as independent units so there are redundancies among them. Formatting for body chapters is based on that of the Weed Science Society of America.

Chapter 1 – Introduction

Weed science is far from a new discipline. Indeed, it could be argued that it is one of the oldest of human endeavors. The practice of cultivating specific plants for food was likely soon followed by the realization that yields could be increased if competing and undesirable plants were removed from the vicinity of the desired plants. However, attention to weeds and their management in range and natural areas is much more recent. It was not until the mid twentieth century that the idea of invasions by non-native species and their impact began to be realized (Elton 1958).

There are a number of definitions for a weed (e.g., Davis and Thompson 2000, Richardson et al. 2000). Generally, the definition is context dependent and plants that are weeds in some systems are not in others. I used the definition developed by the Invasive Species Advisory Committee (ISAC) that defines an invasive weed as a plant that is non-native to the ecosystem of interest, causes either economic or ecological harm, or both, and that the harm outweighs the potential benefits of the species (ISAC 2006).

Since Elton's landmark work, invasive weeds have been identified as causes of reductions in available forage (e.g., Watson and Renney 1974), changes in community

composition (e.g., Tilman 1999, Stohlgren et al. 2003), historic fire cycles (e.g., Whisenant 1990), hydrology (Johnson 1986, Lacey et al. 1989), soil nutrient availability (e.g., Elliot and White 1989), and in wildlife usage (Trammel and Butler 1995, Thompson 1996). Wilcove et al. (1998) estimated that 49% of the listed threatened and endangered species in the US are imperiled by invasive species (but see Gurevitch and Padilla 2004). Hirsch and Leitch (1996) estimated the economic impacts of spotted knapweed (*Centaurea stoebe*) to exceed \$42 million annually in Montana and Leitch et al. (1996) estimated the economic impacts of leafy spurge (*Euphorbia esula*) in 1993 to Montana, North Dakota, South Dakota, and Wyoming to be more than \$129 million annually.

Effective weed management must include an integrated and adaptive approach. This incorporates the idea that no single method of management is sufficient for a given weed, but rather some combination of management techniques will yield the best results at the least costs; both direct and indirect (Shaw 1982). Further, there must be some mechanism for keeping a good record of results (or lack thereof) so that management can adapt as necessary. Another critical component of integrated weed management (IWM) is the concept of prevention. It is much more practicable and cost effective to catch invasions early rather than to wait until they are widespread. The ideal of prevention is to keep invasive species from even arriving in new areas. Given small to non-existent management budgets in range and wildlands, prevention is even more important in these systems.

However, preventing the spread of weeds requires reasonably detailed knowledge about their means of dispersal. In general terms, plants can be moved from one place to

another in one of two ways; through human-mediated means or via the plants inherent dispersal mechanism(s). While both of these factors clearly have strong importance to the development of any prevention program, it is on the latter that this work has focused.

The tumbleweed habit of dispersal is the adaptation where wind breaks and rolls the entire above-ground portion of a senesced herbaceous plant, dropping seed along the way. This dispersal mechanism has evolved convergently in at least nine disparate plant families including Chenopodiaceae, Amaranthaceae, Asteraceae, Brassicaceae, Boraginaceae, Fabaceae, Poaceae (Becker 1978), Lamiaceae (Roche and Wilson 1999), and Asphodelaceae (Heyligers 1999). However, there has been surprisingly little research on tumbleweed dispersal, given the widespread nature of this adaptation.

A number of tumbleweeds have become important weeds. Among their impacts are strong competitive effects on desired vegetation (e.g., Weatherspoon and Schweizer 1969; Watson and Renney 1974; Crompton and Bassett 1985) and even the spread of radioactive waste (Warren 2001). Tumbleweeds are also anecdotally blamed for fence damage due to accumulation of captured plants, and for the same reasons, accused of clogging waterways, and increasing fire hazard.

The focal plant for this work was diffuse knapweed (*Centaurea diffusa*). This plant was introduced from Eurasia in the early 1900s with alfalfa seed (Howell 1959). Since then it has been reported in most of the Western United States and in British Columbia and is considered noxious in most of Western North America. This plant has been referred to as a semelparous perennial. Typically, it only reproduces once during its lifecycle, though it might behave as anything from an annual to a short-lived perennial; largely dependent on available resources (Powell and Myers 1988). While diffuse

knapweed reproduces only by seed, fecundity can be quite high. Seed production has been reported as 925 to 18,248 per plant in British Columbia (Watson and Renney 1974) and 670 to 1201 per plant in Colorado (Beck and Rittenhouse 2002). Available forage in diffuse knapweed infested sites was reported to be reduced by nearly 90% (Watson and Renney 1974, Harris and Cranston 1979). This reduction in productivity is further associated with increased erosion and decreased wildlife populations (Roché and Roché 1988).

Diffuse knapweed reportedly infests over 745,000 ha in 17 western states and has an estimated 16% annual spread rate (Duncan and Jachetta 2005). In Colorado, where my study sites were located, diffuse knapweed was reported to infest approximately 12,000 ha in 1989 (Lacey 1989). By 2005, over 56,000 ha were reported as infested (Figure 1.1) (Colorado Department of Agriculture 2005). Even allowing for errors in mapping and reporting, this is a high rate of spread. Hence, preventing the further spread of this species should be a priority.

A possible means for limiting tumbling dispersal is the selective use of fencing. Nelson (2002) suggested that fences were an overlooked management tool and, to my knowledge, there have been no efforts to use fencing expressly to limit the dispersal of a tumbleweed. Indeed, the initial impetus for this project was a question from a rancher about where fencing could be placed to limit the continued re-introduction of diffuse knapweed onto his range.

Tumbleweed dispersal may be divided into three components. The plant stem must break, making it able to disperse longer distances than otherwise. There must be

sufficient wind to overcome resistance (e.g., slope and vegetation) and move the plant.

Finally, seed must be retained in the plant for some distance and time.

My objectives in this work were as follows:

1. Determine timing of tumbling dispersal for diffuse knapweed and weather factors that correlate with peaks in dispersal (Chapter 2);
2. Investigate the forces necessary to initiate tumbling dispersal of diffuse knapweed and two other tumbleweeds, the effects of soil moisture on that force, and calculate the wind velocities necessary to exert these forces (Chapter 3);
3. Model the spatial movement of tumbling diffuse knapweed and evaluate the fit of model results to observed field data (Chapter 4); and
4. Determine the potential for long-distance diffuse knapweed seed dispersal via tumbling (Chapter 5).

Two sites in Colorado, USA were used for this research; one near Larkspur and the other near Superior (Figure 1.1). The Larkspur site (Figure 1.2a) was on a private ranch while the Superior site (Figure 1.2b) was located on Boulder County Open Space and City of Boulder Open Space. The average elevation at the Larkspur site was 2100 m, ranging from 2,372 to 2,163 m and was 1,743 m and ranged from 1,673 to 1,817 m at the Superior site. Both sites were largely grassland with interspersed shrub and sparse woodland. Based on USGS soil maps, the soils at the Larkspur site were primarily sandy loams with some loamy sand and those at the Superior site were cobbly clay loams.

These sites were chosen for their availability and for their heavy infestations of diffuse
knapweed.

Literature Cited

- Beck, K. G. and L. R. Rittenhouse. 2002. The influence of cattle grazing on diffuse knapweed. *Proc. Weed Sci. Soc. America* **42**: 61-62.
- Becker, D. A. 1978. Stem abscission in tumbleweeds of the Chenopodiaceae: *Kochia*. *Amer. J. Bot.* **65**: 375-383.
- Colorado Department of Agriculture. 2005. Conservation Services Division, Noxious Weed Management Program.
<http://www.ag.state.co.us/CSD/Weeds/mapping/QuarterQuadSurvey.html>
- Crompton, C. W. and I. J. Bassett 1985. The biology of Canadian weeds. *Salsola pestifer*. *Can. J. Plant Sci.* **65**: 379-388.
- Davis, 2000. Eight ways to be a colonizer; two ways to be an invader: A proposed nomenclature scheme for invasion ecology. *Bull. Ecol. Soc. America*. July: 226-230.
- Duncan, C. L. and J. J. Jachetta. 2005. Introduction. Pages 1-7 in C. L. Duncan and J. K. Clark, eds. *Invasive plants of range and wildlands and their environmental, economic, and societal impacts*. Weed Science Society of America, Lawrence, KS.
- Elliot, K. J. and A. S. White. 1989. Competitive effects of various grasses and forbs on ponderosa pine seedlings. *For. Sci.* **33**:356-366.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen & Co. LTD., London, U.K.
- Gurevitch, J. and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? *TREE* **19**: 470-474.

- Harris, P., and R. Cranston. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in western Canada. *Can. J. Plant Sci.* **59**:375-382.
- Heyligers, P. C. 1999. Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and *Trachyantra divaricata* in Australia. *Cunninghamia* **6**:315-329.
- Hirsch, S. A. and J. A. Leitch. 1996. The impact of knapweed on Montana's economy. *Ag. Econ. Rep. No.* 355.
- Howell, J. T. 1959. Distributional data on the weedy thistles in western North America. *Leafl. West. Bot.* **9**:17-29.
- ISAC. 2006. Invasive Species Definition Clarification and Guidance White Paper. <http://www.invasivespeciesinfo.gov/docs/council/isacdef.pdf>
- Johnson, S. 1986. Alien plants drain western waters. *The Nature Conservancy News*, Oct-Nov 1986.
- Lacey, C. A. 1989. Knapweed management: a decade of change. Pages 1-6 in P. K. Fay and J. R. Lacey (eds.), *Proc. Knapweed Symp.*, April 4-5, 1989. Montana State Univ., Bozeman. EB45.
- Lacey, J. R., C. B. Marlow, and J. R. Lane. 1989. Influence of Spotted Knapweed (*Centaurea-Maculosa*) on Surface Runoff and Sediment Yield. *Weed Technology* **3**:627-631.
- Leitch, J. A., F. L. Leistritz, and D. A. Bangsund. 1996. Economic impact of leafy spurge in the upper Great Plains: Methods, models, and results. *Impact Assessment* **14**:419-433.
- Nelson, J. K. 2002. Diffuse knapweed movement – A critical, often overlooked component of control. *Proc. Wes. Soc. Weed Sci.* **55**:54.

- Powell, R. and J. Myers. 1988. The effect of *Sphenoptera jugoslavica* on its host plant *Centaurea diffusa*. *J. App. Ent.* **106**:25-45.
- Richardson, D. A., P. Pysek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions.* **6**: 93-107
- Roché, C. T., and B. F. Roché Jr. 1988. Distribution and amount of four knapweed (*Centaurea* L.) species in eastern Washington. *Northwest Science* **62**:242-253.
- Roché, C. T. and L. M. Wilson. 1999. Mediterranean Sage. Pages 261-270 in R.L. Sheley and J.K. Petroff, eds. *Biology and Management of Noxious Rangeland Weeds*. Corvallis, OR: Oregon State University Press.
- Shaw, W. C. 1982. Integrated weed management – systems technology for pest - management. *Weed Sci.* **30**:2-12 Suppl. 1
- Stolgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology* **1**:11-14.
- Thompson, M. J. 1996. Winter foraging response of elk to spotted knapweed removal. *Northwest Sci.* **70**:10-19.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **78**:81-92.
- Trammell, M. A. and J. L. Butler. 1995. Effect of exotic plants on native ungulate use of habitat. *J. Wildl. Manage.* **59**:808-816.
- Warren, R. W. 2001. Sorption and transport of radionuclides by tumbleweeds from two plastic-lined radioactive waste ponds. *J. of Environmental Radioactivity* **54**:361-376.

- Watson, A. K. and A. J. Renney 1974. The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. Can. J. Plant Sci. **54**:687-701.
- Weatherspoon, D. M. and E. E. Schweizer. 1969. Competition between kochia and sugarbeets. Weed Science **17**: 464-467.
- Whisenant, S. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. Proc. Symp. Cheatgrass invasion, shrub dieoff, and other aspects of shrub biology and management, 4-10. USFS Gen Tech. Rep. INT-276.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience **48**:607-615.

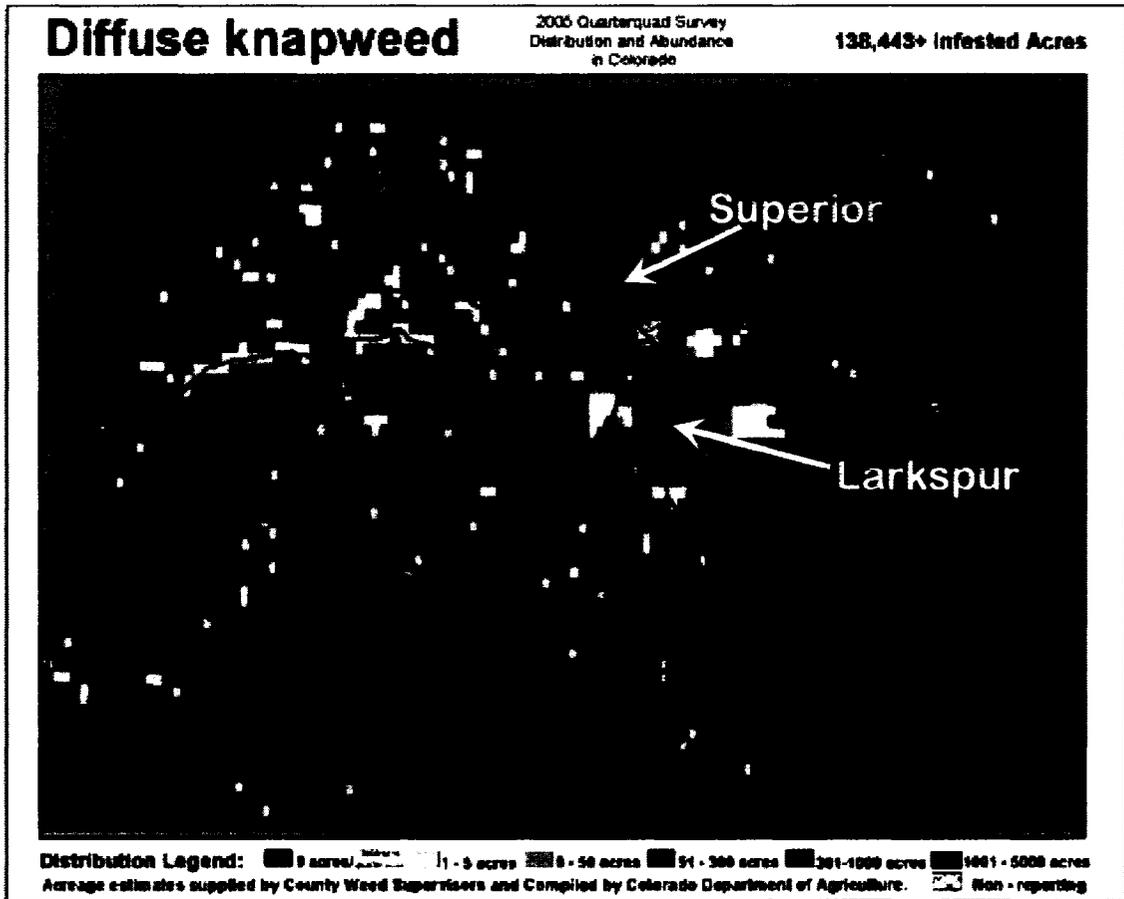
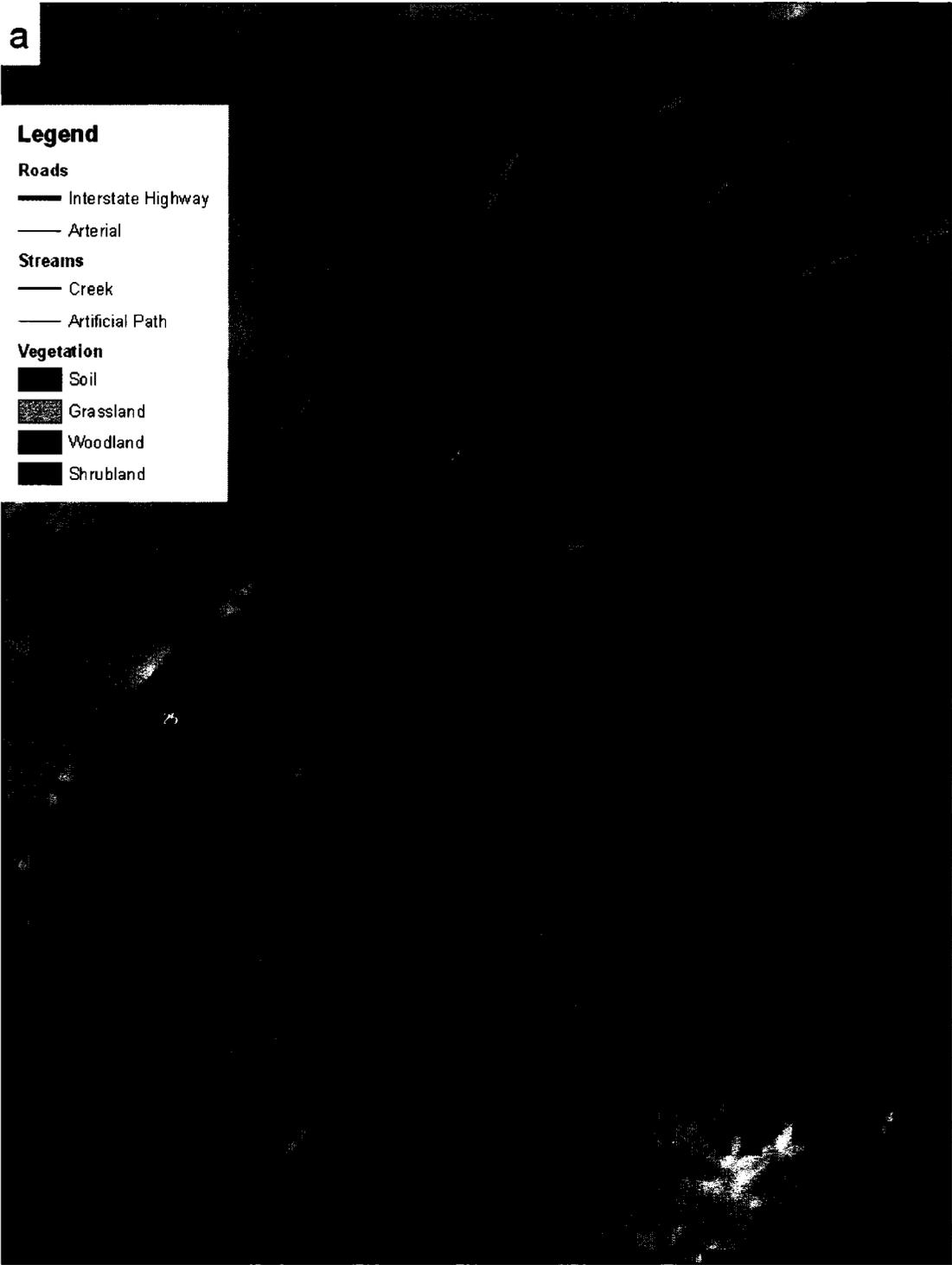
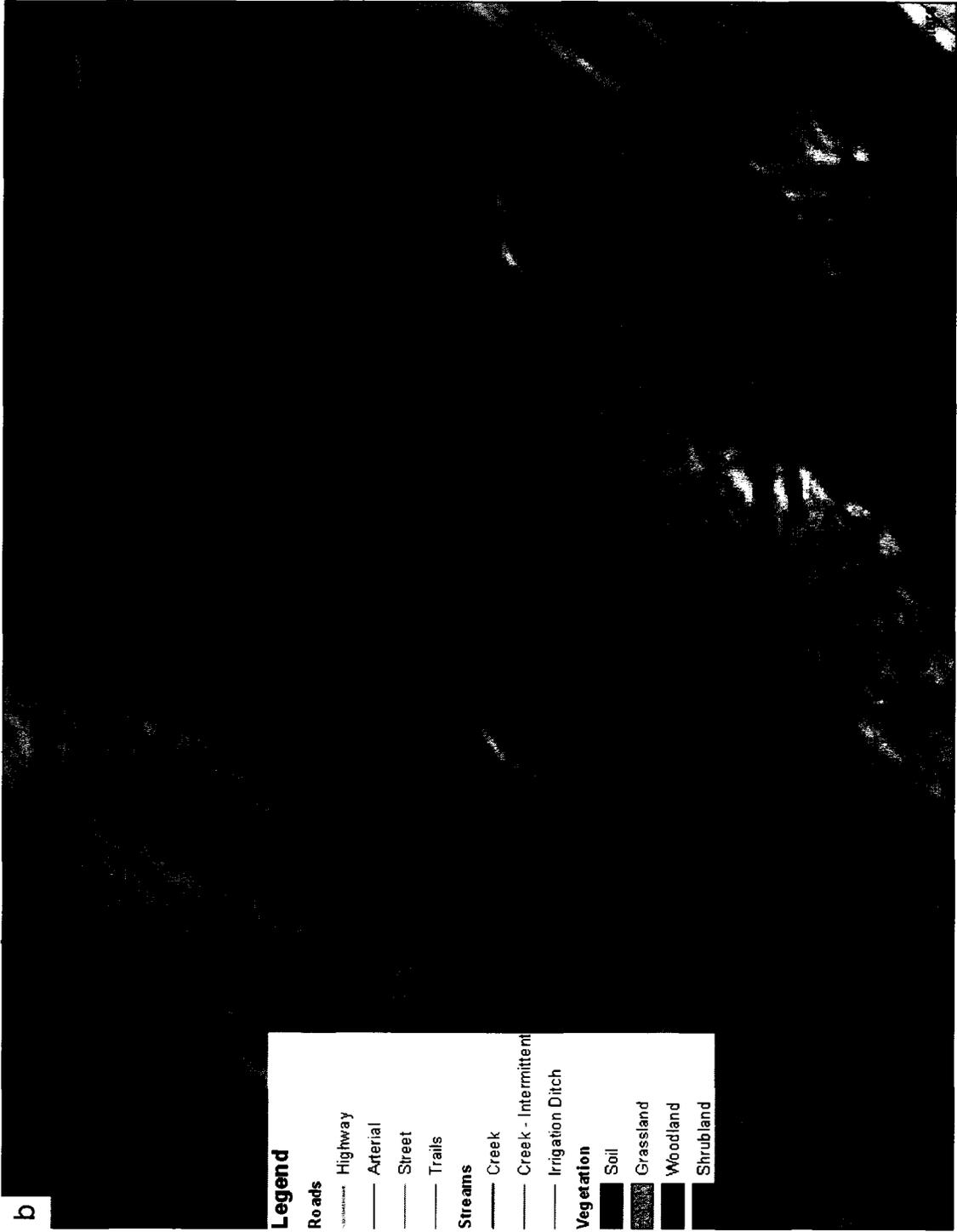


Figure 1.1. The reported extent of diffuse knapweed infestation in Colorado, USA as of 2005. The locations of the field sites used for this research are also indicated.

Figure 1.2. (following two pages) Maps of the study sites used in this research. The sites were located near Larkspur (a) and Superior (b) Colorado, USA. Vegetation data were reclassified from SWreGAP data, road data were from TIGER 2000, stream data from the National Hydrology Data, and elevation data were from USGS digital elevation models.





Chapter 2 – Dispersal Timing and Weather Correlates

Introduction

Diffuse knapweed (*Centaurea diffusa*) is an invasive weed that is considered noxious in most of Western North America. This plant disperses in a tumbleweed manner; after senescence, the stem breaks at or near the soil surface and the plant rolls along the ground in a wind-driven process. Species representing at least nine disparate plant families have evolved this mechanism of dispersal including Chenopodiaceae, Amaranthaceae, Asteraceae, Brassicaceae, Boraginaceae, Fabaceae, Poaceae (Becker 1978), Lamiaceae (Roché and Wilson 1999), and Asphodelaceae (Heyligers 1999). However, very little previous research has sought to elucidate this common dispersal mechanism. To my knowledge, only two studies have investigated the proportion of diffuse knapweed plants tumbling in a given season (Nelson 2002, Beck and Rittenhouse 2002) and only one quantified the timing of that dispersal (Nelson 2002).

Previous work has also shown temporal and spatial variation in the tumbling dispersal of diffuse knapweed. Beck and Rittenhouse (2002) reported that the proportion of diffuse knapweed plants that tumbled during the fall and winter varied from 16 to 49%

over a three-year study and that tumbling was reduced to 9 to 37% when plants were grazed in the mid-spring. Nelson (2002) reported that the proportion of plants tumbling during the fall and winter varied from 45 to 70% across sites in a one-year study and that tumbling dispersal peaked between November 2000 and January 2001, corresponding with the highest frequency of wind speeds exceeding 22.4 m/s (50mph). Both of these studies were conducted near Superior, CO where one of my sites was located.

There were two objectives for this work; first, to make observations of the timing of tumbling dispersal for diffuse knapweed and correlate weather data to dispersal events. The second objective was to formulate hypotheses based on these observations for further investigation.

Methods

My study sites were located on a privately owned ranch near Larkspur, CO and on ranch land administered by Boulder County and the City of Boulder Open Space near Superior, CO. The Larkspur site was more topographically variable than the Superior site and had more shrub and woodland communities sparsely interspersed in the dominant grassland of the site whereas the Superior site was primarily composed of grassland (though this difference is not reflected in the 30 m vegetation data in Figure 1.2). The Larkspur site is also almost 400 m higher in elevation than the Superior site. The soils at the Larkspur site are largely sandy loams while the Superior site is characterized by cobbly clay loams.

From late November 2003 through March 2004 I conducted a pilot study at Larkspur only. As most plants began senescing in September, this was a later start than would be preferable. Weather data for the pilot study were obtained from a station approximately 4.5 km from the site that provides data free to the public (Weather Underground 2004). Data were collected from late September through March 2004-2005 and 2005-2006 at both sites and included data from a weather station (Hobo, Onset Computer Corporation) placed at each site. The Hobo stations were equipped with wind direction, wind velocity, temperature, relative humidity (RH), and soil moisture sensors. Data recorded at 2 second intervals were summarized and logged at 15-minute intervals.

At each site, three locations were selected; one location on a generally windward slope, one on approximately zero slope, and one on a lee slope. The specific location was further dependent on the existence of a patch of diffuse knapweed. At each location, three transects were located at varying compass bearings. Transects were 30 meters long and 20 plants were marked with spray paint along each transect. During the pilot phase, blue paint was determined to be the easiest to relocate irrespective of season. Transects were monitored weekly for presence of marked plants. A plant was considered absent if the plant stem was no longer attached to a root. No attempt was made to relocate dispersed plants during this part of the study.

Analysis. Given the purpose of this work was to make observations and formulate hypotheses for further work, analysis in this chapter is primarily graphical and descriptive in nature. Further, since observations of the number of plants remaining in a given week were dependent on the number the previous week, observations were not independent and any statistical analysis that assumes independence of observations (or their residuals)

would be questionable. Hence, correlations of dispersal events and weather variables were made simply on the basis of visual inspection of graphs. Circular histograms and their statistics were generated with Oriana 2 (v2.02e, Kovach Computing Services) and follow the methods in Fisher (1993). Other graphs were generated using MS Excel (v2002, Microsoft Corporation).

Results

There were small dispersal peaks in 2003-2004 during weeks 13 and 25 (Figure 2.1). Similarly, there were small dispersal peaks during weeks 19 and 25 of 2004-2005 and larger peaks at weeks 6 and 25 of 2005-2006 at the Larkspur site (Figure 2.2a). There were large dispersal peaks during weeks 2 through 5, 10, 11, and 13 of 2004-2005 and weeks 3 through 8, 10, and 11 of 2005-2006 at the Superior site (Figure 2.2b).

Overall, there was a dramatic difference in the proportion of total plants that tumbled between the two sites. Tumbling dispersal occurred with a much higher frequency at the Superior site than at the Larkspur site (Table 2.1). During the pilot study (2003-2004), dispersal events seemed to be correlated with higher wind velocities and particularly with higher gusting (Figure 2.1). That pattern did not appear in 2004-2005 and was inconsistent in 2005-2006 (Figure 2.2). In fact, none of the weather variables seemed to consistently correlate well with dispersal events at the Larkspur site. It should be noted, however, that the Hobo soil moisture sensors failed at both sites, both years that they were deployed. The wind directional vanes failed for both stations during 2005-

2006, so I only obtained reliable wind direction data for 2004-2005 of the study. Further, there were problems with data collection during February of 2006, so no dispersal data are available for week 14 through week 21 period at the Larkspur site.

In contrast, there was a clear correlation of wind gusts and maximum sustained wind speed with dispersal events for the Superior site (Figure 2.2), particularly during 2004-2005. The standard deviation of temperature and the minimum relative humidity also correlated with dispersal events, though the pattern is less evident. During 2005-2006, cattle caused substantial damage to my transects. Nearly all of the marked plants had disappeared from the site before January and the study was terminated at that time for the Superior site. I cannot differentiate between dispersal caused by cattle and dispersal related to weather during that time period for that site. To my knowledge, this is the only time when cattle were in the pastures containing my transects during the entirety of my study.

Wind direction contrasted strongly between the two sites as well (Figure 2.3). Wind direction at the Larkspur site was primarily out of the south-southwest (Figure 2.3a). Wind direction at the Superior site was primarily out of the west (Figure 2.3b). Grouping the data into simple 10 m/s intervals revealed substantial differences in wind direction based on wind speed (Figure 2.3 c-f). Higher winds at Larkspur tended to be from the southwest to west-southwest (Figure 2.3c, e). The most extreme winds at Superior tended to be from the northwest while all other winds tended towards essentially westerly directions. All wind speed intervals were significantly different from each other (Table 2.2). Note that both the Watson's U^2 and Mardia-Watson-Wheeler tests only indicate that there is a difference in distributions. This may reflect differences in

frequency, direction, or some combination (Fisher 1993). Comparisons were made only within site and wind type (sustained or gust).

Discussion and Observations

Despite frustrations with unreliable weather stations (if wind direction and soil moisture are of interest, I do not recommend Hobo weather stations) and the noted problem with dispersal data collection, interesting data and observations can be derived from this study.

There were large differences between the sites in the amount of tumbling dispersal. There was a higher frequency of strong winds and gusts at the Superior site corresponding to a higher proportion of tumbling plants. However, even when strong winds and gusts occurred at the Larkspur site, there was not consistently a corresponding peak in dispersal (Figure 2.2a, c; esp. 2004-2005). There was a contrast in wind direction between the sites as well, though it does not seem likely that this would explain differences in tumbling dispersal. In general, the characteristics that differ between the sites such as wind, vegetation communities and topography may largely explain the differences in the proportion of tumbling dispersal. However, the fact that tumbling at the Larkspur site did not consistently correlate with peaks in winds or gusts suggests that there may be some attribute of the plants themselves that further explains site differences. The hypothesis that there is a difference between the sites in plant stem strength was

explored in Baker et al. (*In Press*). There does not seem to be any consistency in the timing of dispersal events at either site between years.

I made several additional observations. First, close examination of Figure 2.2b and 2.2d reveals what might be a threshold of wind velocity necessary to initiate tumbling dispersal, at least at the Superior site. Data from 2004-2005 are the most reliable for that site due to weather station issues and cattle in 2005-2006 and every time gusts exceeded 25 m/s, there is a corresponding peak in plant dispersal (see Chapter 3). Cattle probably contributed to breaking plant stems during 2005-2006 at the Superior site. Indeed, they were observed to be congregating around the transects, chewing up plastic marker stakes, and even chewing the plastic tags on the plants themselves, pulling and breaking the plants in the process. The variability (std. dev.) of temperature (Figure 2.2g, h) and the minimum relative humidity (Figure 2.2i, j) also correlate with dispersal timing. Both of these factors may contribute to causing stems to become more brittle.

I saw less dispersal at times when the soil was wet; for instance, during snow melt. It seems logical that wet soil provides less of a fulcrum for wind to act against and break plant stems. Additionally, the moisture would diffuse into the senesced plant stems, making them more flexible (see Chapter 3).

While general wind direction and its variability is unlikely an important factor for timing of dispersal, it may be a strong predictor for the direction of movement once the plant stem has broken. It may be possible to predict where tumbling dispersal will and will not occur using wind direction and speed combined with plant community and topography (see Chapter 4).

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Literature Cited

- Baker, D. V., K. G. Beck, B. J. Bienkiewicz, L. B. Bjostad. Forces Necessary to Initiate Dispersal for Three Tumbleweeds. *Invasive Plant Science and Management*. (see Chapter 3)
- Beck, K. G. and L. R. Rittenhouse. 2002. The influence of cattle grazing on diffuse knapweed. *Proc. Weed Sci. Soc. America* **42**: 61-62.
- Becker, D. A. 1978. Stem abscission in tumbleweeds of the Chenopodiaceae: *Kochia*. *Amer. J. Bot.* **65**: 375-383.
- Fisher, N. I., 1993. Statistical analysis of circular data. Cambridge University Press, Cambridge. 277pp.
- Heyligers, P. C. 1999. Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and *Trachyantra divaricata* in Australia. *Cunninghamia* **6**:315-329.
- Nelson, J. K. 2002. Diffuse knapweed movement – A critical, often overlooked component of control. *Proc. Wes. Soc. Weed Sci.* **55**:54.
- Roché, C. T. and L. M. Wilson. 1999. Mediterranean Sage. Pages 261-270 in R. L. Sheley and J. K. Petroff, eds. *Biology and Management of Noxious Rangeland Weeds*. Corvallis, OR: Oregon State University Press.
- Weather Underground. 2004. wunderground.com Station KCOMONU1. Accessed April 2004.

Table 2.1. Proportion of marked diffuse knapweed plants tumbling between the end of September and the end of the following March.

Year	Site	
	Larkspur	Superior
Nov. 2003 – March 2004	7%	---
Sept. 2004 – March 2005	9%	73%
Sept. 2005 – March 2006	26%	83%

Table 2.2. Comparisons of the distributions of sustained and gusting winds at two sites in Colorado.

Site	Wind	Comparison	W(p) ¹	MWW(p) ²
Larkspur	Sustained	<10 to 10-20	2.095(<0.001)	34.342(<0.0001)
		<10 to 20-30	0.416(<0.001)	*
		10-20 to 20-30	0.362(<0.001)	*
Larkspur	Gust	<10 to 10-20	6.496(<0.001)	47.115(<0.0001)
		<10 to 20-30	3.164(<0.001)	78.099(<0.0001)
		10-20 to 20-30	2.894(<0.001)	77.969(<0.0001)
Superior	Sustained	<10 to 10-20	14.794(<0.001)	550.886(<0.0001)
		<10 to 20-30	0.394(<0.001)	*
		10-20 to 20-30	0.392(<0.001)	*
Superior	Gust	<10 to 10-20	51.283(<0.001)	1973.326(<0.0001)
		<10 to 20-30	6.471(<0.001)	234.805(<0.0001)
		<10 to >30	0.593(<0.001)	18.274(0.0001)
		10-20 to 20-30	0.459(<0.001)	9.076(0.011)
		10-20 to >30	0.525(<0.001)	13.444(0.001)
		20-30 to >30	0.487(<0.001)	13.696(0.001)

¹Watson's U² test

²Mardia-Watson-Wheeler test

*Not estimable due to sample size.

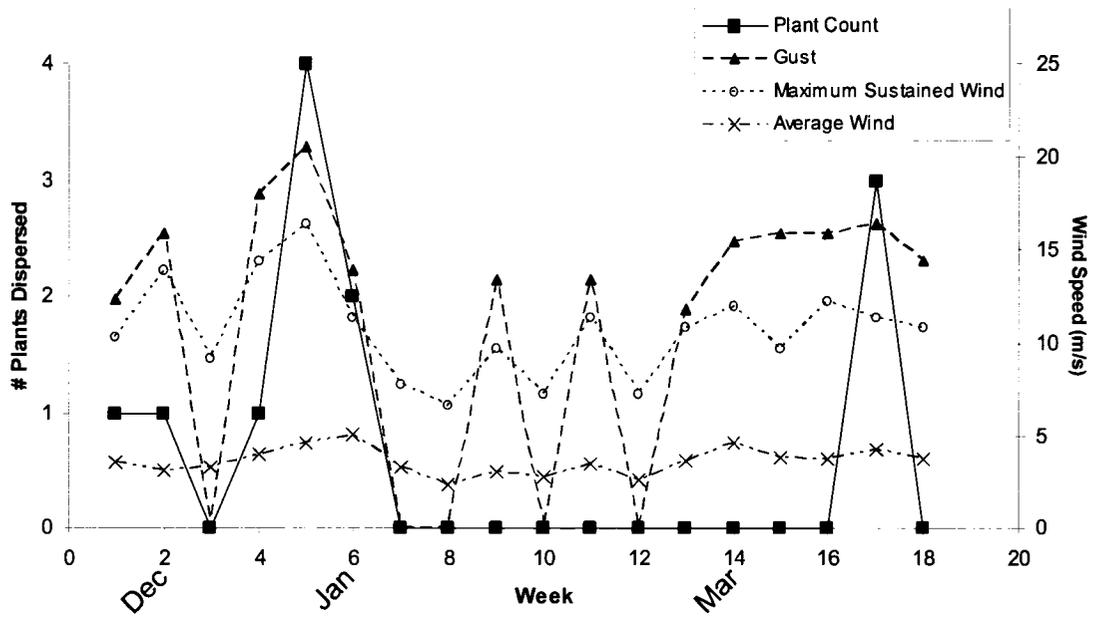
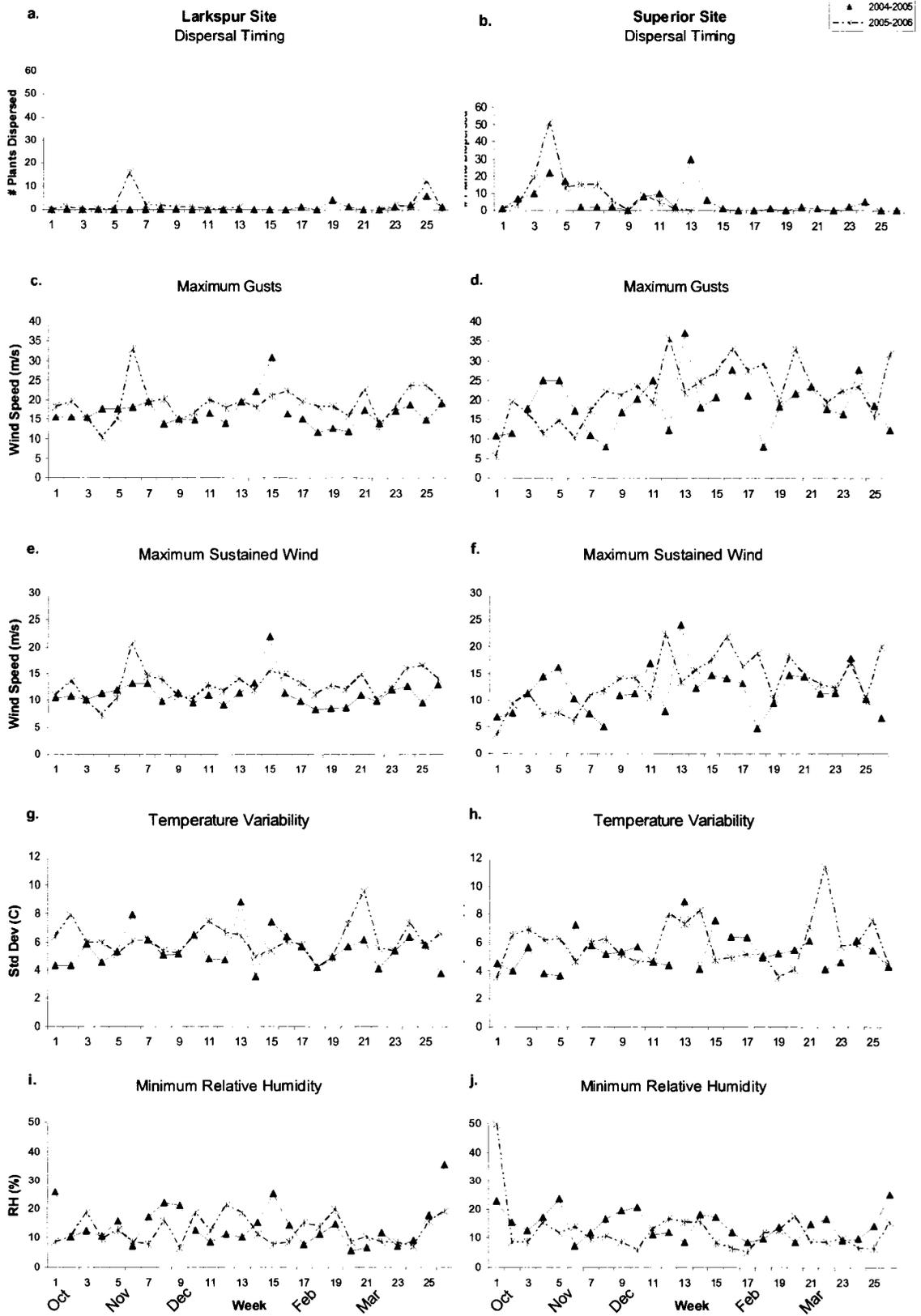
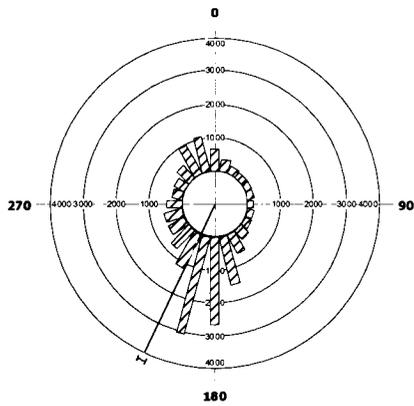


Figure 2.1. Timing of diffuse knapweed tumbling dispersal and corresponding wind speeds during a pilot study near Larkspur, CO. The first week of data collection began 24 November 2003. The horizontal axis is labeled to correspond with weeks in subsequent years (Figure 2.2).

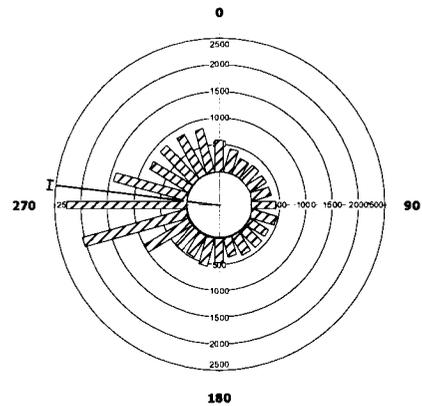
Figure 2.2. (Following page) Timing of diffuse knapweed tumbling dispersal (a,b) compared with maximum wind gusts (c, d), maximum sustained wind (e, f), variability in temperature (g, h), and minimum relative humidity for a site near Larkspur, Colorado (first column) and a site near Superior, Colorado (second column). Week 1 began the last week of September. Weather variables were selected for correlations with dispersal peaks at one or both sites after visual inspection of all recorded weather variables.



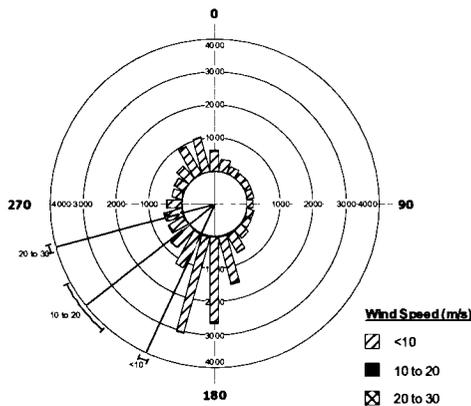
a. Larkspur Overall Wind



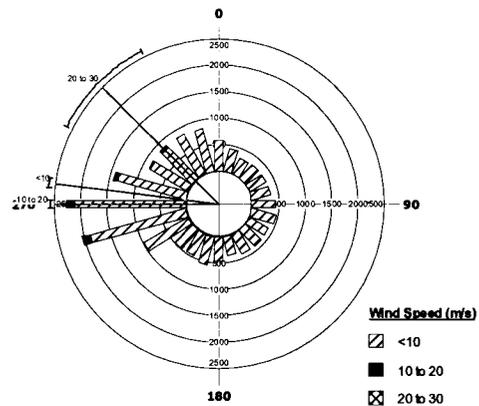
b. Superior Overall Wind



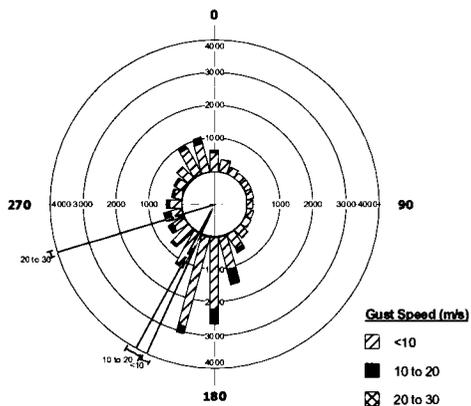
c. Larkspur Sustained Wind



d. Superior Sustained Wind



e. Larkspur Gusts



f. Superior Gusts

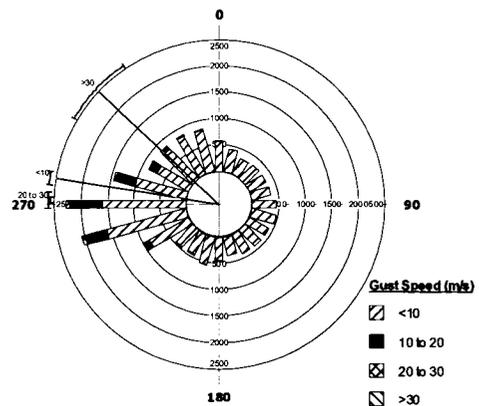


Figure 2.3. Mean wind and gust directions for two sites in Colorado. Data were collected from 26 September, 2004 through 27 March, 2005. All directional data exclude observations with zero wind speed. Arcs reflect 95% confidence intervals for the mean vector. Zero is north and bars reflect the frequency of wind from a given direction.

Chapter 3: Forces Necessary to Initiate Dispersal for Three Tumbleweeds

Introduction

The tumbleweed mechanism of dispersal is characterized when the entire above-ground portion of a senesced herbaceous plant breaks and rolls, dropping seed along the way in a wind-driven process. The point at which the plant breaks is typically at or near the soil surface. This dispersal mechanism has evolved in at least nine disparate plant families including Asteraceae, Amaranthaceae, Asphodelaceae, Brassicaceae, Boraginaceae, Chenopodiaceae, Fabaceae, Lamiaceae, and Poaceae (Becker 1978, Heyligers 1999, Roché and Wilson 1999). Despite the widespread nature of this adaptation, little research on tumbling dispersal has been published. A number of tumbleweeds including diffuse knapweed (*Centaurea diffusa*), kochia (*Kochia scoparia*) and Russian thistle (*Salsola tragus* and *S. iberica*), among others, are considered noxious or invasive in much of western North America. These weeds compete with desired vegetation (Weatherspoon and Schweizer 1969; Watson and Renney 1974; Crompton and Bassett 1985) and may contribute to the spread of radioactive waste (Warren 2001).

They are also anecdotally blamed for fence damage, clogged waterways, and increased fire hazard due to accumulation of plants.

Diffuse knapweed, kochia, and Russian thistle are widespread and are still spreading. For instance, diffuse knapweed was reported to infest approximately 12,000 ha (30,000 ac) in 1989 (Lacey 1989) and by 2005, over 56,000 ha (138,000 ac) were reported as infested in Colorado (Colorado Department of Agriculture 2005). Rapid response and early eradication are important components of integrated management, and knowledge of the environmental conditions that are conducive to the spread of these plants could be valuable in this endeavor. For instance, the drought that has affected large areas of the west over the last several years could increase tumbleweed dispersal if dry stems were more brittle and dry soil provided a stronger fulcrum for wind force to act against. If this were true, managers should increase prevention efforts during periods of drought.

Conceptually, there are three components to tumbling dispersal. First, sufficient force must be exerted to break the main stem of plants; thereby initiating the process. Second, the plant must move across the landscape. Thirdly, seed must be retained in the plant for some distance and time. Seed dispersal of diffuse knapweed plants that do not tumble is similar to that of spotted knapweed (*C. stoebe*); seed is simply shaken out of heads to fall near the parent plant (Watson and Renney 1974). Stallings et al. (1995) investigated seed retention in Russian thistle plants with time and distance. On average, 51% of Russian thistle seed was retained in plants recovered after traveling 2,209 m in summer fallow wheat fields in one year and 26% after traveling 1,771 m in the next year. Further, they found that 61% of seed were retained on plants that did not tumble during

the 6 and 12 weeks of the first and second years of the study, respectively (Stallings et al. 1995). I am aware of no work addressing the plant movement and seed retention components of tumbling dispersal for kochia. In this work, I focused on the forces necessary to initiate dispersal.

Previous work has shown temporal and spatial variation in the tumbling dispersal of diffuse knapweed. Beck and Rittenhouse (2002) reported that the proportion of diffuse knapweed plants that tumbled during the fall and winter varied from 16 to 49% over a 3 year study and that tumbling was reduced 9 to 37% when plants were grazed in the early summer. Nelson (2002) reported that the proportion of plants tumbling during the fall and winter varied from 45 to 70% across sites in a 1 year study. Both of these studies were conducted near Superior, CO. I made further observations during the falls and winters from 2004 through 2006 at two sites. At a site near Superior, CO, on average 78% of diffuse knapweed plants tumbled (unpublished data). However, observations near Larkspur, CO (approximately 100 km south-southeast of Superior) showed only an average of 18% of plants tumbling (unpublished data).

There are undoubtedly a variety of factors and interactions that influence the strength of senesced tumbleweed stems and, hence, the likelihood of tumbling dispersal. These factors may include plant physiology, soil type, soil organic matter, stem fatigue due to varying wind direction and velocity, stem decay, solar radiation, and soil moisture. To my knowledge, the only previously published work examining the force required to initiate tumbling and related factors is that of Becker's (1978) investigation of the anatomical, histochemical, and mechanical aspects of stem abscission in kochia. He

concluded that, while desiccation, anatomical changes, and decay were important factors, the physical force exerted by wind was the primary factor causing stems to break.

I had five objectives in this work. The first was to estimate the stem strength of the three species of tumbleweed (i.e., the force necessary to break the main stem at the soil surface thereby initiating tumbling dispersal). The second was to determine the effects of soil moisture on the stem strength. The hypothesis was that increasing soil moisture would cause senesced plant stems to be more flexible and, hence, greater forces would be required to induce stem failure. My third objective was to determine if there was a difference in stem strength between diffuse knapweed plants collected from two field sites. I hypothesized that the observed differences in tumbling dispersal at my field sites would be at least partially explained by differences in stem strength. The fourth objective was to estimate the force exerted by wind (hereafter referred to as drag effect) on diffuse knapweed. Finally, my fifth objective was to use estimated drag effect to relate stem breaking strength to wind velocity for all species.

Methods

Sites, Collection and Rearing. Bolting rosettes of diffuse knapweed, kochia and Russian thistle were collected and transplanted into 3.8 L (1 gal) pots with their native soil in early June of 2004 and 2005. Bolting rosettes were used to control for the unpredictability of whether a diffuse knapweed plant grown from seed or rosette would bolt and bloom in a given year. Diffuse knapweed plants were obtained from a site near

Larkspur, CO and from a site near Superior, CO. Forty-five plants were collected from each site in 2004 and 65 in 2005. Kochia and Russian thistle plants were collected from agricultural fields within Colorado State University's Agricultural Research, Demonstration, and Education Center (ARDEC, Fort Collins, CO). Twenty-five kochia and Russian thistle plants were collected in 2004 and 45 in 2005. Potted plants were placed into 46 cm (18 in) high wood frames and wood mulch was packed between pots to minimize the effects of temperature fluctuation on root growth. Plants were maintained outdoors under drip irrigation at ARDEC and monitored to ensure they were receiving sufficient water to prevent wilting. At the onset of senescence (late August), plants were transferred to a greenhouse and allowed to complete senescence with no further water added.

To obtain concurrent weather observations, a weather station¹ equipped with an anemometer and directional vane was placed at each site from late September, 2004 through March, 2005 and for the same period the following season.

Treatments. After plants senesced, each was assigned to a post-senescent water treatment in a completely random design. A minimum of 10 plants was assigned to each water treatment per year based on a simple statistical power calculation and available greenhouse space. Due to small 2004 sample size, there were two treatments: water and no-water. Plants assigned to the water group received 145 ml (4.9 oz) of water two times per week for 8 weeks, while those in the no-watered groups received no water for the same period. More plants and space were available in 2005; therefore an additional water level was added and a minimum of 20 plants of each species was assigned to this treatment. Plants assigned to the highest water level treatment received 145 ml every 2

days for the 8-week post-senescence period. The moderate level of water (145 ml, twice per week) was based on the 55 year average precipitation during September and October for the collection sites (about 5 cm (2 in) per month). Separate groups of diffuse knapweed plants were randomly selected for the site difference trials and wind tunnel tests. The ultimate sample size (n) for each treatment is shown in Table 3.1. Sample sizes within treatment were roughly equal between years.

Measuring Breaking Strength. At the end of the 8-week treatment period, the horizontal force necessary to induce stem failure was measured. Failure was defined as the point at which the plant stem broke and the plant could freely tumble. Measurements were completed within 3 days of the cessation of treatments and plants within species were measured within a few hours of each other.

Horizontal force was measured with a device composed of a vertical beam, a crank, pulley and a tubular scale (Figure 3.1). The pulley was mounted to the beam and was adjustable in height so force exerted was horizontal. A 13.6 kg test weight (30 lb) line was attached from the crank through the pulley to the scale. A short piece of line was wrapped around the plant stem and attached to the other end of the scale. The point of attachment was a visually estimated, vertical coordinate of the centroid of the plant canopy; in essence the center of the wind shadow of each plant. The crank was used to gradually increase the horizontal force exerted on the plant until the plant stem failed. Stem failure typically occurred at or near the soil surface. The force, rounded to the nearest 0.01kg, and the height (cm) on the stem at which the line was attached were both recorded. The measured force was multiplied by the height of attachment to calculate the breaking moment (M_B), which was the dependent variable for this analysis. The plant

size was characterized by the canopy diameter (at its widest) and the stem diameter (at the soil surface). These diameters were measured as possible covariates for analysis.

Estimating Drag Effect. A wind tunnel was designed and constructed to carry out investigations under controlled wind conditions (Appendices A and B). This wind tunnel was capable of generating air flow velocities from 0 to 8 m/s (0 to 17.9 mph). Air flow was monitored with a hot-film probe, in conjunction with a constant temperature anemometer². The test section of the tunnel was equipped with a proximity sensor³ calibrated to monitor wind drag effects on a plant. The output from this sensor was logged to a personal computer and was sampled at 1-second intervals. Thirty samples were used to calculate the temporal average of the acquired data.

The proximity sensor's output can range from 0.000 to 10.000 DCV over a calibration proximity range of 3 mm (0.12 in), thereby giving proximity accuracy to 3 μ m. The proximity was the distance between the sensor and a sensor target; a metal plate that was spring-mounted and furnished with a mount employed to test (individual) plants (Appendix A, Figure A.2). Given that force is directly proportional to change in proximity, this device was calibrated to provide information on wind drag exerted on a plant. During calibration, known force was applied to the system using the same device used to measure stem strength. During wind tunnel experiments, the proximity was measured for calm and with wind (3.3 m/s (7.4 mph)) conditions and the difference in proximity was converted into the drag force, using the calibration conversion factor. This factor is analogous to, for instance, the conversion factor between Kg-m and N-m. This methodology was based on those of Kawakita et al. (1992) who estimated forces exerted on a roof by wind.

Measurements were carried out for each diffuse knapweed plant. Kochia and Russian thistle were not included in this experiment as it was not feasible to construct a wind tunnel large enough to accommodate these species. The wind velocity selected for testing was chosen to represent moderate wind conditions and to ensure repeatability of wind tunnel measurements. The following equation relates the aerodynamic overturning moment to the wind speed U and the remaining principal independent variables:

$$M_B = \left(\frac{1}{2}\rho U^2\right) C_M A\sqrt{A} \quad [3.1]$$

where M_B is the overturning moment associated with stem breaking, ρ is air mass density (approximately 1.066 kg/m^3 at 1500 m (4921 ft) elevation (Lide 1992-1993)), U is wind speed, C_M is the moment coefficient and $A\sqrt{A}$ is volume, while A is a reference area.

Because the purpose of this work was to relate wind speed to the breaking moment (force), there was no need to uniquely estimate the moment coefficient and volume or area. In fact, determining these parameters would be problematic as volume in the equation refers to solid volume. Hence, these variables can be combined as is expressed in Equation 3.2, where Ψ is the product of the moment coefficient and volume, hereafter referred to as the wind drag effect parameter, or drag effect.

$$M_B = \left(\frac{1}{2}\rho U^2\right)\Psi \quad [3.2]$$

Analysis: Data were *ln* transformed to meet assumptions associated with normal distribution and equality of residuals and subjected to ANOVA with covariates and regression using SAS v9.1 (Proc GLM, The SAS Institute 2005). Collection site, canopy diameter, and stem diameter were the covariates included for soil moisture effects and for evaluating site differences. The regressors for the analysis of drag effect were plant height, canopy diameter and plant weight. The experimental unit was an individual plant.

Backward model selection was used and began with inclusion of all main effects and two-way interactions. Effects were eliminated by lack of significance or estimability due to sample size.

Results and Discussion

Water Effects on Stem Strength. The model including all three species showed no year effect and a strong water by species interaction ($p < 0.0001$). Therefore data were pooled over the 2 years of the study and analyses conducted by species.

Russian thistle stem strength was not affected by water treatments but water was the only significant effect for kochia ($p = 0.0015$) (Table 3.1).

For diffuse knapweed, collection site ($p = 0.0121$), water treatment ($p < 0.0001$), and the interaction between site and stem diameter ($p = 0.0356$) were significant effects. Though stem diameter was not a significant main effect ($p = 0.1066$), it was included in the model due to the interaction. The mean (\ln) breaking strengths (\pm SE) for diffuse knapweed from Sites 1 and 2 were 1.91 kg*cm (± 0.2) and 1.29 kg*cm (± 0.22), respectively. Site comparisons within water treatment were not conducted due to insufficient sample size.

My hypothesis that stem strength would increase with increasing soil moisture was based on three premises. First, moist soil is soft and provides less of a fulcrum for the wind (or force) to act upon. Second, moisture absorbed from the soil by stems would cause the stems to be more flexible. Third, it could be hypothesized that long-distance

dispersal would be more adaptive when the local habitat is least suitable, i.e., if water were less available. If the immediate locale of the parent plant is very dry, it is not well-suited to seedling establishment and survival, therefore it might be more adaptive for seeds to be dispersed over greater distances.

Site Effects on Diffuse Knapweed Stem Strength. The experiments to determine the basis for observed site differences in tumbling dispersal showed that stem strength depended on site ($p = 0.0005$) and stem diameter ($p < 0.0001$) and that the effect of stem diameter was not dependent on site ($p = 0.9042$). On average, plants from the Larkspur site require 57% more force (back-transformed data) to break than those from Superior (Table 3.1). However, only 32% of the variance in stem strength was explained by the model that included site and stem diameter as parameters. Stem diameter depended on site ($p = 0.0397$). The average diameter (\pm SE) of Larkspur plant stems was 5.5 mm (\pm 0.2) (0.22 in) and 5 mm (\pm 0.2) (0.2 in) for Superior plant stems. However, the small difference in stem diameter between sites and the low R-square suggest that there are other factors involved. Further, the question of why there is a difference in stem diameter between sites remains.

I noted two important differences between the sites. First, what appeared to be putative hybrids between diffuse knapweed and spotted knapweed were present at Larkspur but not at Superior. It seems reasonable that hybridization with a plant that does not disperse via the tumbling mechanism might increase the stem strength of progeny. Spotted knapweed has not been reported to disperse by tumbling. A test of this hypothesis controlling for stem diameter showed no difference ($p=0.9924$) in stem strength between diffuse knapweed plants and putative hybrids within the Larkspur site

refuting this hypothesis. However, as there were only nine putative hybrids, this result is tentative and further research is needed to determine the possible effects of hybridization.

Second, 33 of the 47 plants from Superior that I reared from the bolting stage showed symptoms of damage by the root-borer biological control agent *Cyphocleonus achates*. There was no evidence of this damage on plants from Larkspur. The larvae of this biocontrol agent are root-borers. Because the damage caused by these larvae is proximate to the location at which I observed most of the non-infested plants breaking, it is likely that this damage could further weaken the plants, making them more likely to tumble. My test comparing the infested and non-infested plants within the site showed no effect ($p=0.7881$) controlling for stem diameter refuting this hypothesis. However, I am again limited by sample size and this potential effect of the biocontrol agent on dispersal warrants further investigation. It would indeed be ironic if a promising biological control agent increases long-distance dispersal of the plant.

Drag Effect. Analysis of drag effect estimates showed that the drag effect (\ln transformed) depended on plant height ($p<0.0001$), plant weight ($p<0.0001$) and their interaction ($p<0.0001$) (Table 3.2, R-square=0.796). These are fairly intuitive results, particularly if the weight of the plant represents the density of the plant structure. It was surprising, however, that the plant canopy diameter was not significant ($p=0.976$, slope=-0.00015), as I expected that the height and canopy would describe the plant profile with which the wind interacts.

With the estimated drag effect and Equation 3.2, I calculated the wind velocity equivalents of breaking forces (Table 3.1). For diffuse knapweed, plants in dry soil required more than twice the wind velocity to break than do those under moist soil

conditions. Kochia plants under moderate soil moisture conditions required approximately 73% greater wind to break than the other two treatments. Calculations for kochia and Russian thistle assume that the plant characteristics that dictate drag effect (i.e., height, weight and their interaction) are similar to those for diffuse knapweed. Hence, these findings should be taken only as rough approximations.

The generalization of my results is limited by several factors. I conducted my tests 8 weeks after plants senesced. While this time period was based on field observations of dispersal timing, it is somewhat arbitrary. It is likely that stem strength varies with time after senescence, even within my chosen treatments. I also kept soil moisture reasonably constant and soil moisture fluctuation might also have an important effect. Because my tests consisted of gradually increasing, unidirectional force, the effects of fatigue due to variability in wind velocity and direction are not reflected in my data and could dramatically reduce stem strength over time. Wind in the field is turbulent and highly variable, even over relatively short time periods. This factor might substantially affect stem strength. However, the calculated wind speeds necessary to break plant stems are largely within the range of wind gusts observed at my field sites (Table 3.3). Arguably, it is wind gusts that are most important for fatiguing and breaking plant stems. Finally, soil characteristics such as texture and organic content as well as decay of the root and lower stem may be important, but were not measured in this work.

Despite these qualifications, it is clear that soil moisture has a strong effect on the stem strength of both diffuse knapweed and kochia. These results suggest that long-distance dispersal of diffuse knapweed may be increased during autumns of high soil moisture compared to dry autumns. Further, the moisture would facilitate germination

and seedling establishment. In contrast, long-distance dispersal of kochia may be increased during autumns characterized by low or no precipitation. Awareness of the environmental conditions that are well-suited for dispersal of these plants can be an important management tool. For instance, sites that experience higher moisture in the fall as well as strong winds might be particularly prone to long-distance dispersal of diffuse knapweed while drier or extremely wet sites may maximize kochia dispersal. These data can also be used to assess the vulnerability of sites to rapid dispersal and infestation by tumbleweeds.

There are several aspects of this work that should be further investigated. Becker (1978) and Zeroni et al. (1978) reported on the physiological basis for stem failure that characterizes the tumbleweed mechanism of dispersal in the *Kochia* genus and Becker (1969) for *Psoralea*. Similar work is needed for diffuse knapweed and Russian thistle. This work would be of particular interest for diffuse knapweed given the temporal and site-based variation in the proportion of tumbling versus non-tumbling plants shown in my observations and by Beck and Rittenhouse (2002) and Nelson (2002).

Sources of Materials

¹Hobo, Onset Computer Corporation

²Hotwire anemometer, model 407123, Extech Instruments.

³GageProx 8mm unshielded proximity sensor, Kaman Instruments.

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Literature Cited

- Beck, K. G. and L. R. Rittenhouse. 2002. The influence of cattle grazing on diffuse knapweed. *Proc. Weed Sci. Soc. America* **42**: 61-62.
- Becker, D. A. 1969. Stem abscission in the tumbleweed, *Psoralea*. *Amer. J. Bot.* **55**: 753-756
- Becker, D. A. 1978. Stem abscission in tumbleweeds of the Chenopodiaceae: *Kochia*. *Amer. J. Bot.* **65**: 375-383.
- Colorado Department of Agriculture. 2005. Conservation Services Division, Noxious Weed Management Program.
<http://www.ag.state.co.us/CSD/Weeds/mapping/QuarterQuadSurvey.html>
- Crompton, C. W. and I. J. Bassett 1985. The biology of Canadian weeds. *Salsola pestifer*. *Can. J. Plant Sci.* **65**: 379-388.
- Heyligers, P. C. 1999. Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and *Trachyantra divaricata* in Australia. *Cunninghamia* **6**:315-329.
- Lacey, C. A. 1989. Knapweed management: a decade of change. Pages 1-6 in P. K. Fay and J. R. Lacey (eds.), *Proc. Knapweed Symp.*, April 4-5, 1989. Montana State Univ., Bozeman. EB45.
- Lide, D. R. ed. 1992-1993. Geophysics, Astronomy, and Acoustics. *Handbook of Chemistry and Physics*, CRC Press: 14-13.
- Kawakita, S., B. Bienkiewicz, and J. E. Cermak. 1992. Aeroelastic model study of suspended cable roof. *Journal of Wind Engineering and Industrial Aerodynamics.* **41-44**: 1459-1470.

- Nelson, J. K. 2002. Diffuse knapweed movement – A critical, often overlooked component of control. *Proc. Wes. Soc. Weed Sci.* **55**:54.
- Roché, C. T. and L. M. Wilson. 1999. Mediterranean Sage. Pages 261-270 in R. L. Sheley and J. K. Petroff, eds. *Biology and Management of Noxious Rangeland Weeds*. Corvallis, OR: Oregon State University Press.
- Stallings, G. P., L. W. Lass, C. A. Mallory-Smith, and D. C. Thill. 1995. Plant movement and seed dispersal of Russian thistle (*Salsola iberica*). *Weed Science* **43**:63-69.
- Warren, R. W. 2001. Sorption and transport of radionuclides by tumbleweeds from two plastic-lined radioactive waste ponds. *J. of Environmental Radioactivity* **54**: 361-376.
- Watson, A. K. and A. J. Renney 1974. The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. *Can. J. Plant Sci.* **54**:687-701.
- Weatherspoon, D. M. and E. E. Schweizer. 1969. Competition between kochia and sugarbeets. *Weed Science*. **17**: 464-467.
- Zeroni, M., T. Arzee, and E. Hollander. 1978. Abscission in the tumbleweed *Kochia indica*: ethylene, cellulase, and anatomical structure. *Botanical Gazette*: **139**:299-305.

Table 3.1. Force and calculated wind velocities necessary to break tumbleweed stems in a single event (SE = standard error; N = sample size).

Species	Force ^a <i>lnkg*cm</i>	SE	N	Calculated Wind m/s (mph) ^b
Diffuse knapweed				
Larkspur	2.42a	0.09	46	34.2 (76.5)
Superior	1.97b	0.09	47	27.3 (61.1)
Diffuse knapweed				
0 H ₂ O ^c	2.65a	0.21	16	37.4 (77)
M H ₂ O ^c	0.97b	0.19	20	16.1 (36)
H H ₂ O ^c	1.04b	0.21	16	16.7 (37.4)
Kochia				
0 H ₂ O ^c	3.24a	0.23	22	31.9 (71.4)
M H ₂ O ^c	4.12b	0.25	20	49.6 (111)
H H ₂ O ^c	2.78a	0.27	17	25.4 (56.8)
Russian thistle				
0 H ₂ O ^c	2.62a	0.32	16	27.5 (61.5)
M H ₂ O ^c	2.71a	0.32	16	28.8 (64.4)
H H ₂ O ^c	2.54a	0.25	26	26.5 (59.3)

^aDifferent lower case letters denote significant differences at $\alpha=0.05$. Comparisons were made only within species and, in the case of diffuse knapweed, separately for the site and water experiments. Due to small sample size, I did not make site comparisons within water treatment. Lsmeans are reported for diffuse knapweed.

^bWind calculations for kochia and Russian thistle assume that the plant characteristics that dictate drag effect are similar to those for diffuse knapweed.

^c Water treatments for the eight week treatment period: 0 H₂O is no water; M H₂O is 145 ml twice per week; H H₂O is 145 ml every 2 days.

Table 3.2. Drag effect regression parameter estimates for post-senescence diffuse knapweed plants collected from two sites in Colorado in 2004 and 2005. Drag effect, or the force exerted by wind on a plant, was estimated using a wind tunnel and \ln transformed for analysis.

Parameter	Estimate	SE	p-value
Intercept	-5.551	0.2838	<0.0001
Height	0.058	0.0069	<0.0001
Weight	0.108	0.0146	<0.0001
Height*Weight	-0.002	0.0003	<0.0001

Table 3.3. Wind observations at two sites in Colorado. Observations were made from late September 2004 through March 2005 (denoted 2004) and late September 2005 through March 2006 (denoted 2005).

Site	Year	Sustained Winds (m/s)		Gusts (m/s)	
		Avg.	Range Weekly max	Avg.	Range Weekly Max
Larkspur	2004	3.8	8.4 to 21.9	6	11.7 to 30.8
	2005	4.2	7.2 to 20.6	6.4	10.4 to 32.8
Superior	2004	3.2	4.6 to 24.1	5.2	8 to 36.9
	2005	3.4	3.5 to 22.5	5.7	5.6 to 35.6



Figure 3.1. Device used to measure breaking strength. Force was applied via a crank (a) through a pulley (b) and measured by a tubular scale (c). The pulley was adjustable in height to keep applied force horizontal. Force when the stem breaks was multiplied by the height of line attachment (d) to obtain the moment of breaking or stem strength.

Chapter 4: Movement Patterns of an Invasive Tumbleweed

Introduction

Invasive weeds cause decreases in available forage (e.g., Watson and Renney 1974), changes in plant community composition (e.g., Tilman 1999, Stohlgren et al. 2003), historic fire cycles (e.g., Whisenant 1990), hydrology (Johnson 1986, Lacey et al. 1989), soil nutrient availability (e.g., Elliot and White 1989), and reduction in wildlife usage (Trammel and Butler 1995, Thompson 1996). Wilcove et al. (1998) estimated that 49% of all listed threatened and endangered species and 57% of listed plants in the US are imperiled by invasive species (but see Gurevitch and Padilla 2004). Economic impacts of invasive weeds are high. For example, Hirsch and Leitch (1996) estimated the economic impacts of spotted knapweed (*Centaurea stoebe*) to exceed \$42 million annually in Montana alone and Leitch et al. (1996) estimated the economic impacts of leafy spurge (*Euphorbia esula*) in 1993 to Montana, North Dakota, South Dakota, and Wyoming to exceed \$129 million annually.

A critical component of integrated weed management (IWM) is the concept of prevention. Finding and addressing invasions early rather than waiting until they are

widespread is much more practicable and cost effective. The ideal is to prevent invasive species from arriving to new areas. Prevention is particularly important in systems such as range and wildlands because management budgets are often insufficient to address established weed infestations. However, if we are to be successful in preventing the spread of weeds, we must know something about how they get from one place to another.

The tumbleweed habit of dispersal is characterized when the entire aboveground portion of a senesced herbaceous plant breaks and rolls, dropping seed along the way in a wind-driven process. This dispersal mechanism has convergently evolved in at least nine disparate plant families including Chenopodiaceae, Amaranthaceae, Asteraceae, Brassicaceae, Boraginaceae, Fabaceae, Poaceae (Becker 1978), Lamiaceae (Roche and Wilson 1999), and Asphodelaceae (Heyligers 1999). There is surprisingly little research on tumbleweed dispersal, given the widespread nature of this adaptation.

A number of tumbleweeds have become important weeds. Among their impacts are strong competitive effects on desired vegetation (e.g., Weatherspoon and Schweizer 1969; Watson and Renney 1974; Crompton and Bassett 1985) and even the spread of radioactive waste (Warren 2001). Tumbleweeds are also anecdotally blamed for pasture fence damage due to accumulation of captured plants, and for the same reasons, accused of clogging waterways, and increasing fire hazard.

The focal plant for this work was *Centaurea diffusa*. Available forage in *C. diffusa* infested sites can be reduced by nearly 90% (Watson and Renney 1974, Harris and Cranston 1979). In addition to loss in productivity, there are increased erosion and decreased wildlife populations (Roché and Roché 1988).

C. diffusa was reported to infest over 745,000 ha in 17 western states and has an estimated 16% annual spread rate (Duncan and Jachetta 2005). In Colorado, where my study sites were located, *C. diffusa* was reported to infest approximately 12,000 ha in 1989 (Lacey 1989) and over 56,000 ha by 2005 (Colorado Department of Agriculture 2005). Even allowing for inaccuracies in mapping and reporting, this is rapid spread. Thus, reducing or preventing the further spread of this species should be a priority.

A possible means for limiting tumbling dispersal is the selective use of barrier fences. Nelson (2002) stated that fences were an overlooked management tool and, to my knowledge, there have been no efforts to use fencing expressly to limit the dispersal of a tumbleweed. Indeed, the initial impetus for this project was a question from a rancher about where fencing could be placed to limit the continued re-introduction and spread of *C. diffusa* onto his range.

Mechanistically, tumbleweed dispersal is very similar to secondary seed dispersal by wind where seed can be rolled along the ground by wind after falling from the parent plant. Secondary seed dispersal models such as those by Greene and Johnson (1997) and Schurr et al. (2005) might also be applied to tumbleweeds. The goal of such models was to estimate dispersal distances for seed blown across snow (Greene and Johnson 1997), or sand (Schurr et al. 2005). I know of no movement modeling efforts directed at the dispersal of tumbleweeds.

There is also some analogy between modeling the movement of tumbleweeds and modeling the movement of pollution clouds over complex terrain such as that by Hepner and Finco (1995). However, such models used diffusion-based approaches to model the movement of gaseous clouds in three dimensions and individual particles are assumed to

be without mass. These models also do not incorporate direct interaction with vegetation; a factor that could have a profound effect on the movement of tumbleweeds.

My objectives in this research were (1) to identify the major factors controlling dispersal of a tumbleweed, (2) to develop a model to predict movement across varied terrain and vegetation, and (3) to compare model results to observed dispersal patterns. If successful, the model will be used to guide placement of barriers to dispersal such as short, mid-pasture fences.

Methods

Field Sites. I selected two study sites in Colorado, USA for use in this research. One was on a private ranch near Larkspur, CO (north of Colorado Springs) (Figure 4.1a) and the other was on Boulder County Open Space property near Superior, CO (southwest of Boulder) (Figure 4.1b). The two sites were largely grassland and both were heavily infested with *C. diffusa*. The Larkspur site was approximately 400 m higher in elevation than the Superior site and had more shrub and woodland interspersed within its extent (though this is not fully reflected in Figure 4.1).

I placed a weather station (Hobo, Onset Computer Corporation) at each site. Each weather station was equipped with wind direction and speed, temperature, and humidity sensors and set to record every 5 minutes from October 2006 through April 2007.

GIS Data. I used USGS 10 m Digital Elevation Models (DEM) for both sites. These data were projected in UTM Zone 13N, NAD 83 and all subsequent data were matched to

this grain and projection. Southwest reGAP (SWreGAP) data (USGS National Gap Analysis Program 2004) were used for my vegetation cover data. Based on my observations, these data showed the best accuracy for both of my study sites when compared with the USGS National Land Cover Dataset (NLCD 1992) and the Colorado Vegetation Model (CVM) (Theobald et al. 2004). SWreGAP data are 30 m and were resampled to 10 m using the nearest neighbor algorithm to standardize them to the other datasets. After resampling, these data were reclassified into one of four categories; soil, grass, woodland (forest), and shrub (Table 4.1).

Wind data were derived from the meteorological model, MicroMet (Liston and Elder 2006). For my purposes, MicroMet was configured to generate two ASCII text files, wind direction and wind speed, which were converted to raster datasets. MicroMet begins by interpolating weather observations within an extent and then adjusts those values for known relationships with topography. I used 0.58 and 0.42 for the slope and curvature weights, respectively, as suggested by Liston and Elder (2006). The weather inputs to MicroMet were the mean wind direction and the 95th percentile of sustained wind speed measurements. This selection for wind speed was based on two premises: (1) I assumed that, while gusts may be important for breaking stems and initiating tumbling dispersal, sustained wind is more important for movement and (2) that wind events or storms, rather than the everyday, background wind, are important for movement. These assumptions are based on field observations of tumbling. During my time in the field, it seemed that the only time substantial movement occurred was during strong, sustained winds. I felt that the 95th percentile of sustained wind would be a reasonable

representation of major wind events that would drive dispersal without overly biasing wind calculations by inputting the maximum sustained winds.

All final surfaces were clipped from 6 by 8 km to the geographic extent of validation data plus a 1 km buffer on all sides. The final extent for the Larkspur site was 3 (east-west) by 3.7 km and 3.75 (east-west) by 2.7 km for the Superior site.

Movement Threshold Estimation. I collected 53 and 54 plants from my field sites as bolting rosettes in early June of 2004 and 2005, respectively, and transplanted them with their field soil into 3.8 L pots. They were reared outdoors with drip irrigation sufficient to prevent wilting until senescence began. Plants were transferred to a greenhouse and allowed to complete senescence without any additional water. After senescence was complete, I broke the stems near the soil surface and used a wind tunnel to estimate the minimum wind speed (m/s) necessary to move a plant.

Plants were placed in the wind tunnel with the stems upwind and wind speed gradually increased until tumbling movement was initiated. The wind speed at that moment was recorded. Wind tunnel air flow was monitored with a hot-film probe, in conjunction with a constant temperature anemometer (Hotwire anemometer, model 407123, Extech Instruments). This procedure was conducted for all plants on each of two surfaces; soil (fine gravel and sand) and grass. The grass was grown in flats and was also allowed to senesce before trials. Grass height was reasonably uniform at approximately 20 cm.

Observed Movement Data. I collected data on the movement of individual plants from October, 2006 through April, 2007 for comparison with modeled movement (hereafter referred to as validation data). Individual plants were clipped, marked with blue

spraypaint and fluorescent orange survey tape, labeled with unique numbers and released at various points within the extent of large pastures at each of my field sites. Release points were selected to provide plants with the maximum possible movement distance within the pastures, i.e., the upwind edges of pastures based on wind observations of the previous 2 years (Figure 4.1). While this may have introduced some bias into these data, I did not want to artificially restrict observations due to a lack of access to neighboring properties. A minimum of 3 plants were released at each point. GPS coordinates (Garmin GPSMAP 60CSx) were collected (UTM Zone 13N, NAD83) for each release point by averaging 30 points. The sites were searched by foot and the subsequent locations of released plants recorded with the same GPS methodology. My original intent was to search the sites at least every 4 weeks and release additional plants at each visit, however, weather precluded frequent visits. Plants found lodged in shrubs or fences such that movement was unlikely to continue were re-released at another location. Otherwise, plants were left where they were found and these locations could be considered release points for a new observation period.

Model. I developed a simple, mechanistic model to predict tumbling movement patterns of *C. diffusa* using geographic information system software (ArcGIS v9.2, ESRI) (Figure 4.2). This model predicts pathways of movement based on a source infestation of the plant, vegetation, topography, the estimated movement threshold modified by slope and vegetation, and wind speed and direction as modeled by MicroMet. In simplest terms, my model calculates whether or not there is sufficient physical force at a given location exerted by wind to overcome the resistance to movement exerted by landcover and slope. If the force exceeds the resistance, the model projects the direction of travel.

Based on my own observations, I assumed that shrubs present a barrier to tumbling plants while all other landcover types would allow plant movement if there was sufficient wind in a given cell. Wind speed was adjusted from the weather station observation height to a height of 0.2 m using the log wind profile (Sutton 1953, Monteith 1975, Goudrian 1977, Oke 1987, Stull 1988, Monteith and Unsworth 1990, Geiger et al. 2003):

$$u_z = \frac{u_*}{\kappa} \ln\left(\frac{z}{z_0}\right) \quad [4.1]$$

Where u_z is the wind speed at height z , u_* is the friction speed, κ is von Karman's constant (≈ 0.41), and z_0 is roughness length (a measure of surface roughness). In tall vegetation such as forests, an additional variable, d (zero plant displacement), is sometimes subtracted from z and is approximately 0.63 of the height of the roughness elements (Monteith 1975, Monteith and Unsworth 1990). However, this is only valid if the height at which wind speed is being calculated is at least $d + z_0$ (Sutton 1953). Since the height at which a plant experiences wind is much less than $d + z_0$, particularly in woodland cover types, d is not included here. I assumed a roughness length of 0.001 for grass, 0.003 for soil, and 1.0 for woodland. These values are the lower end of ranges given by Oke (1987) and are thus conservative in their estimation of the effect of vegetation on wind speed. I chose to use the lower estimates because roughness length depends on wind speed for these vegetation types with higher wind speeds resulting in lower roughness lengths due to a 'flattening' of the vegetation at high wind speeds (Sutton 1953). Friction velocity (u_*) is constant only for a given wind profile (Sutton 1953, Monteith 1975, Goudrian 1977, Oke 1987, Stull 1988, Monteith and Unsworth 1990, Geiger et al. 2003), so it was calculated separately for each cell using the observed

speed at station height. Values of u^* were used to calculate the wind speed at the height at which most plants experience wind. One half of the average height and canopy diameter of plants from my sites was 0.198 m (SE=0.45). Hence, 0.2 m was an approximate midpoint of both standing and prone plants and was a reasonable approximation for the height at which plants generally experienced wind.

The estimated movement threshold on soil was used for cover types such as dry lakebeds and roads, and the grass movement threshold was used for all grass and woodland cover types (Table 4.2). The woodland cover types such as ponderosa pine (*Pinus ponderosa*) that occur at my field sites are fairly open and typically have an understory component of grass and herbaceous vegetation. Therefore, I assumed that these cover types would not present the physical barrier that shrubs do. However, as wind speed is substantially reduced in woodland, grass and woodlands are not ultimately treated equivalently by the model.

The effect of slope was estimated using the following, well-established physical relationship:

$$F_s = F_l + mg \sin \alpha \quad [4.2]$$

where F_s is the force necessary to move an object up or down a slope; F_l is the force necessary for movement on a level; m is mass; g is acceleration due to gravity and α is the angle of the slope (positive or negative). This relationship requires that the wind speed threshold estimate be converted to units of force (N). From aerodynamics and wind engineering, the following equation relates the aerodynamic overturning moment to the wind speed and the remaining principal independent variables:

$$M_B = \left(\frac{1}{2} \rho U^2\right) C_M A \sqrt{A} \quad [4.3]$$

where M_B is the overturning moment associated with stem breaking, ρ is air mass density, U is wind speed, C_M is the moment coefficient and $A\sqrt{A}$ is volume, while A is a reference area. However, the units of a moment are in terms of force-length (e.g. N-m), so this might not be the most reliable means of calculating the force exerted on an average plant by a given wind speed. However, based on the established relationship in Equation 4.3 it seems reasonable to hypothesize a simple relationship of force with the square of wind speed.

Therefore, to develop a conversion between wind speed and force, I chose to estimate this relationship empirically with a subset of the plants used to estimate the movement threshold. Seven plants were visually selected from the plants used in estimating movement thresholds that were a representative range of plant sizes and shapes. The test section of the wind tunnel was equipped with a proximity sensor (GageProx 8mm unshielded proximity sensor, Kaman Instruments) calibrated to monitor wind drag effects on a plant. The output from this sensor was logged to a personal computer and sampled at 1-second intervals. Thirty samples per plant were used to calculate the temporal average of the acquired data. Output voltage ranged from 0.000 to 10.000 DCV over a calibration proximity range of 3 mm, giving proximity accuracy to 3 μm . The proximity was the distance between the sensor and a sensor target. The latter was a metal plate spring-mounted and furnished with a mount employed to test (individual) plants. Given that force is directly proportional to change in proximity, this device was calibrated to provide a conversion between wind speed and force exerted on a plant. During calibration, known force was applied to the system. These methods are similar to those used by Kawakita et al. (1992). Proximity was measured for wind speeds

of 0, 1.9, 3.4, 5.3, and 7.2 m/s conditions and the difference in proximity was converted into force, using the calibration conversion factor. These velocities were chosen for repeatability and represented approximately the full range achievable with the wind tunnel. Data for individual plants were regressed separately and the average parameter estimates used for converting wind speed to force.

Surfaces representing movement potential for plants were generated using wind data observed at the sites for selected time periods of observed plant movement. Movement potential was calculated by determining if there was sufficient wind to overcome vegetation type and slope. If movement could occur, the cell value was wind speed beyond the minimum speed necessary for movement at that cell. To convert values of wind force (N) used for calculating movement potential back to wind speed for more intuitive interpretation, I simply inverted the regression equation. Otherwise, the cell was assigned a value of NODATA; signifying a barrier to dispersal. (See Appendix C for metadata and Appendix D for documentation including map algebra syntax).

Prediction envelopes for directional movement were derived from the range of wind directions calculated by MicroMet for an observed movement period. Each envelope consisted of an acute triangle with a plant release point as its vertex. The legs were of arbitrary length at the maximum and minimum values of wind direction within the final model extent for each site and each validation period as modeled by MicroMet. I considered simply using confidence limits of the mean wind direction; however, even 99% confidence intervals were only 4 to 5 degrees in width. This narrow width seemed overly restrictive. Further, using the range of predicted output from MicroMet that a plant might encounter was a more consistent modeling approach.

I developed a second, locally based model for travel direction as well. Specifically, I used a method analogous to Individual Based Movement Modeling that I refer to as the surfacing technique. This model obtained local wind direction from the MicroMet output and drew a 5 m vector (half the grain of the surfaces) in that direction. The process repeated until a barrier (NODATA) value in the movement potential grid was encountered. Using vectors avoided the problem of 8-neighbors/8 possible directions in a raster data format. Allowing local variation in movement direction might increase the accuracy of overall movement direction and pattern. This effort was conducted manually for a few select movement observations as a preliminary assessment of the method's viability. Three lines were drawn. The first was the explicit predicted pathway based on wind direction. The other two represented prediction bounds based on the 99% confidence interval of mean wind direction.

Model results were deemed positive if (1) the observed relocation point for a plant fell within the prediction envelope and (2) there were no barriers modeled by the movement potential surface between the release and relocation points. Another prediction of the model is that plants should stop only where the movement potential surface predicted a barrier; either as a result of shrubs or insufficient wind. This prediction was evaluated by getting the value of the movement potential surfaces at each relocation point.

Analysis. Analyses of the wind-force data were performed with SAS (v9.1 The SAS Institute, PROC GLM). Data from individual plants were regressed with the change in proximity as the dependent variable and wind speed as the independent variable beginning with the full quadratic model and proceeding with backward model selection.

Resulting regression coefficients were averaged to derive a general model for converting wind speed to force.

Circular means and wind roses were generated with Oriana 2 (v2.02e, Kovach Computing Services 2007).

Results

Experimental parameters. From the wind tunnel trials, the mean (SE) movement thresholds for plants (n=104) were 3.8 m/s (0.1) on soil and 4.9 m/s (0.1) on grass.

Model inputs were simply the means for the two surfaces.

The empirically derived model for the wind-force relationship was (Table 4.2):

$$f = (\beta_0 + \beta_1 u^2 + \beta_2 u) \eta \quad [4.4]$$

where β s are regression coefficients, u is wind speed and η is the calibration conversion factor. Since the β estimates and η are known constants, Equation 4.4 can be reduced to:

$$f = \beta_0 + \beta_1 u^2 + \beta_2 u \quad [4.5]$$

and the inverse for back-converting is:

$$u = \frac{-\beta_2 + \sqrt{\beta_2^2 - 4(\beta_1)(\beta_0 - f)}}{2(\beta_1)} \quad [4.6]$$

Model results. I chose two validation sampling periods from each site for comparisons with predictions; one of a relatively short time span and one over a longer period.

Sampling periods were selected such that they were temporally non-overlapping though they include at least some of the same plants. The validation periods were (A) 20

November, 2006 through 28 March, 2007 and (B) 28 March, 2007 through 12 April, 2007 for the Larkspur site; and (C) 7 March, 2007 through 4 April, 2007 and (D) 5 April, 2007 through 19 April, 2007 for the Superior site. The weather station at the Superior site failed, so weather data were acquired from a weather station 3 km from the site (Weather Underground 2007).

Overall, the envelopes did not perform well at predicting the travel direction of tumbling plants. Only 4 of 37 observed relocation points fell within the predicted bounds with an additional three plants relocated within 3 m of an envelope (Table 4.3, Figure 4.3). The performance of the envelopes can also be evaluated by plotting the distance of relocation points from prediction envelopes versus the Euclidian (minimum) distance traveled (Figure 4.4). The worst case scenario is for a plant to travel in the direction opposite from that predicted. In this case, the distance from the relevant envelope and the travel distance for the plant are the same and its position in Figure 4.4 would fall on a line with slope of one. This method of assessing prediction accuracy is admittedly qualitative. However, observations near or on a line with slope equal to one demonstrate poor model performance, while those closer to the vertical axis show better support of the model. In addition, error in angle of travel is amplified with distance, but so is the width of the prediction envelopes. With this method of assessment, there were six observations that had traveled 50 m or more and were less than 20 m outside respective envelopes. There were five observations not shown in Figure 4.4 that were greater than 200 m from their respective prediction envelopes. Four of these fell near the line (slope = 1) while the fifth had traveled 1,602 m and was 305 m from the prediction envelope.

The results of the surfacing technique (a series of local predictions of travel direction) were similar to the more generalized envelopes, though with narrower prediction bounds (Figure 4.3a, b).

There were no plants that went beyond a predicted barrier to dispersal; however, only one of the relocation locations was at a point that the model predicted no movement would occur. The values of the movement potential surfaces at relocation points were at the approximate mid-point of the range of wind speeds beyond the movement threshold for the Larkspur site and at the lower end of the range for the Superior site (Table 4.4). However, the range of wind speeds beyond the movement threshold for the Superior site was substantially higher than those for the Larkspur site (Table 4.4).

Discussion

To my knowledge, there have not been any previous efforts to model the movement of a tumbleweed. As mentioned earlier, the closest analogy I am aware of is that of secondary seed dispersal. Secondary seed dispersal modeling efforts have been focused on dispersal distances on simple surfaces (Greene and Johnson 1997, Schurr et al. 2005). My emphasis has been on modeling restrictions to dispersal in complex terrain and complex surfaces.

It would seem to be intuitive that tumbleweed movement direction would closely follow wind direction. Based on these results, however, this seems to be true in only a very general sense. Most of the plants moved in a direction not completely contrary to

observed winds (Figure 4.3). Some of the poor performance of directional prediction at the Superior site may be attributable to the failure of the weather station and my resulting use of data from a weather station 3 km distant. Even so, predictions made based on weather data from a functioning station at the Larkspur site were substantially less accurate than I expected. It is also possible that mean wind direction was not representative of the winds that caused plant movement. The architecture of a plant could also affect the movement direction. For instance, most of these plants are taller than wide. This ovoid shape could incrementally change the direction of travel; an effect that would increase with distance traveled.

It came as something of a surprise that the surfacing technique did not show more promise. I feel that incorporating local variation in wind direction into the model is a stronger modeling approach. However, instantaneous wind direction does not vary greatly as modeled by MicroMet.

As with any modeling endeavor, there were a number of assumptions that went into building my model. One key assumption was that all of a given cover type (i.e., soil, grass, shrub, or woodland) is uniform and temporally static in its effects. Clearly, there can be both spatial and temporal variation in all of these landcover types that might either restrict or facilitate tumbling movement. It is likely that a plant could become stuck in a given set of conditions and that re-initiation of movement would take a great deal more force than the model currently incorporates in its predictions. Winter weather serves to flatten the previous summer's growth in grassland. Hence, movement at a given location in the late winter or early spring might require substantially less wind. Also, if a plant is available to tumble during snow cover, tumbling could be maximized. For instance, if a

plant grew in a location where wind cleared the snowfall and subsequently tumbled while a snowdrift covered shrubs, the plant could easily disperse well beyond where the model would predict a barrier.

The MicroMet outputs of wind speed and direction are a critical basis for this model. Therefore, the inputs for this meteorological model are key assumptions and must be carefully considered. I chose to input the mean wind direction. Other options are modes or the median. A local mode such as the direction of highest frequency, or the median wind direction are alternatives for predicting the direction of plant movement.

All but one of the plants stopped at locations where the model instead predicted movement *would* occur. This indicates that the model substantially overpredicts movement. This overprediction may be largely attributable to the choice of the 95th percentile of observed wind speed. Some of these may also be a result of inaccuracies in the SWreGAP dataset or local variation in vegetation structure. Small patches of shrubs or variations in vegetation might be enough to present a barrier to plant movement, but would not appear in data with a 30 m grain. Examination of the movement potential surfaces reveals that all of the regions where movement was predicted not to occur are where there is shrub cover type according to SWreGAP. This indicates that modeled resistance to movement on soil, grass, and woodland types based on the movement thresholds and topography is overcome by wind speed in all locations within the extent. Refinement and further testing of the model should systematically vary the inputs to MicroMet. It would be interesting if there is a point at which the input percentile of wind speed more accurately predicts stopping points and if this percentile is consistent between sites (though the latter seems unlikely). It is possible, however, that increasing the

accuracy of this model would necessitate creating a temporally explicit model. This could incorporate varying wind speed and direction rather than using a generalized weather condition over a given period of time.

The ultimate goal of this research was to take advantage of and supplement natural barriers to movement for the purpose of reducing the dispersal and spread of an invasive weed. If such natural barriers can be modeled, the spatial placement of barriers that mimic snow fences in function would be facilitated. Therefore, the exact direction a given plant will travel is less important than is knowledge and predictability of restrictions to dispersal. Though application to management at this point is limited and premature, this model provides a first effort and a good basis for future work.

Reliable information on the dispersal of invasive species is critical for a more proactive approach to management. Efforts in invasive species management are all too often reactive and extremely costly. When possible, preventing the introduction and spread of these species has greater potential for success in reducing the impacts and associated costs of management. Given the mechanistic basis for my model, it has the potential for broad application to the variety of species that disperse in this manner. If the accuracy of predictions can be improved, the model could be tested with other species simply by estimating a movement threshold for those species.

Future work should focus on several factors I have alluded to above. One priority is to determine which wind directions are important for plant movement. For instance, I used an overall mean wind direction. It is possible that the wind direction for a relatively short time period after the plant stem breaks dictates the direction of travel. A plant may be caught by local topographical or vegetation variation and re-initiation of movement

unlikely. Also, a mode of wind direction might be a more accurate predictor of plant movement direction. For instance, the mode in Figure 4.3a appears to be more representative of observed movement direction than the mean. However, this does not hold for the cases in Figures 4.3b, c, and d where there is no obvious, explicit relationship between observed wind direction and plant movement direction. There may also be means or modes of high winds that would better correlate with plant movement direction.

Another avenue of further research should be to more explicitly incorporate local variation in both space and time. The surfacing technique was a preliminary attempt to incorporate the spatial variation in wind direction. The shortcomings of this technique may be attributable to inaccuracies in the inputs to MicroMet as well as low instantaneous, spatial variability in modeled wind direction. Since wind varies more in time than in space (at least as modeled by MicroMet), extending the model to be temporally explicit might increase accuracy. However, this would also dramatically increase model complexity. For instance, decisions and assumptions would have to be made about the length of the time step, how far a plant would go during that time step and the entire modeling process repeated for every time step.

The wind speed inputs to MicroMet should be systematically altered to determine what inputs result in more accurate modeling of the movement potential. Once a reasonable prediction is achieved, it should be tested against other data or other sites. For instance, if the 75th percentile of observed wind speed provides the best fit to plant movement at the Larkspur site, that fit could be compared to predictions based on the 75th percentile at the Superior site. Alternatively, and perhaps more importantly, there may be a simple threshold of observed wind speed that indicates movement will occur and the

frequency at which that threshold is exceeded is an important factor in tumbling dispersal. Also, additional weather stations at study sites could improve the accuracy of MicroMet's outputs.

Finally, an important part of future work will be to collect detailed data of plant movement from several sites and years along with reliable, local weather data. These data should also include detailed observations describing the immediate local (<10 m) of post-release plant locations. This information could help to elucidate the influence of vegetation and topographical factors on plant movement that are unlikely to be well-represented by available raster datasets due to spatial resolution. These data will aid in gaining greater insight into the important factors influencing tumbling dispersal and allow the use of alternative approaches such as diffusion-based modeling.

Literature Cited

- Becker, D. A. 1978. Stem abscission in tumbleweeds of the Chenopodiaceae: *Kochia*.
Amer. J. Bot. **65**: 375-383.
- Colorado Department of Agriculture. 2005. Conservation Services Division, Noxious
Weed Management Program.
<http://www.ag.state.co.us/CSD/Weeds/mapping/QuarterQuadSurvey.html>
- Crompton, C. W. and I. J. Bassett 1985. The biology of Canadian weeds. *Salsola pestifer*.
Can. J. Plant Sci. **65**: 379-388.
- Duncan, C. L. and J. J. Jachetta. 2005. Introduction. Pages 1-7 in C. L. Duncan and J. K.
Clark, eds. Invasive plants of range and wildlands and their environmental,
economic, and societal impacts. Weed Science Society of America, Lawrence,
KS.
- Elliot, K. J. and A. S. White. 1989. Competitive effects of various grasses and forbs on
ponderosa pine seedlings. For. Sci. **33**:356-366.
- Geiger, R., R. H. Aron, and P. Todhunter. 2003. The climate near the ground, 6th edition.
Rowman and Littlefield Publishers, Inc., Lanham, MD.
- Goudrian, J. 1977. Crop micrometeorology. Center for Agricultural Publishing and
Documentation, Wageningen, The Netherlands.
- Greene, D. F., and E. A. Johnson. 1997. Secondary dispersal of tree seeds on snow. J. of
Ecology **85**:329-340.
- Gurevitch, J. and D. K. Padilla. 2004. Are invasive species a major cause of extinctions?
TREE **19**: 470-474.

- Harris, P., and R. Cranston. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in western Canada. *Can. J. Plant Sci.* **59**:375-382.
- Hepner, G. P. and M. V. Finco. 1995. Modeling dense gaseous contaminant pathways over complex terrain using a geographic information system. *Journal of Hazardous Materials.* **42**: 187-199.
- Heyligers, P.C. 1999. Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and *Trachyandra divaricata* in Australia. *Cunninghamia* **6**:315-329.
- Hirsch, S. A. and J. A. Leitch. 1996. The impact of knapweed on Montana's economy. *Ag. Econ. Rep. No. 355.*
- Johnson, S. 1986. Alien plants drain western waters. *The Nature Conservancy News*, Oct-Nov 1986.
- Kawakita, S., B. Bienkiewicz, and J. E. Cermak. 1992. Aeroelastic model study of suspended cable roof. *Journal of Wind Engineering and Industrial Aerodynamics.* **41-44**: 1459-1470.
- Lacey, C. A. 1989. Knapweed management: a decade of change. Pages 1-6 *in* P. K. Fay and J. R. Lacey (eds.), *Proc. Knapweed Symp.*, April 4-5, 1989. Montana State Univ., Bozeman. EB45.
- Lacey, J. R., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaureamaculosa*) on surface runoff and sediment yield. *Weed Technol.* **3**:627-631.
- Leitch, J. A., F. L. Leistritz, and D. A. Bangsund. 1996. Economic impact of leafy spurge in the upper Great Plains: Methods, models, and results. *Impact Assessment* **14**:419-433.

- Liston, G. E., and K. Elder. 2006. A meteorological distribution system for high-resolution terrestrial modeling (MicroMet). *J. Hydrometeorology* 7:217-234.
- Monteith, J. L. 1975. *Vegetation and the atmosphere*. Academic Press, London.
- Monteith, J. L., and M. Unsworth. 1990. *Principles of Environmental Physics*, 2nd edition. Edward Arnold, London.
- Nelson, J. K. 2002. *C. diffusa* movement – A critical, often overlooked component of control. *Proc. Wes. Soc. Weed Sci.* 55:54.
- NLCD 1992. National Land Cover Dataset. <http://landcover.usgs.gov>
- Oke, T. R. 1987. *Boundary layer climates*, 2nd edition. Methuen and Co., New York.
- Roché, C. T., and B. F. Roché Jr. 1988. Distribution and amount of four knapweed (*Centaurea* L.) species in eastern Washington. *Northwest Science* 62:242-253.
- Roché, C. T. and L. M. Wilson. 1999. Mediterranean Sage. Pages 261-270 in R. L. Sheley and J. K. Petroff, eds. *Biology and Management of Noxious Rangeland Weeds*. Corvallis, OR: Oregon State University Press.
- Schurr, F. M., W. J. Bond, G. F. Midgley, and S. I. Higgins. 2005. A mechanistic model for secondary seed dispersal by wind and its experimental validation. *J. of Ecology* 93:1017-1028.
- Stolgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology* 1:11-14.
- Stull, R. B. 1988. *An introduction to boundary layer climates*. Kulwer Academic Publishers, Dordrecht, The Netherlands.
- Sutton, O. G. 1953. *Micrometeorology*. McGraw-Hill Book Co, London.

- Theobald, D. M., N. Peterson, and W. Romme. 2004. The Colorado Vegetation Model: Using National Land Cover Data and Ancillary Spatial Data to Produce a High Resolution, Fine-Classification Map of Colorado (v8). 4 February. Unpublished report, Natural Resource Ecology Lab, Colorado State University.
- Thompson, M. J. 1996. Winter foraging response of elk to spotted knapweed removal. *Northwest Sci.* **70**:10-19.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **78**:81-92.
- Trammell, M. A. and J. L. Butler. 1995. Effect of exotic plants on native ungulate use of habitat. *J. Wildl. Manage.* **59**:808-816.
- USGS National Gap Analysis Program. 2004. Provisional Digital Land Cover Map for the Southwestern United States. Version 1.0. RS/GIS Laboratory, College of Natural Resources, Utah State University.
- Warren, R. W. 2001. Sorption and transport of radionuclides by tumbleweeds from two plastic-lined radioactive waste ponds. *J. Environmental Radioactivity* **54**:361-376.
- Watson, A. K. and A. J. Renney 1974. The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. *Can. J. Plant Sci.* **54**:687-701.
- Weather Underground. 2007. wunderground.com Station KCOSUPER3. Accessed June, 2007.
- Weatherspoon, D. M. and E. E. Schweizer. 1969. Competition between kochia and sugarbeets. *Weed Sci.* **17**: 464-467.
- Whisenant, S. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. *Proc. Symp. Cheatgrass invasion, shrub dieoff, and*

other aspects of shrub biology and management, 4-10. USFS Gen Tech. Rep.
INT-276.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying
threats to imperiled species in the United States. *BioScience* **48**:607-615.

Table 4.1. Reclassification from SWreGAP values to generalized values used in modeling restrictions to the tumbling dispersal of *C. diffusa*.

Site	SWreGAP Description	Model Classification
Larkspur	Rocky Mountain Montane Dry-Mesic Mixed Conifer Forest and Woodland	Woodland
	Rocky Mountain Montane Mesic Mixed Conifer Forest and Woodland	Woodland
	Rocky Mountain Ponderosa Pine Woodland	Woodland
	Rocky Mountain Gambel Oak-Mixed Montane Shrubland	Shrub
	Western Great Plains Foothill and Piedmont Grassland	Grass
	Western Great Plains Riparian Woodland and Shrubland	Shrub
	Western Great Plains Floodplain Herbaceous Wetland	Grass
	Open Water	Soil
	Developed, Open Space - Low Intensity	Woodland
	Developed, Medium - High Intensity (Road)	Soil
	Agriculture	Soil
	Invasive Perennial Grassland	Grass

Superior	Western Great Plains Cliff and Outcrop	Soil
	Rocky Mountain Ponderosa Pine Woodland	Woodland
	Rocky Mountain Gambel Oak-Mixed Montane Shrubland	Shrub
	Rocky Mountain Lower Montane-Foothill Shrubland	Shrub
	Inter-Mountain Basins Mixed Salt Desert Scrub	Shrub
	Western Great Plains Foothill and Piedmont Grassland	Grass
	Western Great Plains Shortgrass Prairie	Grass
	Western Great Plains Riparian Woodland and Shrubland	Shrub
	Western Great Plains Floodplain Herbaceous Wetland	Grass
	Open Water	Soil
	Developed, Open Space - Low Intensity	Woodland
	Developed, Medium - High Intensity (Road)	Soil
	Agriculture	Soil
	Recently Burned	Grass
	Invasive Perennial Grassland	Grass

Table 4.2. Parameter estimates for the derivation of a conversion between wind speed and force exerted on a plant by wind speed. With the exception of the R-square, which is reported as a range, parameter estimates are reported as the means from regressions on individual plants (n=7). The general form of the regression is: $f = \beta_0 + \beta_1 u^2 + \beta_2 u$ where u = wind speed and the entire equation was multiplied by a constant to convert from wind tunnel measurements to force (N).

Parameter	Estimate	SE
β_0	0.004	0.002
β_1	0.021	0.006
β_2	0.022	0.007
R-square (range)	0.991 to 0.999	

Table 4.3. Assessment of prediction envelopes with relocation points. Test periods are: (A) 20 November, 2006 through 28 March, 2007 at Larkspur, CO; (B) 28 March, 2007 through 12 April, 2007 at Larkspur, CO; (C) 7 March, 2007 through 4 April, 2007 at Superior, CO; (D) 5 April, 2007 through 19 April, 2007 at Superior, CO.

Test Period	# Relocated	#Relocated w/in envelopes	Nearest misses
(A)	15	2	3 m (180 m travel dist.) 1 m (30 m travel dist.)
(B)	17	2	2 m (10 m travel dist.)
(C)	4	0	none
(D)	6	0	20 m (490 m travel dist.)

Table 4.4. Values of predicted wind speed beyond minimum necessary for movement (from movement potential surfaces) at relocation points compared to range of possible values. Test periods are: (A) 20 November, 2006 through 28 March, 2007 at Larkspur, CO; (B) 28 March, 2007 through 12 April, 2007 at Larkspur, CO; (C) 7 March, 2007 through 4 April, 2007 at Superior, CO; (D) 5 April, 2007 through 19 April, 2007 at Superior, CO. SE = standard error.

Test Period	Predicted Range (m/s)	Mean Value (m/s)	SE	MicroMet Input (m/s)
(A)	0, 7.2	4.3	0.27	10
(B)	0.1, 7.6	4.5	0.27	10.4
(C)	11.5, 21.4	13.2	0.11	22.4
(D)	13.5, 24.6	14.9	0.08	24.6

Figure 4.1. (following two pages) Maps of the study sites used in this research showing plant release points for model validation. The sites were located near Larkspur (a) and Superior (b) Colorado, USA. Vegetation data were reclassified from SWreGAP data, road data were from TIGER 2000, stream data from the National Hydrology Data, and elevation data were from USGS digital elevation models.

a

Legend

× Release Points

Roads

— Interstate Highway

— Arterial

Streams

— Creek

— Artificial Path

Vegetation

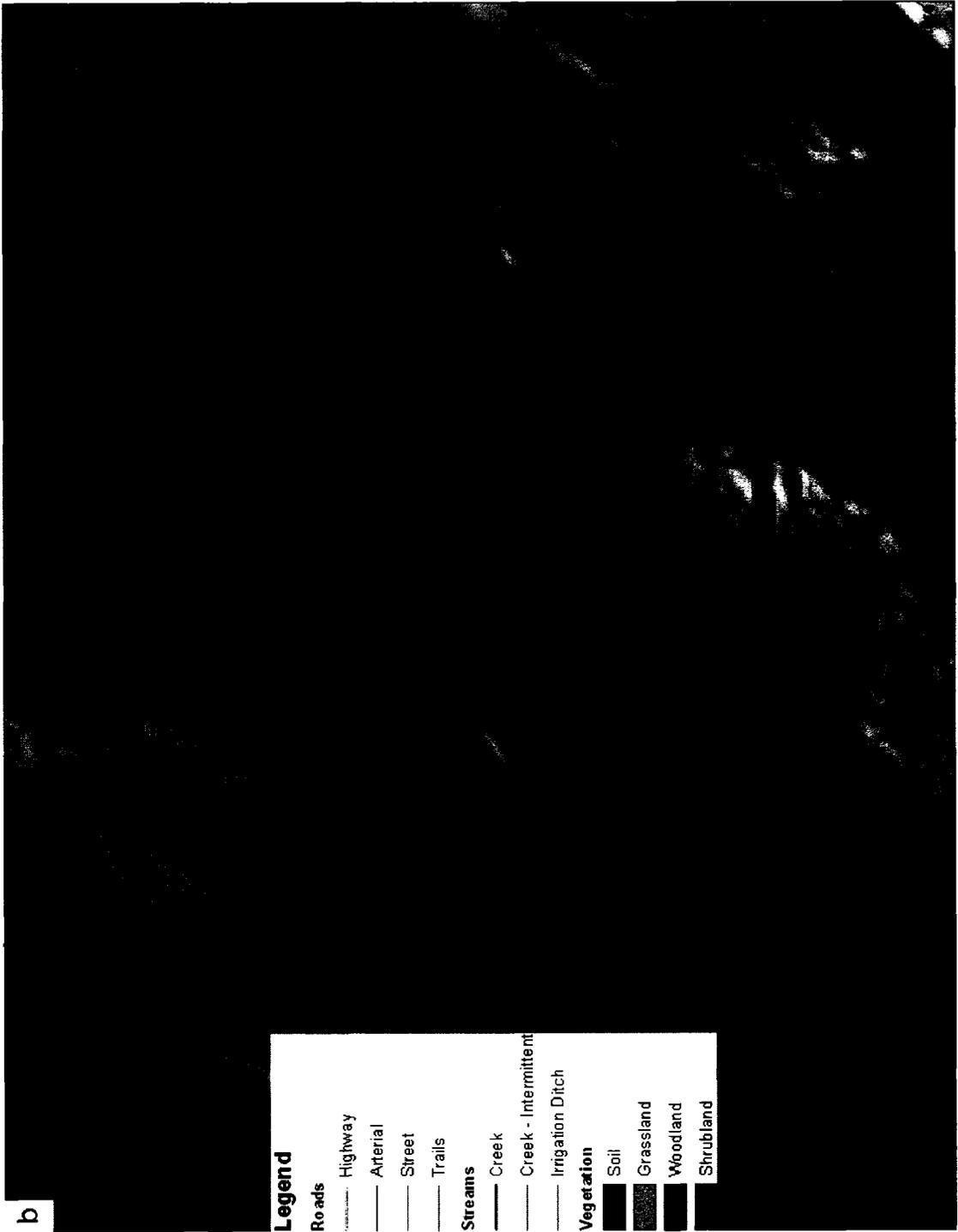
■ Soil

■ Grassland

■ Woodland

■ Shrubland





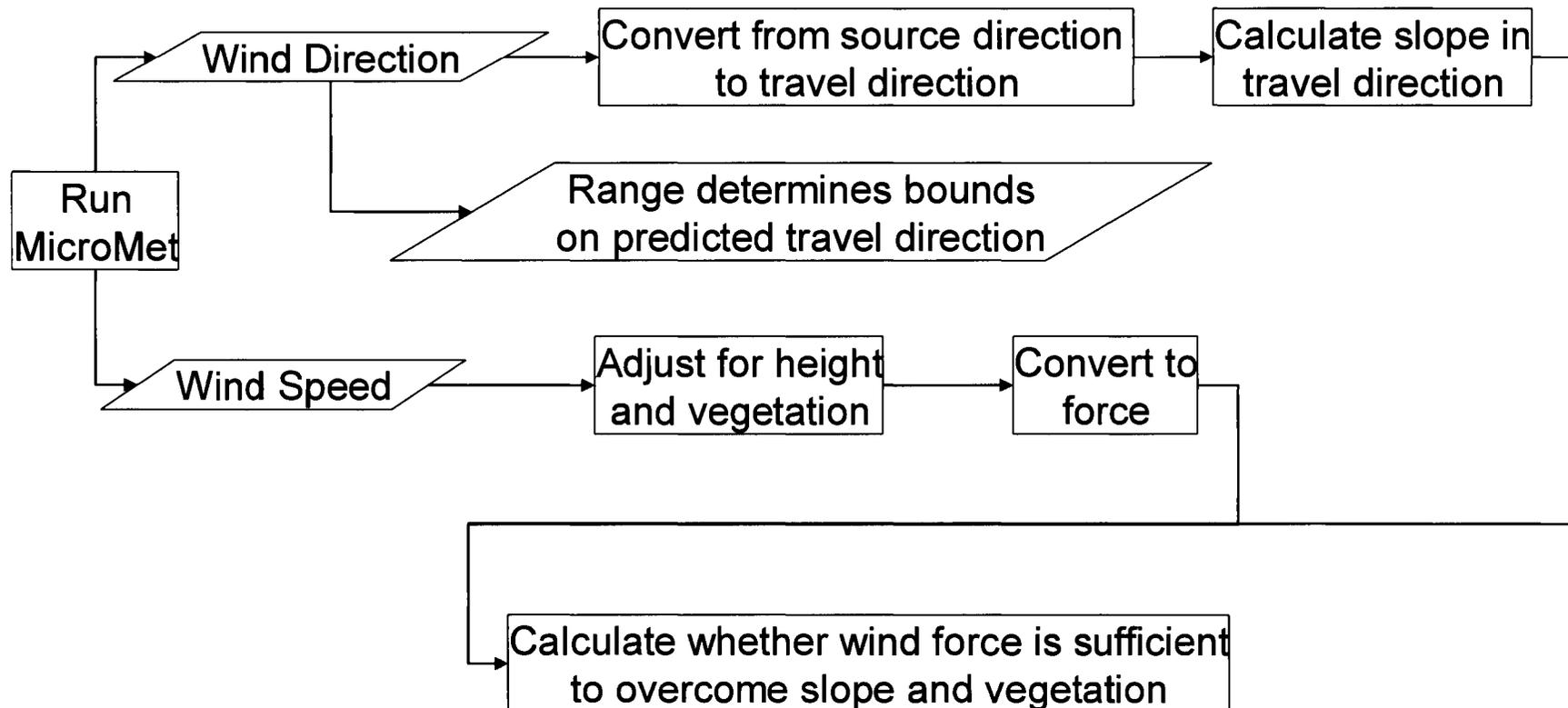
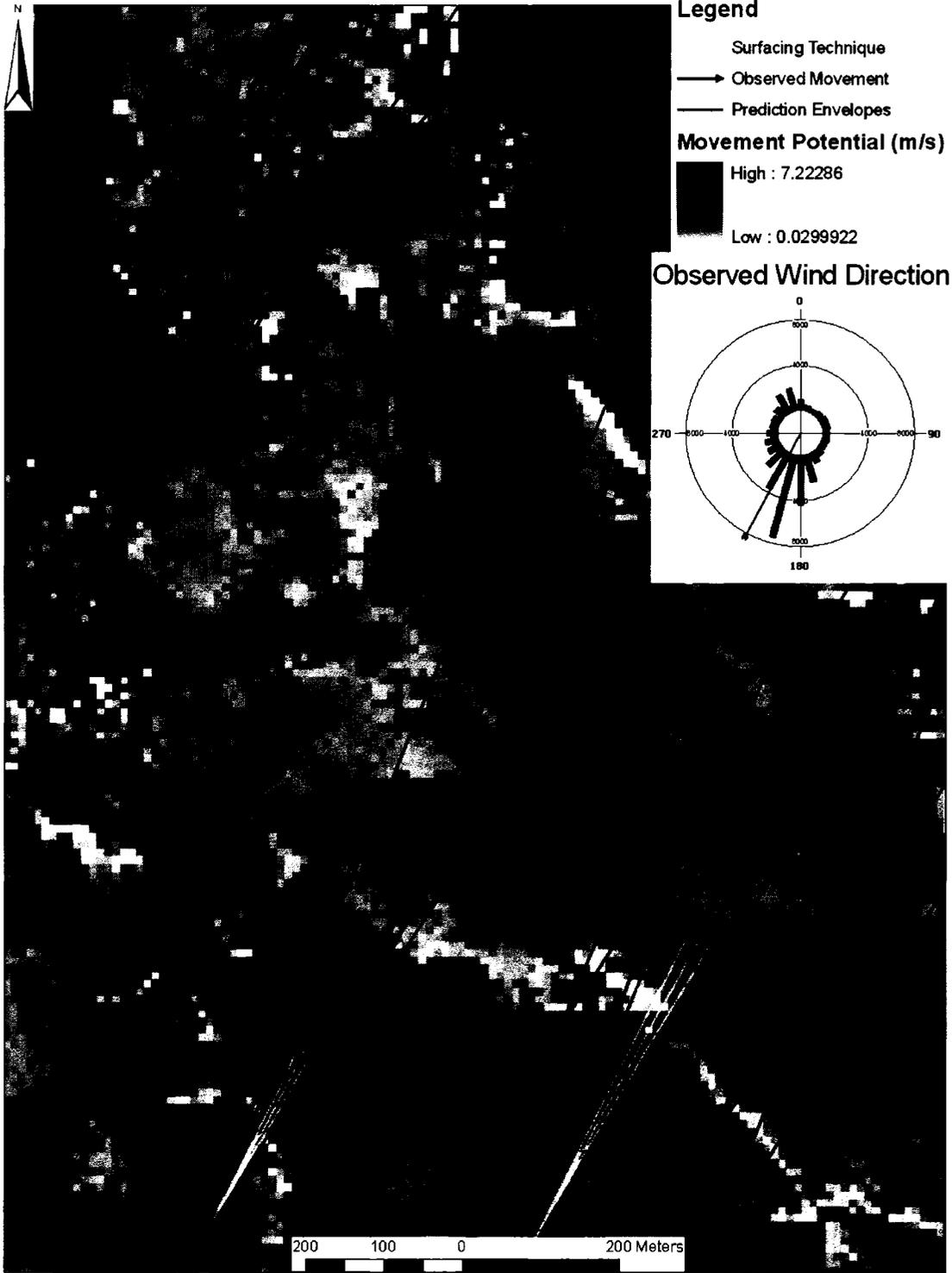
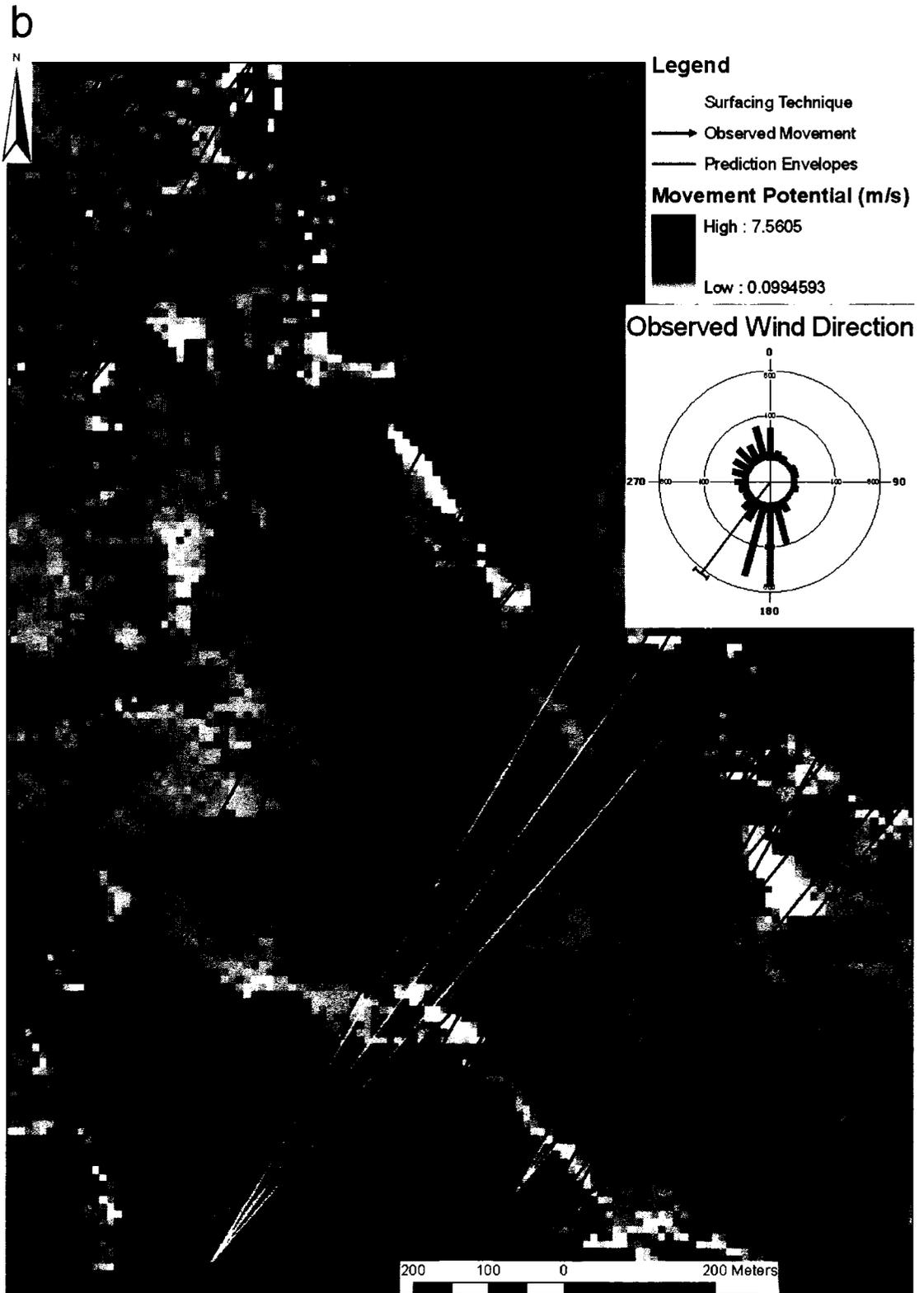


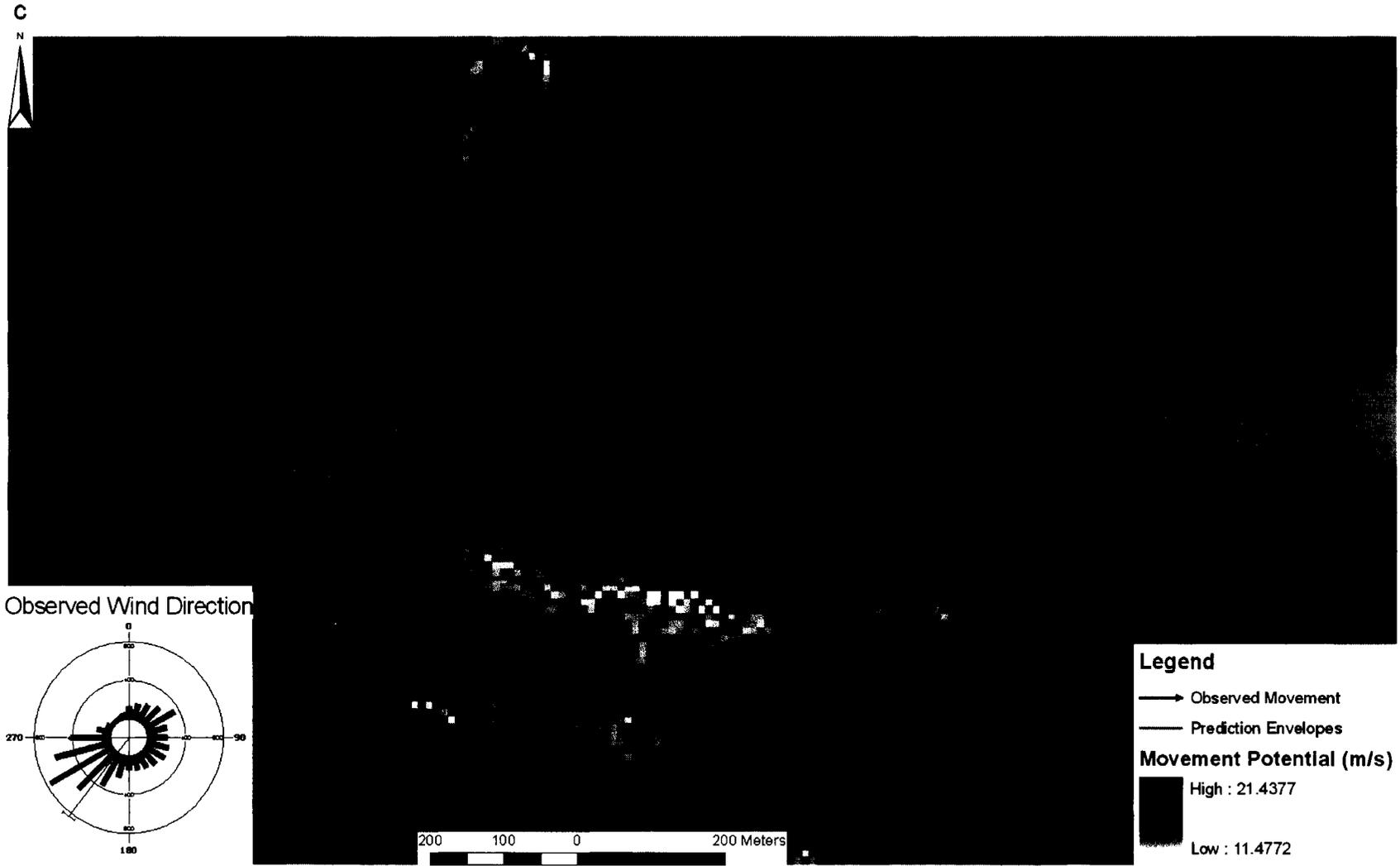
Figure 4.2. Model flowchart.

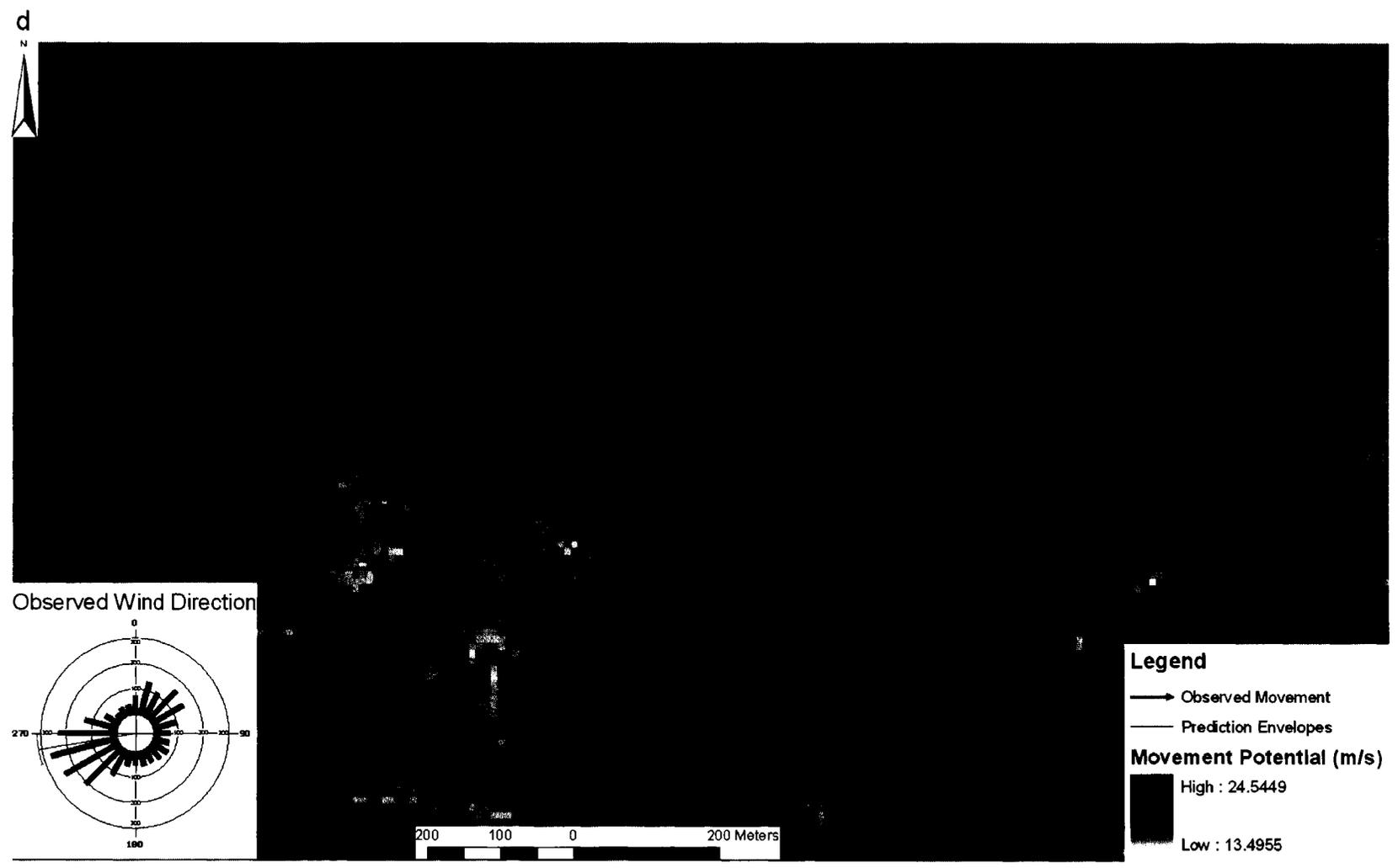
Figure 4.3. (Following 4 pages) Movement potential surfaces and movement direction prediction envelopes compared to observed movement. Green indicates predicted barriers to tumbling movement. Test periods are: (a) 20 November, 2006 through 28 March, 2007 at Larkspur, CO; (a) 28 March, 2007 through 12 April, 2007 at Larkspur, CO; (c) 7 March, 2007 through 4 April, 2007 at Superior, CO; (d) 5 April, 2007 through 19 April, 2007 at Superior, CO. Initial tests of the surfacing technique are shown in a and b.

a









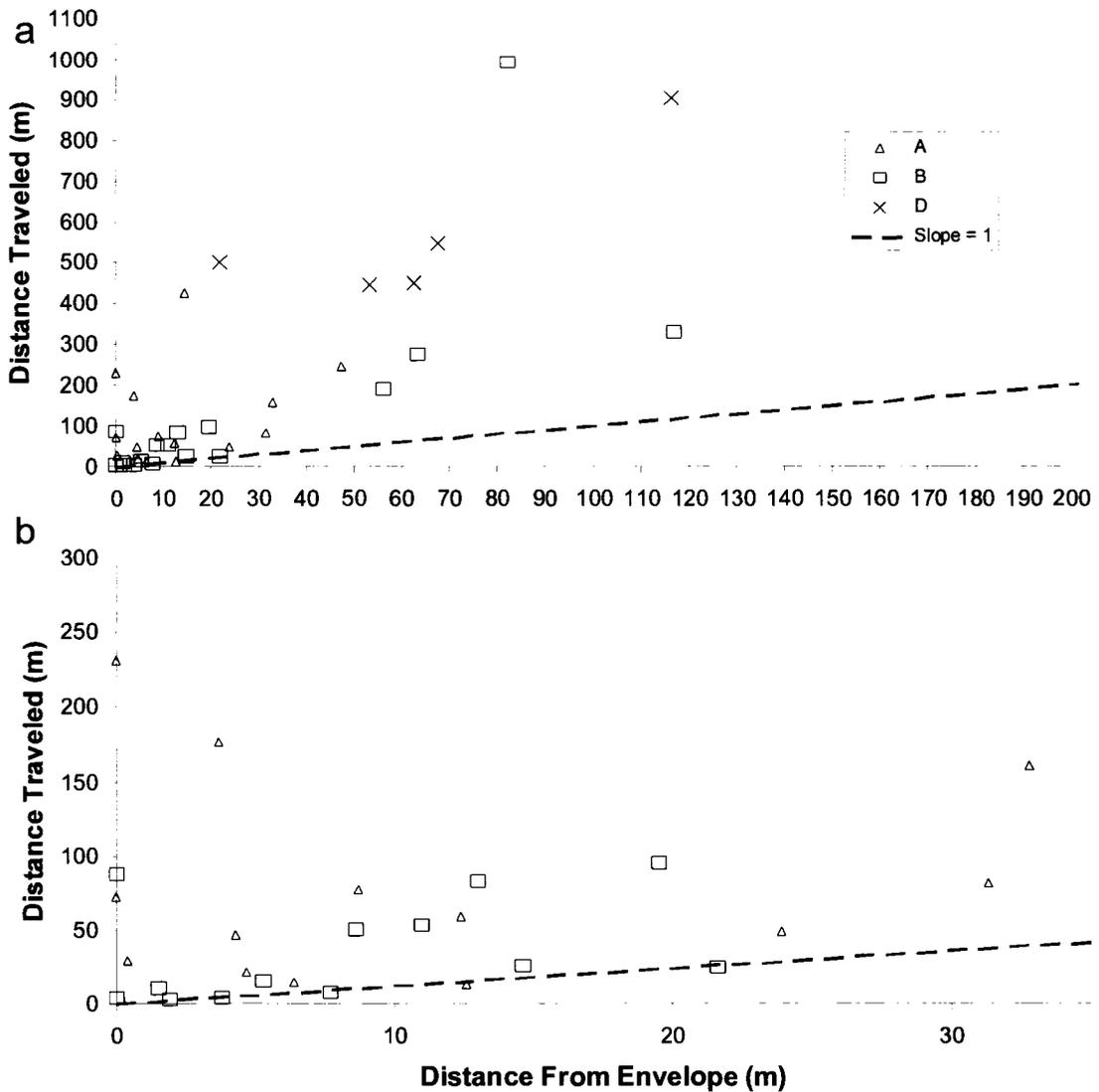


Figure 4.4. Distance of observations from respective directional prediction envelopes versus their travel distance. Figure b simply offers a closer view of observations near the origin. Test periods are: (A) 20 November, 2006 through 28 March, 2007 at Larkspur, CO; (B) 28 March, 2007 through 12 April, 2007 at Larkspur, CO; (D) 5 April, 2007 through 19 April, 2007 at Superior, CO. Five observations that were greater than 200 m from their respective envelopes are not shown. Four of these fell near the line of slope = 1, while the fifth was 305 m outside its envelope after traveling 1,602 m.

Chapter 5: Seed Dispersal of *Centaurea diffusa* via the Tumbleweed Mechanism

Introduction

Wind dispersal of seed has received strong attention in recent years (see reviews by Nathan and Muller-Landau (2000) and Levin et al. (2003), and the special section of the 11 August, 2006 issue of Science). The first international conference on movement ecology was held in June, 2007 in Israel. One mechanism of seed dispersal that remains little-studied is that of a tumbleweed. The tumbleweed mechanism of dispersal is characterized by the entire above-ground portion of a senesced herbaceous plant breaking and rolling, dropping seed along the way in a wind-driven process. The point at which the plant breaks is typically at or about the soil surface.

To my knowledge, only two works have been published on tumbleweed seed dispersal distances (Mehlman 1993, Stallings et al. 1995) and neither of these developed dispersal models. Tumbleweeds have evolved in at least nine disparate plant families including Chenopodiaceae, Amaranthaceae, Asteraceae, Brassicaceae, Boraginaceae, Fabaceae, Poaceae (Becker 1978), Lamiaceae (Roche and Wilson 1999), and Asphodelaceae (Heyligers 1999). Many of these are economically or ecologically

important invasive weeds, or both. The invasive weed *Centaurea diffusa* is one of these and is legally designated as noxious in most of Western North America.

While I know of no other research that has modeled seed dispersal for a tumbleweed, secondary dispersal of seed by rolling along a substrate is a similar process. Mechanistic models of secondary seed dispersal such as those developed by Greene and Johnson (1997) and Schurr et al. (2005) might have potential for modeling the distances that tumbleweeds will travel. However, a tumbleweed may or may not retain seed for the full distance that the plant skeleton will move. Therefore, such models do not seem to have direct application to modeling seed dispersal distances for a tumbleweed. I used an analytical approach as an initial effort in modeling seed dispersal distances of *C. diffusa*.

Objectives of this work were to use wind tunnel and field experiments to measure seed dispersal distances for *C. diffusa* as a tumbleweed and evaluate the predictability of seed dispersal distances and the potential for long distance dispersal (LDD). For a tumbleweed, LDD may be defined relative to seed dispersal distances in the absence of tumbling. Without tumbling, primary seed dispersal is unlikely to be more than a few meters.

Methods

Field. Study Sites were established near Larkspur and Superior, Colorado, USA. In September, 2004 a fence 60 m long and 1.5 m tall was erected at each site. Also in September, 60 *in situ* plants were located upwind of each fence, tagged and painted.

Plant height, canopy diameter and stem diameter at the soil surface were recorded along with GPS (Garmin MAP76S, average of 30 points) coordinates (UTM Zone 13N, NAD83) for each plant and each end of the fence. An estimate of plant volume was derived from the plant height and canopy diameter measurements using the formula for a prolate spheroid. The fences were monitored weekly through March, 2005, and any plant caught by the fence was collected and its distance from one end of the fence noted. The Pythagorean Theorem was used to calculate distance from a plant's origin to its capture point based on their respective coordinates. This process was repeated the following for September 2005 through March 2006.

To quantify seed loss in plants that did not tumble, I randomly collected plants from the vicinity of marked plants at 6-week intervals beginning in September 2005 and ending in March 2006 for a total of five collection dates. Ten plants were collected from each site at each sampling date for a total of $n=100$. I collected the plant closest to the point reached by taking a random number of steps in a random direction from a haphazard starting point that was generated independently for each individual. The same size characteristics as above were measured for each plant.

Wind Tunnel. Twenty haphazardly selected plants were transplanted from my study sites into pots in June of 2005 and reared outdoors with adequate water to prevent wilting. When senescence began, the plants were moved to a greenhouse and allowed to complete senescence.

I designed and constructed a wind tunnel for this and related experiments. The test section of this tunnel was 8 m in length. A transparent, adhesive surface (carpet masking) was placed adhesive side up in the test section of the tunnel, a plant was placed

in the tunnel and wind sufficient to move the plant was generated. This was repeated three additional times such that each plant ($n=19$) tumbled a total of 30.5 m across the adhesive surface. New adhesive was used for each run, and paper towel was placed over the seed to secure it on the adhesive, and to provide a light background to aid seed counting.

Estimating Seed per Plant. All matured heads from each collected or relocated plant were clipped into a tray and counted. Thirty capitula (or all if fewer than 30) were randomly selected and the number of seed counted in each. The average seed per capitulum multiplied by the number of heads was my estimate for total seed per plant. This estimate was made for all field-collected plants as well as for plants used in the wind tunnel trials. I also noted whether there was any evidence of biocontrol insect damage to the capitula and whether the capitula had opened or not. A capitulum was defined as open if the tips of its bracts were wider than the base of the capitulum.

Analyses. I used two analytical approaches. I first focused exclusively on the tunnel data to develop a model of cumulative seed deposition (or rain) with distance. A script developed with the R Statistical Package (v2.4.1) was used to iteratively estimate parameters for cumulative seed deposition. The script used a non-linear routine that assumed a Poisson error distribution to estimate parameter values and their variance (the script is included in Appendix D). I estimated initial values of all three parameters based on visual inspection of graphs.

My second and broader approach was to develop models to predict the number of seed remaining in a plant and used a balanced bootstrap method (Manley 2007) to estimate confidence intervals for parameters and predictions. This approach was used (1)

to develop two competing models (linear and exponential decay) for seed retention in plants with distance and (2) to develop a model for seed retention in plants over time. For the distance models I used multiple regression (SAS v9.1; PROC GLM) on the tunnel data to develop an initial model of the number of seed remaining in a plant (untransformed and natural log transformed data) with distance. The independent variables used in the regression were distance, stem diameter and plant volume. Bootstrapped predictions were compared to data from field collections.

Similarly, I used multiple regression on the non-dispersed data to develop an initial model of seed retention in plants with time and used bootstrapping to estimate confidence intervals for seed retention over time.

Lastly, I used the non-dispersed data to examine the correlation of seed with biocontrol insects and whether or not capitula were open.

Results & Discussion

Cumulative Seed Deposition. On average, 8% (SE = 1.6) of the total seed were lost from plants in the wind tunnel trials. This simple statistic alone suggests that there is a strong potential for LDD of diffuse knapweed; seed dispersal distances in the hundreds of meters if not more. Upon examination of the graph of the number of seed observed with distance tumbled (not shown), two patterns became apparent. The first was that, as the plant tumbled, seed were not only deposited simply by falling from capitula, but also as entire capitula and even branches that broke from the plant and were deposited. This

latter process results in a large number of seed being deposited at sporadic intervals. This is analogous to the findings of Mehlman (1993) who investigated the tumbleweed dispersal of a Fabaceous species. He found that fewer seed pods remained on plants that had tumbled longer distances, though the maximum distance he recorded was only 160 m (Mehlman 1993). He did not, however, explicitly quantify seed dispersal in this work.

Secondly, there were clear periodic modes in the data associated with the length of the wind tunnel. Specifically, there seemed to be few seed deposited at the beginning of a given run and the rate of deposition increased to a point and leveled off. This pattern suggested that there was a relationship between the velocity of the plant and the number of seed deposited. This pattern was also intuitively appealing, as I would expect that the greater forces (centrifugal and otherwise) at greater tumbling velocity to increase seed deposition rates. Therefore, I hypothesized that the following model would adequately describe cumulative seed deposition over the 30.5 m of the experiment:

$$s_{loss} = (\alpha - \beta z) \left(\frac{d}{d_{half} + d} \right) \quad [5.1]$$

where α is the maximum rate of seed deposition, β is the rate at which α declines with distance, z is overall distance, d is distance since the beginning of a run and d_{half} is the distance since the beginning of a run at which a plant reaches half of its maximum velocity. The first factor in brackets represents linear seed loss with distance while the second represents the dependency of the seed loss rate on the velocity of the plant. Note that the velocity factor contains only distance values; thereby illustrating that I assumed a relationship between velocity and location in the wind tunnel.

The process of capitula being deposited from plants was more stochastic. The most extreme example occurred where several heads dropped at once, resulting in 108

seed deposited within one linear cm. Therefore, I chose to evaluate the accuracy of this model first with data resulting from seed dropped directly from plants (excluding data resulting from dropped capitula) as an initial assessment. The model's predictive ability was further evaluated with the entire dataset.

Finally, I simplified Equation 5.1 by eliminating the velocity component as follows:

$$s_{loss} = \alpha - \beta z \quad [5.2]$$

This allowed me to determine the importance of velocity in Equation 5.1 and its impact on accurately predicting cumulative seed deposition.

I evaluated the accuracy of the models by plotting predicted versus observed and performing a linear regression analysis (SAS v9.1; PROC GLM; The SAS Institute) (Table 5.1). All three of these models demonstrate a high degree of predictive capability as indicated by R-square values of essentially 1 as well as minimal bias indicated by slope estimates of essentially one and low associated standard errors. In fact, I was surprised by the high accuracy of model predictions given the high variability of observations, particularly variability introduced by the seemingly stochastic process of capitula dropping from plants. It is important to note that residual plots from these accuracy assessments indicate that variance is not homogeneous; therefore standard errors and p-values may be questionable in their accuracy.

There are, however, several limitations to these models. All three are based on the cumulative seed deposition of 19 plants over 30.5 m and four runs. Given plant characteristics such as stem diameter and plant volume were not included, my inference is limited to those 19 plants cumulatively. Further, those 19 plants were reared in pots

with adequate water. While I made efforts to simulate a field setting by using field soil and keeping the plants outdoors while they were growing, the additional water and probable difference in root-zone soil temperatures may have influenced plant growth and seed production relative to plants in a more natural setting. On the other hand, potted plants may require additional water simply to survive compared to field plants. In addition, for all three models, β (the rate of decline in seed deposition with distance) is assumed to be linear. A more realistic assumption might be that of an exponential decline. A linear β will ultimately force predicted seed deposition to be negative beyond some distance. Moreover, it is likely that those seed that are easily dislodged from the plant would be rapidly deposited while those that are more tightly held might remain in the plant for much greater distances.

In spite of these limitations, seed deposition, particularly cumulative, can be accurately predicted as a function of distance and tumbling velocity. It is also apparent that the velocity factor in the model is not necessary for accurate prediction. This is fortunate, since the velocity of plants would be a difficult parameter to estimate for further application of these models. Therefore, I suggest that the two parameter model is the better of those tested for its simplicity without a substantial sacrifice in accuracy or precision.

Seed Dispersal Distance. While the initial full model of the number of seed retained in a plant had strong explanatory power ($R^2 = 0.841$), the model also showed strong evidence for a relationship between residual error variance and predicted values, with error variance decreasing sharply with increased predicted values. Predicted values fell into three relatively discrete groups so the dataset was divided three ways and the full model

analyzed for each distinct data set. The full model analysis within each sub-dataset showed relatively constant error variance with predicted values. Therefore, a weighted regression analysis was performed on the entire dataset with regression weights defined according to an additional variable w :

$$w = \frac{1}{MSE_i} \quad [5.3]$$

where MSE_i is the mean squared error associated with the individual regression performed on sub-dataset i . Such weighting has been previously cited as an acceptable remedial measure for instances of unequal variance (Neter et al. 1996). Equation 5.3 served as an initial approximation for regression weights. The weights were further iteratively adjusted until the model residuals appeared to adequately satisfy the assumptions of linear regression. The following was the resulting model:

$$N_{seed} = \beta_0 + \beta_1 z + \beta_2 s + \beta_3 v + \beta_4 zs + \beta_5 zv + \beta_6 sv + \beta_7 zsv \quad [5.4]$$

where β_s are regression coefficients, z is distance (m), s is stem diameter (mm), and v is plant volume (cm³).

This methodology was repeated for an exponential decay model with the following result:

$$N_{seed} = e^{\beta_0 + \beta_1 z + \beta_2 s + \beta_3 v + \beta_4 zs + \beta_5 zv + \beta_6 sv + \beta_7 zsv} \quad [5.5]$$

All parameter estimates for Equations 5.4 and 5.5 were significantly different from zero at $\alpha = 0.0001$.

The parameters of both of these models and their respective means were estimated from 1000 bootstrapped datasets and output to a spreadsheet. The spreadsheet was used to produce bootstrapped percentile confidence limits of predicted seed retention at observed distances for comparison with field data (Table 5.2, Figures 5.1, 5.2) and to

obtain distributions of predicted maximum dispersal distances (Figure 5.3). The 95 percentile confidence limits for the linear model were 187 and 260 m and 935 to 1,812 m for the exponential decay model.

Since no plants were recovered from fences at the Larkspur site, all of my truthing data for distances dispersed came from the Superior site. A total of 34 plants that had traveled a known distance were recovered in 2 years. This number included eight plants that were incidentally recovered from a pasture fence well beyond the fence I erected to capture plants. Since these plants were recovered coincidentally, I was not able to collect GPS coordinates at their recovery points (I was in the field for other reasons and did not have a GPS unit). Therefore, the travel distance was recorded as the shortest distance they could have traveled to encounter the pasture fence. The distance traveled by plants recovered from my fence ranged from 11 to 71 m while the distance traveled by plants recovered from the pasture fence ranged from 222 to 1,039 m.

When compared to field data, neither the linear nor the exponential decay model predicted seed retention with distance well. Only five observations fell within the 95 percentile confidence limits of either the linear or exponential decay model. Three additional observations were within 32 seeds of a confidence bound (Table 5.2). Two of these were the plant with the largest number of total seed observed in a dispersed plant and the plant that traveled the longest distance (1,039 m). These observations were within 32 and 8 seeds of the lower confidence bound of the exponential decay model, respectively. This may suggest that the exponential decay model better predicts extreme dispersal events. The rest of the observations were substantially overpredicted by both models. Interestingly, and despite very wide confidence intervals, none of the plants

recovered from the fence I erected fell within the prediction bounds of either model. All but one of the plants recovered from the pasture fence were reasonably well predicted by the linear model. The distances reported for these plants probably represent minimum distances traveled without greatly underestimating them.

Overpredictions were probably due largely to the fact that the tunnel plants used to develop the models were reared with adequate water while the field plants were experiencing drought and/or biocontrol. Neither of these effects was accounted for in these models. While neither stem diameter nor plant volume differed between tunnel and field plants, the difference in total seed between tunnel plants and non-dispersed field plants collected in September was greater than an order of magnitude with an average of 2,446 seeds and 207 seeds, respectively. Seed production has been reported as 925 to 18,248 per plant in British Columbia (Watson and Renney 1974) and 670 to 1,201 per plant in Colorado (Beck and Rittenhouse 2002). The difference between these previously reported values strongly indicates that seed production may be substantially lower in Colorado than BC. However, Beck and Rittenhouse (2002) also conducted their research at the Superior site. Therefore, the tunnel plants may represent potential seed production in more favorable growing conditions.

To follow up on the hypothesis that the overprediction of dispersal distances by both the linear and exponential decay models is largely due to differences in fecundity, I conducted separate regression analyses on each individual plant from the tunnel dataset with distance as the only regressor. There was virtually no difference between linear and exponential decay models in values of R-square. For most of the plants a large proportion of the variance was explained by distance alone. Out of 19, one R-square

value was 0.5, one was 0.74, 17 were 0.84 or greater and 12 were 0.9 or greater. The plant for which the regression resulted in an R-square of 0.5 lost only 55 of 2,908 seed, 36 of which were from dropped heads within 2 cm. An ANOVA on the distance parameter estimates did not detect dependence of the rate of seed loss from a plant on the plant ($p = 0.763$), stem diameter ($p = 0.542$), plant volume ($p = 0.3$) or the interaction between stem diameter and plant volume ($p = 0.44$). This finding lends support to the above hypothesis and further suggests that fecundity may be an important determining factor in LDD of seed by this plant.

Despite the differences between tunnel and field plants, I felt that using the tunnel data might yield a better model as there was no information on seed in plants prior to dispersing for the field plants. Time since senescence is another factor that is not accounted for in this model. Indeed, given these differences, it is surprising how well the models performed. In most cases, observed values were within tens of meters of the predicted confidence limits. If the rate of seed loss were the same in field and tunnel plants, I would expect plants with greater fecundity to have the potential to disperse seed to much greater distances. The relatively small difference between predictions and observations suggests that the rate of seed loss is greater in the tunnel plants versus the field plants. One clear difference between these two groups is the tunnel plants were tumbled across a hard surface (the wood surface of the wind tunnel), while field plants generally tumble across grassland. It is reasonable to expect that the interaction with a hard surface would cause plants to lose seed at greater rates. It may also be that plants with higher fecundity simply lose seed more rapidly with distance tumbled.

Retention of Seed in Non-Dispersed Plants. Linear regression of seed ($\ln +0.0001$ transformed) retained in plants with time resulted in the following model:

$$\ln T_{seed} = \beta_0 + \beta_1 t + \beta_2 s \quad [5.6]$$

where β s are regression parameter estimates, t is time (weeks since senescence) and s is stem diameter (mm). All parameter estimates were significant at $\alpha=0.01$. The parameters of this model and their respective means were estimated from 1,000 bootstrapped datasets and output to a spreadsheet. The spreadsheet was used to produce bootstrapped percentile confidence limits of predicted seed retention over time (Figure 5.2) and a distribution of the half-life of seed retention in a plant (Figure 5.3). The lower and upper bootstrapped 95 percentile confidence limits for seed half-life are 3.3 and 14.1 weeks, respectively. This implies that plants that tumble late in the dispersal season still pose a strong threat for LDD and rapid spread of this invasive plant.

Biocontrol and Open Capitula. The ANCOVA of seed remaining in individual capitula (square root transformed) (SAS v9.1; PROC MIXED with collection site as a random effect) resulted in the same model as that for the non-dispersed data. I began with a model including time of collection (weeks since senescence), stem diameter, plant volume, open capitula (Y/N), seed biocontrol (Y/N), and all two-way interactions and used backward model selection. There was no evidence that the number of seed in capitula depended on the number of open capitula ($p = 0.44$) or the presence of biocontrol ($p=0.76$). This finding conflicts with those of Seastedt et al. (2003) who found that the presence of biocontrol agents strongly correlated with reduced seed production. Given the observational nature of my data, I can only speculate about the reasons for the lack of significance of these variables. As has been mentioned earlier, this region has been

experiencing historic drought over the last 8 to 10 years. I would expect open capitula to more easily lose seed; however, an overall decrease in seed production due to the drought might mask differences between open and closed capitula. Similarly, while the majority of those heads that exhibited evidence of seed-feeding biological control insects had no seed in them, there were also a large number of capitula with no seed and no evidence of biocontrol damage. These latter might be a result of drought. Further, there might be a cumulative affect of biocontrol that is not reflected in my data. The lack of direct damage to a given capitula does not necessarily mean that it was not affected by the presence of insect damage elsewhere on the plant. I have also observed a prevalence of *Cyphocleonus achates*, a root-boring biocontrol, at the Superior site. All of the plants collected from that site showed damage attributable to a seed-feeder (probably *Larinus minutus*) to at least one capitula. There could certainly be an effect on seed production due to *C. achates* and possibly a synergistic affect of both insects (Seastedt 2003). Finally, there were a surprising number of seed in very small capitula where I expected to find none. This may lead to bias in some sampling methods.

Summary. There is a clear potential for LDD of *C. diffusa* seed via tumbling. To my knowledge, this is one of only two works that quantify seed dispersal of a tumbleweed and is the only work for this species. The timing of tumbling dispersal varies substantially in time and space and can occur at any time from fall through early spring (Beck and Rittenhouse 2002, Nelson 2002, Baker et al. IN REVIEW). My data show that seed are retained in non-dispersed plants for sufficient time to pose a continuing threat of LDD throughout the dispersal season. Indeed, even during drought

and in the presence of relatively intense biological control, I found seed in plants that tumbled 200 to 300 m and in one plant that had tumbled over 1 km. It is interesting that a linear model achieved the best accuracy in predicting LDD. Yet, it is not an unreasonable hypothesis that seed loss from a tumbling plant occurs at a constant rate. According to my exponential decay model, which may better capture extreme dispersal events, seed may be retained in plants as far as 1800 m in moist years. Stallings et al. (1995) estimated that, on average, 51% of the seed of the tumbleweed *Salsola iberica* was retained in plants recovered after traveling 2,209 m in summerfallow wheat fields in one year and 26% after traveling 1,771 m in the next year. Their estimates of seed retained in plants were based on a plant weight regression of 9 and 13 plants for the first and second years, respectively. This sample size and methodology is error prone; so, as they point out, these estimates may not be reliable. However, due to the minute size of *S. iberica* seed, true counts are prohibitive.

I suggest that the distance *C. diffusa* plants will tumble may be more limiting to LDD than seed retention in plant. Nelson (2002) reported finding plants at distances of 1,500 m with an average distance tumbled of 400 m. My data suggest that plants certainly have the potential to retain seed to those distances. Therefore, preventing tumbling may have a strong impact on the spread of this species. I concur with Nelson's (2002) suggestion that fences may be an overlooked management tool for this invasive weed as well as other tumbling plants. Preventing the spread of weeds is an important component of integrated weed management. To be effective in prevention efforts, scientists and managers need to be informed about the dispersal of target species. The

data I have presented provide unprecedented work on the dispersal capability of an important invasive weed.

Acknowledgements

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Literature Cited

- Baker, D. V, B. J. Bienkiewicz, K G. Beck, and L. B. Bjostad. IN REVIEW. Forces necessary to initial dispersal for three tumb weeds. *Invasive Plant Science and Management*.
- Beck, K. G. and L. R. Rittenhouse. 2002. The influence of cattle grazing on diffuse knapweed. *Proc. Weed Sci. Soc. America* **42**: 61-62.
- Becker, D. A. 1978. Stem abscission in tumbleweeds of the Chenopodiaceae: Kochia. *Amer. J. Bot.* **65**: 375-383.
- Greene, D. F., and E. A. Johnson. 1997. Secondary dispersal of tree seeds on snow. *J. of Ecology* **85**:329-340.
- Heyligers, P. C. 1999. Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and *Trachyantra divaricata* in Australia. *Cunninghamia* **6**:315-329.
- Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: A theoretical perspective. *Ann. Rev. Ecology Evolution and Systematics* **34**:575-604.
- Manly, B. F. J. 2007. *Randomization, Bootstrap, and Monte Carlo Methods in Biology*. New York, NY: Chapman and Hall / CRC. 455pp.
- Mehlman, D. W. 1993. Tumbleweed dispersal in Florida sandhill Baptisia (Fabaceae). *Bull. Torrey Bot. Club.* **120**:60-63.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* **15**:278-285.

- Nelson, J. K. 2002. Diffuse knapweed movement – A critical, often overlooked component of control. *Proc. Wes. Soc. Weed Sci.* **55**:54.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied Linear Statistical Models*. Fourth Edition, St. Louis, MO: WCB McGraw Hill, Inc., 1408pp.
- Roché, C. T. and L. M. Wilson. 1999. Mediterranean Sage. Pages 261-270 in R.L. Sheley and J.K. Petroff, eds. *Biology and Management of Noxious Rangeland Weeds*. Corvallis, OR: Oregon State University Press.
- Schurr, F. M., W. J. Bond, G. F. Midgley, and S. I. Higgins. 2005. A mechanistic model for secondary seed dispersal by wind and its experimental validation. *J. of Ecology* **93**:1017-1028.
- Seastedt, T. R., N. Gregory, and D. Buckner. 2003. Effect of biocontrol insects on diffuse knapweed (*Centaurea diffusa*) in a Colorado grassland. *Weed Science* **51**:237-245.
- Stallings, G. P., L. W. Lass, C. A. Mallory-Smith, and D. C. Thill. 1995. Plant movement and seed dispersal of Russian thistle (*Salsola iberica*). *Weed Science* **43**:63-69.
- Watson, A. K. and A. J. Renney 1974. The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. *Can. J. Plant Sci.* **54**:687-701.

Table 5.1. Wind tunnel cumulative seed deposition models, their parameter estimates, and accuracy assessment. Model 1 excludes seed deposited as a result of entire capitula breaking from plants. Model 2 includes all deposited seed. Model 3 includes all data and does not include a tumbling velocity factor. α = maximum rate of seed deposition; β = rate at which α declines with distance; d_{half} = distance since a tumbling event began that a plant reaches half of its maximum velocity.

Model	Parameter			Accuracy Assessment			
	α (Var.)	β (Var.)	d_{half} (Var.)	R ²	Slope	SE	p-value
1	2.339(9e-7)	0.051(3.9e-9)	1.508(4.3e-5)	0.999	1.001	0.001	<0.0001
2	1.681(2.1e-7)	0.028(1.8e-10)	0.198(6.1e-7)	0.999	1.002	0.001	<0.0001
3	1.475(1.3e-7)	0.023(9.6e-13)	---	0.999	1.001	0.001	<0.0001

Table 5.2. Comparisons of observed dispersal distances with predicted percentile confidence limits from linear and exponential decay models of seed dispersal. Twenty-six comparisons were greater than 100 from a 95 percentile confidence limit of either model and are not shown. Observations within 95 percentile limits are highlighted in bold.

Observed		Seed Percentiles				
Dist (m)	# Seed	Model	2.5th	50th	97.5th	Avg.
305	18	linear	-988	-468	36	-480
		<i>-e</i>	521	692	1219	994
222	25	linear	35	407	768	403
		<i>-e</i>	808	987	1219	994
258	25	linear	-409	27	456	20
		<i>-e</i>	668	846	1080	854
272	58	linear	-581	-119	331	-129
		<i>-e</i>	620	797	1031	805
252	93	linear	-335	90	508	84
		<i>-e</i>	690	868	1103	876
256	94	linear	-384	48	474	41
		<i>-e</i>	675	854	1088	861
35	2104	linear	2322	2391	2453	2389
		<i>-e</i>	2136	2201	2264	2203
1039	3	linear	-10,065	-8258	-6462	-8288
		<i>-e</i>	11	30	80	34

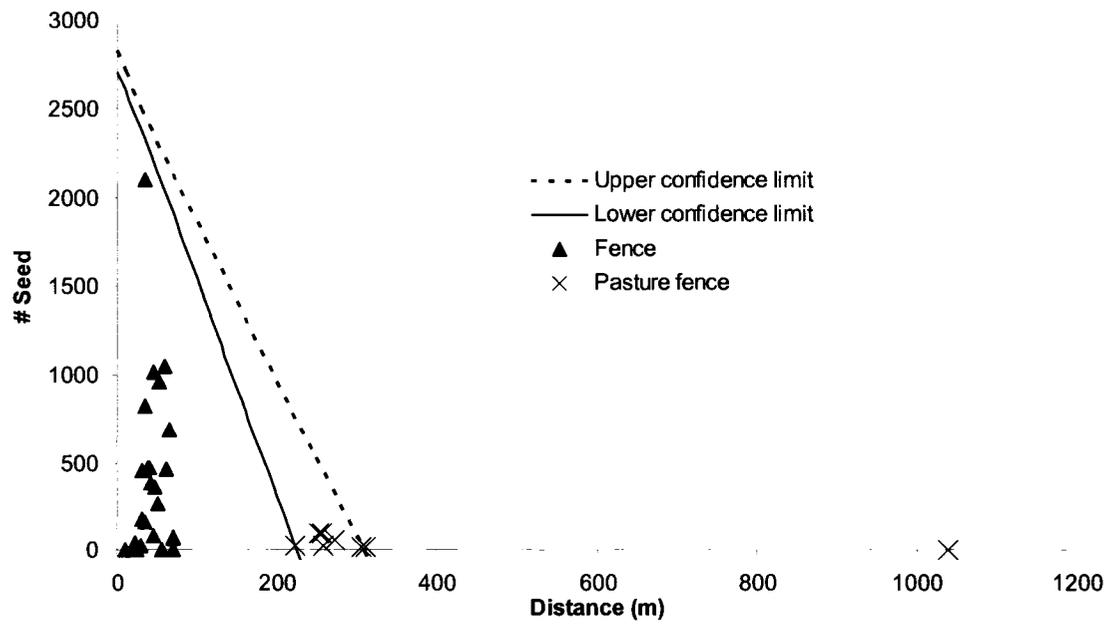


Figure 5.1. Observed seed retained in plants with distance compared to 95 percentile confidence limits predicted by a linear dispersal model derived from 1,000 bootstrap replicates.

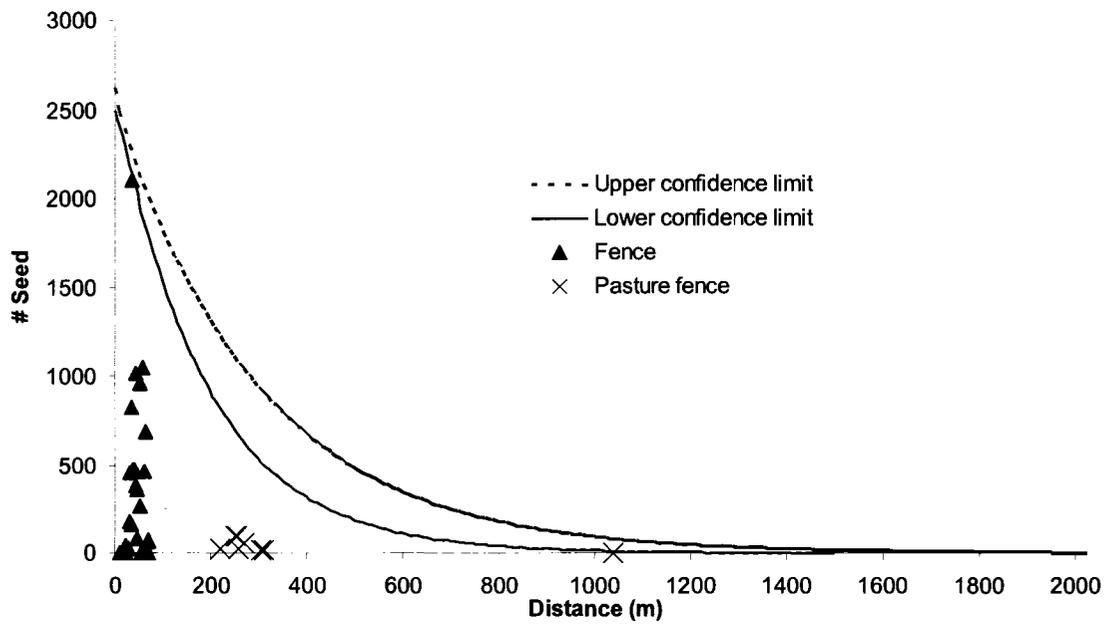


Figure 5.2. Observed seed retained in plants with distance compared to 95 percentile confidence limits predicted by a exponential decay dispersal model derived from 1,000 bootstrap replicates.

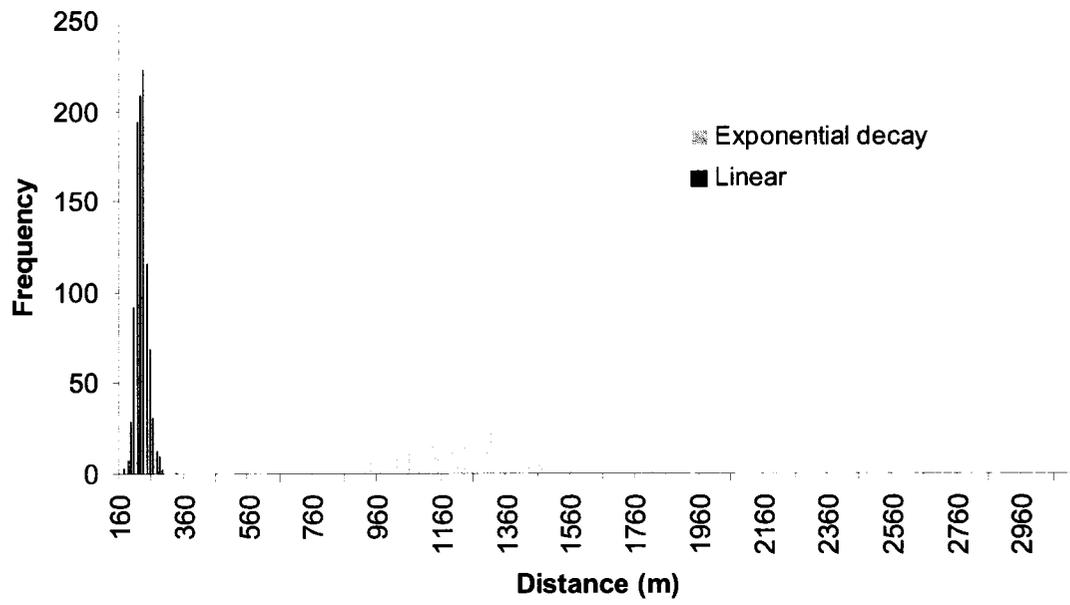


Figure 5.3. Bootstrapped distributions of maximum seed dispersal distance as predicted by linear and exponential decay models for diffuse knapweed.

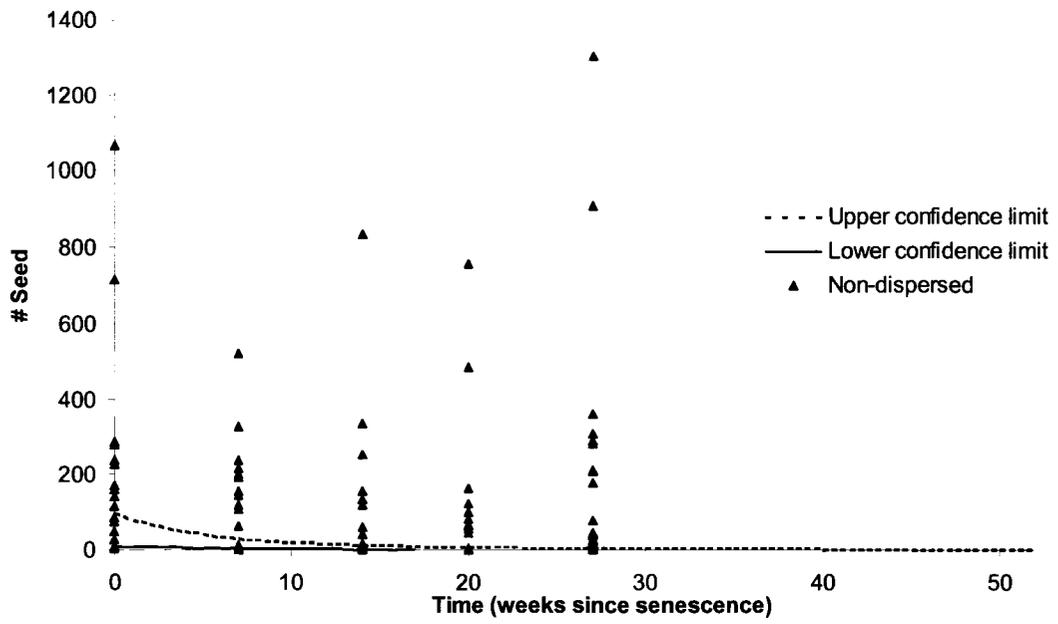


Figure 5.4. Observed seed retained in non-dispersed plants with time compared to predicted 95 percentile confidence limits derived from 1,000 bootstrap replicates.

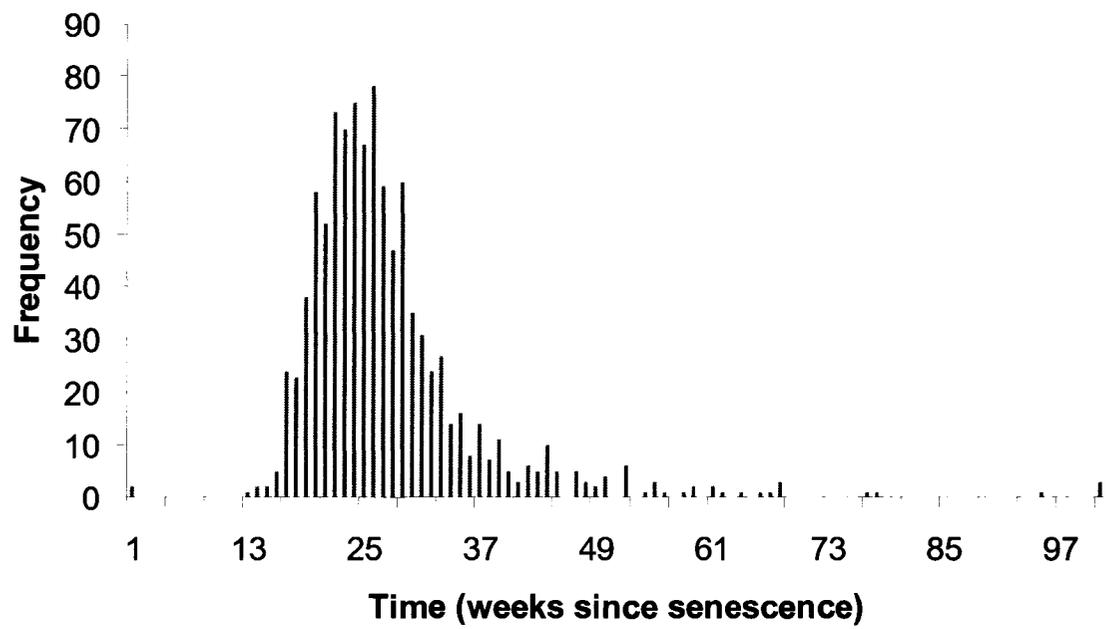


Figure 5.5. Bootstrapped distribution of the half-life of seed retention in non-dispersed diffuse knapweed plants.

Chapter 6: Summary and Future Directions

The central premises of this work have been twofold. One is that invasive weeds pose serious issues that warrant management. The second is that prevention is a key component of integrated weed management and that effective prevention requires detailed information about dispersal.

Attention to dispersal ecology and to the issues of invasive weeds has strongly increased within the last couple of decades. For instance, the first international symposium on movement ecology was held in June, 2007 and the journal *Science* devoted a special section to this subject in its 11 August, 2006 issue. However, to my knowledge research on dispersal and research on invasive weeds have not been combined to any large degree.

Tumbleweed dispersal may be considered from three general aspects: (1) initiation, (2) movement of the plants and (3) the deposition of seed. Plant movement requires sufficient force to break plant stems, thereby initiating tumbling dispersal. This may be caused by wind or by animals; I have focused on wind. Primary seed dispersal

may be local from a plant that has not yet tumbled, or it may be over long distances via the tumbling mechanism.

The specific objectives of this research were to:

1. Determine timing of tumbling dispersal for diffuse knapweed and weather factors that correlate with peaks in dispersal at two Colorado locations (Chapter 2);
2. Investigate the forces necessary to initiate tumbling dispersal of diffuse knapweed and two other tumbleweeds, the effects of soil moisture on that force, and calculate the wind velocities necessary to exert these forces (Chapter 3);
3. Model the spatial movement of tumbling diffuse knapweed and evaluate the fit of model results to observed field data at two Colorado locations (Chapter 4); and
4. Determine the potential for long-distance diffuse knapweed seed dispersal via tumbling (Chapter 5).

Dispersal timing and weather correlates

That the timing of tumbling is highly variable in space and time and that there does not seem to be any year-to-year consistency in the timing of dispersal at a given site was not surprising. However, while wind, particularly gusts, is certainly correlated with peaks in dispersal, this pattern was not as clear as one might expect and inconsistent between sites. There was substantially more tumbling dispersal at my Superior site than at Larkspur. There were certainly more high wind events at the Superior site, but even during high winds at the Larkspur site there were not strong peaks in dispersal. This led

me to hypothesize that there was something about the biology of the plants that was different between the sites.

Due to equipment failures, I only had 1 year of reliable weather data and even that year had no reliable data for soil moisture. Since soil moisture had a strong effect on stem strength under controlled conditions, this would be an important variable to track in the field. It would also be interesting to continue observations on timing over a long time period with reliable weather stations. However, the equipment and weekly checks were costly and time consuming. For example, the minimum one can expect to pay for weather stations is \$1500 each and the weekly checks required at least 4 hours of driving each if I did them. Therefore, such an endeavor would need to be weighed against the possible benefits of further observational data. It is possible that even long-term data would not reveal anything more than the variability that I have already noted.

Forces necessary to initiate tumbling dispersal

Prior to this research, nothing had been published that documented the forces necessary to break the stem (stem strength) of diffuse knapweed. The only work I am aware of that investigated the stem strength of a tumbleweed was that of Becker (1978). This work focused on kochia and did not directly relate forces to wind speed nor did it explicitly report the forces themselves. Rather, it focused on factors that might influence stem strength.

I found that soil moisture dramatically decreased stem strength. This is the opposite of the effect my data showed for kochia, which is consistent with the findings of

Becker (1978). I did not have the necessary space or sample size to test the change of stem strength with time since senescence. All of my data reflect tests conducted 8 weeks after senescence had completed.

Estimates of stem strength and equivalent wind speeds are shown in Chapter 3, Table 3.1. All of these estimates are likely overestimates. In the field, wind direction and speed can vary substantially even over short time intervals. This variation probably has the effect of fatiguing and weakening plant stems. It is also a factor that would be very difficult to simulate in a manipulative experiment. One option would be to take the device I used to break plant stems into the field at various times throughout the dispersal season to sample plants under realistic conditions.

My data also support the hypothesis, based on differences in quantity of tumbling dispersal, that there was a difference in the stem strength between sites. Stem strength of plants reared in a common garden was substantially higher for plants collected from the Larkspur site than those from the Superior site and I observed much less tumbling dispersal at the Larkspur site. The ultimate cause of the difference in stem strength is unclear. I suggest that root-boring biocontrol agents (observed at the Superior site), plant hybridization (observed at the Larkspur site), or some combination may be contributing factors.

The difference could be tested more rigorously by conducting a controlled, factorial experiment in a common garden. The factors would be species (e.g., diffuse knapweed, diffuse hybrid, spotted knapweed) and biocontrol agent (Y/N). This would be an important avenue to pursue as knowledge of factors contributing to dispersal aid in risk assessment and prevention efforts. In addition, it is important to know whether a

promising biocontrol option is actually increasing tumbling dispersal by weakening stems. However, if tumbling is increased but seed production is strongly reduced or eliminated by these insects, this may not be a serious concern. Therefore, this experimental design should include estimating seed production.

Movement modeling

I developed a conceptually simple, mechanistically-based model for the movement of tumbling diffuse knapweed plants. This model uses the variation in wind direction calculated by the meteorological model, MicroMet to predict the direction of tumbleweed movement. MicroMet uses topography and observed wind direction and speed as its inputs. My model calculates movement potential and barriers to dispersal based on vegetation, slope in wind direction, and the empirically-derived, minimum wind speed for plant movement. I compared model predictions to observed movement at my two field sites.

It came as a surprise to find that general wind direction does not closely predict movement direction of diffuse knapweed. I used mean observed wind direction as input to Micromet and the range of values output by that model was my prediction envelope for the directional movement of tumbling plants. These envelopes were 10° to 15° wide, yet very few field observations were within these relatively broad predictions. Failure of directional predictions at the Superior site may be attributable to the failure of my on-site weather station. This necessitated the acquisition of data from a station 3 km from my observations of movement. However, even with weather observations from my station at

the Larkspur site, predictions were not greatly improved. Even if they were, the utility of predictions would be questionable if they required weather observations from within 10s to 100s of meters.

Directional predictions might be improved by allowing local variation in the model. One way this could be accomplished is to make local predictions over short distances based on wind direction and iterate these through the geographic extent to obtain a dispersal path (i.e., an individual-based modeling approach). However, my initial exploration of this technique did not improve prediction accuracy as instantaneous wind direction does not vary greatly in space as modeled by MicroMet. Complexity could be further added by using weather observations over shorter time intervals such that temporal variation in weather is incorporated. Both of these refinements could substantially affect model results. However, a temporally explicit model requires decisions on the length of the time step and plant travel distance per time step. Both of these would be challenging to justify and could have large impacts on model results. Building a temporally explicit model would also substantially increase computational time. Another alternative is to modify the surfacing technique I used to randomly get directions from the observed distribution of wind directions rather than the wind direction surface output by MicroMet. This would incorporate the variability of wind directions and could be a reasonable compromise between the surfacing technique and a fully temporally explicit model.

While the observed stopping point of a plant was successfully predicted in only one case and dispersal is overpredicted for all other observations, movement potential surfaces show promise that further refinement will yield application to management.

Such surfaces could aid in efforts to restrict dispersal such as the placement of fences. I chose the 95th percentile of observed wind speed as the input for MicroMet. This results in modeled wind speeds that are sufficient to move plants everywhere in the extent except where it is assumed that movement cannot occur, irrespective of wind speed (i.e., where shrub vegetation types create barriers to movement).

Seed dispersal

To my knowledge, there have been no previously published studies that developed models for the seed dispersal of a tumbleweed. Stallings et al. (1995) documented estimates of seed remaining in plants based on the weights of the plants and plant travel distance, but theirs are the only published data that estimate seed dispersal for a tumbleweed prior to my efforts.

I developed two analytical models and tested them against field observations. Neither model performed very satisfactorily, though inaccurate predictions may be largely due to differences in fecundity between plants used to develop the models and those used to test model predictions. A linear model was better supported by the data than was an exponential decay model, although the most extreme dispersal observation was better predicted by the exponential decay model. At first glance, it seems counterintuitive that a linear model would outperform a log model in predicting seed dispersal distance. However, mechanistically, a linear rate of seed deposition from a rolling plant is plausible and my model of cumulative seed loss in a wind tunnel is linear

and highly accurate. It is also a common problem in seed dispersal modeling that models are able to predict only one aspect of the dispersal curve such as the mode or tail (Nathan and Muller-Landau 2000). This may be true for my models as well, though I have insufficient data at the longest distances to reach any conclusions.

In conclusion, this work has resulted in substantially more information about the dispersal of diffuse knapweed than has previously been reported. In particular, there are two main conceptual arenas to which my work has contributed; prevention and seed dispersal. Most emphasis in efforts to prevent the spread of invasive species have focused on early detection and rapid response. However, successful prevention must ultimately include a focus on the dispersal of organisms and very little work in the field of weed science has investigated dispersal. While there has been a great deal of progress made in seed dispersal research during the last 1 to 2 decades, the tumbleweed mechanism of dispersal has been largely overlooked. Indeed, reviews such as those by Nathan and Muller-Landau (2000) and Levin et al. (2003) have not mentioned this mechanism.

It is premature to claim strong management application for my work, particularly for the seed dispersal and spatial movement models. However, the wind speeds necessary to initiate dispersal can be used to assess the vulnerability of a site to high dispersal and spread rates. Areas where wind exceeds 16 to 17 m/s on a regular basis from October through March are much more likely to see high rates of tumbling dispersal.

I have also shown that, even in a drought year in a location that has seen repeated introductions of a number of biocontrol insects, seed can occasionally be dispersed over 1 km and more commonly over 200 to 400 m. In addition, I only relocated 34 of the 120 marked plants. The fact that it is easier to re-locate plants that traveled shorter distance suggests that longer distance dispersers are underrepresented in these data.

Finally, to the degree possible, I have endeavored to have a mechanistic basis for my models. This allows the potential application of these models, and certainly of the methods, to other species of the tumbleweed guild; a group of plants (often weeds) that is represented in at least nine disparate plant families (Becker 1978, Roché and Wilson 1999, Heyligers 1999).

Special Thanks

I would like to express my sincere gratitude to Deputy Winston Boswell of the Boulder County Sheriff's Office for his role in the investigation and recovery of items stolen from my vehicle at the Superior site last spring. His professionalism and communication were exemplary! Among the items stolen and recovered were my laptop computer, data backups, and a field notebook without which I could not have completed my dissertation.

Literature Cited

- Becker, D. A. 1978. Stem abscission in tumbleweeds of the Chenopodiaceae: *Kochia*.
Amer. J. Bot. **65**: 375-383.
- Heyligers, P. C. 1999. Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and
Trachyandra divaricata in Australia. *Cunninghamia* **6**:315-329.
- Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and
evolution of seed dispersal: A theoretical perspective. *Ann. Rev. Ecology
Evolution and Systematics* **34**:575-604.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their
determinants and consequences for recruitment. *Trends in Ecology & Evolution*
15:278-285.
- Roché, C. T. and L. M. Wilson. 1999. Mediterranean Sage. Pages 261-270 in R. L.
Sheley and J. K. Petroff, eds. *Biology and Management of Noxious Rangeland
Weeds*. Corvallis, OR: Oregon State University Press.
- Stallings, G. P., L. W. Lass, C. A. Mallory-Smith, and D. C. Thill. 1995. Plant movement
and seed dispersal of Russian thistle (*Salsola iberica*). *Weed Sci.* **43**:63-69.

APPENDICES

Appendix A: The Weed Tunnel

Diffuse knapweed (*Centaurea diffusa*) is one of the many weeds that disperse in a tumbleweed manner. Sometime after the growing season the plant stem breaks at or about the soil surface and the above-ground portion of the plant is rolled along the ground in a wind-driven process dropping seed along the way. This mechanism of dispersal is not uncommon. In fact, there are species that have evolved the tumbling habit representing at least nine different plant families (Becker 1978, Roche and Wilson 1999, Heyligers 1999). Yet there has been very little previous research published elucidating the importance of this dispersal mechanism. My research establishing the forces necessary to break and disperse diffuse knapweed plants as well as seed dispersal distances is, to my knowledge, unique. In conducting this research I found it necessary to design and construct an experimental wind tunnel. This design and construction was largely of a trial and error nature. In this paper I outline this process in the hopes of supporting similar future efforts and helping other researchers avoid some of the mistakes and difficulties I encountered as a novice in aerodynamics.

I began the process with the simple construction of a fan blowing air through a 7 by 3 by 3 foot plywood-walled tube, or test section. The fan was six-bladed, 3 feet in

diameter and belt driven, powered by a $\frac{1}{2}$ hp, 8 amp, variable speed DC motor. The chief issues that made this design untenable were insufficient flow velocity and highly uneven air flow in cross section. While it was not surprising that there was uneven flow given the use of an axial fan, the size and longevity of the dead spot in the center of the test section was a surprise. Though I never had any difficulties with the laminar flow, the measured flow velocity in the periphery was approximately 7 m/s while there was no measurable flow in the center. Further, this dead area was nearly 2 feet in diameter and encompassed the entirety of the area in which measurements were to be made. I attempted to mitigate this with baffling and the addition of a honeycomb. However, neither of these changes, nor several variations of them, had substantial effect on the evenness of flow.

My final design made a number of changes resulting in even cross-sectional flow and a maximum velocity of approximately 8 m/s. There were two changes that were the most significant breakthroughs in correcting the problems described above. First, making the change to a sucking rather than blowing design corrected the issues with uneven cross-sectional flow. To my chagrin, I found that simple web searches yielded much more useful information from my perspective than literature searches. The second major change was to utilize the Venturi effect to increase the velocity of the flow. In addition, for the purposes of mobility and storage, this tunnel is modular and each section is structurally independent and on casters (Figure A.1). The following sections detail the final design.

Contraction Section. The contraction section was a simplification of those in more advanced tunnels (Bradshaw and Mehta 2003, Neuman 2006, Anonymous 2007a, Anonymous 2007b) and provided the first step in making use of the Venturi effect to accelerate air flow (Figure A.1). The first stage rapidly contracted incoming flow from 78 by 78 inches to 36 by 36 inches over 18 inches in flow direction. The second stage contracted much more gradually from 36 by 36 inches to 28 by 24 inches over 36 inches of flow length. This design maximized the contraction ratio while the second stage reduced the turbulence introduced by the contraction (Bradshaw and Mehta 2003, Neuman 2006, Anonymous 2007a, Anonymous 2007b). This section was mounted on locking casters.

Test Section & Instrumentation. As the name implies, this was the working section of the tunnel. At the upwind end of this section immediately adjacent to the Contraction Section was the honeycomb (Figure A.1). This was composed of stacked 10 inch lengths of 1.5 inch, PVC pipe. The honeycomb produced some degree of backpressure that served to force the flow to become more laminar and even as it entered the experimental space. The experimental space was approximately 72 by 24 by 28 inches (L by W by H). It was slightly taller than wide to allow for the addition of realistic surfaces (such as grass or soil) for different experiments. LexanTM windows were placed both in the side and top for monitoring and illumination of experiments.

The tunnel was equipped with both an anemometer and a proximity sensor (Figure A.1). I used a hot wire anemometer¹ mounted on a telescoping rod. The small

size (0.5 inch in diameter) and telescoping rod enabled me to measure wind speed proximate to the test plant without appreciably affecting the flow.

The proximity sensor² was mounted beneath the floor of the tunnel and detected the proximity of a spring mounted plate to which individual plants could be mounted (Figure A.2). As change in proximity is directly proportional to force, this allowed me to measure the force exerted by wind on individual plants. The springs were four flat brass strips; one on each corner of the plate. This design minimized twisting and sideward movement while allowing movement toward or away from the sensor. Further, brass does not develop a memory when flexed, i.e., it returns to its previous position more reliably than sheet metal rather than staying bent. A digital voltmeter (DVM)³ was used to read proximity sensor output. The DVM was further capable of outputting to a PC for logging.

The test section was later lengthened by three, 8 foot sections of simple wood construction for seed dispersal experiments.

Expansion/Fan Section. This section was composed of three parts; the expansion, a settling chamber, and the fan (Figures A.1, A.3, A.4). The expansion went from 28 by 24 inches to 48 by 48 inches in 20 inches of flow length and provided the final part in the use of the Venturi effect. The settling chamber allowed debris to settle out of the flow before going through the fan. The fan blade was galvanized steel and was 4 feet in diameter with 6 blades at 40 degree angles and was capable of moving 31,630 cubic feet per minute (CFM) at its maximum rated rotations per minute (RPM) of 600. The blade was belt driven by an 18.5 amp, 1 to 2.5 hp, variable speed, DC motor (a surplus

treadmill motor). By using this relatively light motor I could use a common 120V circuit rather than being restricted to 220V circuits. The pulley on the blade was 18 inches in diameter while the motor pulley was 1.75 inches in diameter. This approximate 10:1 ratio allowed the small motor to handle the large blade as well as enabling finer control over the flow velocity. The motor was operated with a treadmill controller and mounted in a box (Figure A.5). The box was further equipped with an ammeter, voltmeter, and cooling fan for safety and to help protect the AC circuit, the controller, and the motor from overload. The weight of the fan necessitated constructing a steel frame mounted within the wood housing of the section (Figure A.3).

The final result was a versatile, relatively low-cost, reliable wind tunnel that served my purposes very well. It could also be stored in as little as 11 by 12 feet of floor space. My hope is that researchers with similar needs will find the information provided here useful in their own work and that it will help prevent the numerous false-starts in the trial-and-error process I experienced in building my own wind tunnel from scratch.

Materials

¹Hotwire anemometer, model 407123, Extech Instruments.

²GageProx 8mm unshielded proximity sensor, Kaman Instruments.

³Triplett Model 2103, Triplett Corporation, www.triplett.com

Acknowledgements

I would like to express my gratitude to Bogusz Bienkiewicz and Lou Bjostad for their expert advice; to Jerry Lang for his help with the electrical system; and Van Baker and Brett Ochs for their help in construction and problem-solving.

Literature Cited

- Anonymous. 2007a. The Wind Tunnel. <http://sln.fi.edu/flights/first/tunnel1.html>.
Accessed August, 2007.
- Anonymous. 2007b. The New AAE Wind Tunnel.
<http://www.lboro.ac.uk/departments/tt/research/aerodynamics/windtunnel/tunnel2.html>. Accessed August, 2007.
- Becker, D. A. 1978. Stem abscission in tumbleweeds of the Chenopodiaceae: *Kochia*.
Amer. J. Bot. **65**: 375-383.
- Bradshaw, P. and R. D. Mehta. 2003. Wind Tunnel Design.
<http://navier.stanford.edu/bradshaw/tunnel/index.html>. Access August, 2007.
- Heyligers, P. C. 1999. Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and *Trachyandra divaricata* in Australia. *Cunninghamia* **6**:315-329.
- Neuman, C. M. 2006. <http://www.trentu.ca/academic/geography/featuresExpl.html>.
Accessed August, 2007.
- Roché, C. T. and L. M. Wilson. 1999. Mediterranean Sage. Pages 261-270 in R. L. Sheley and J. K. Petroff, eds. *Biology and Management of Noxious Rangeland Weeds*. Corvallis, OR: Oregon State University Press.

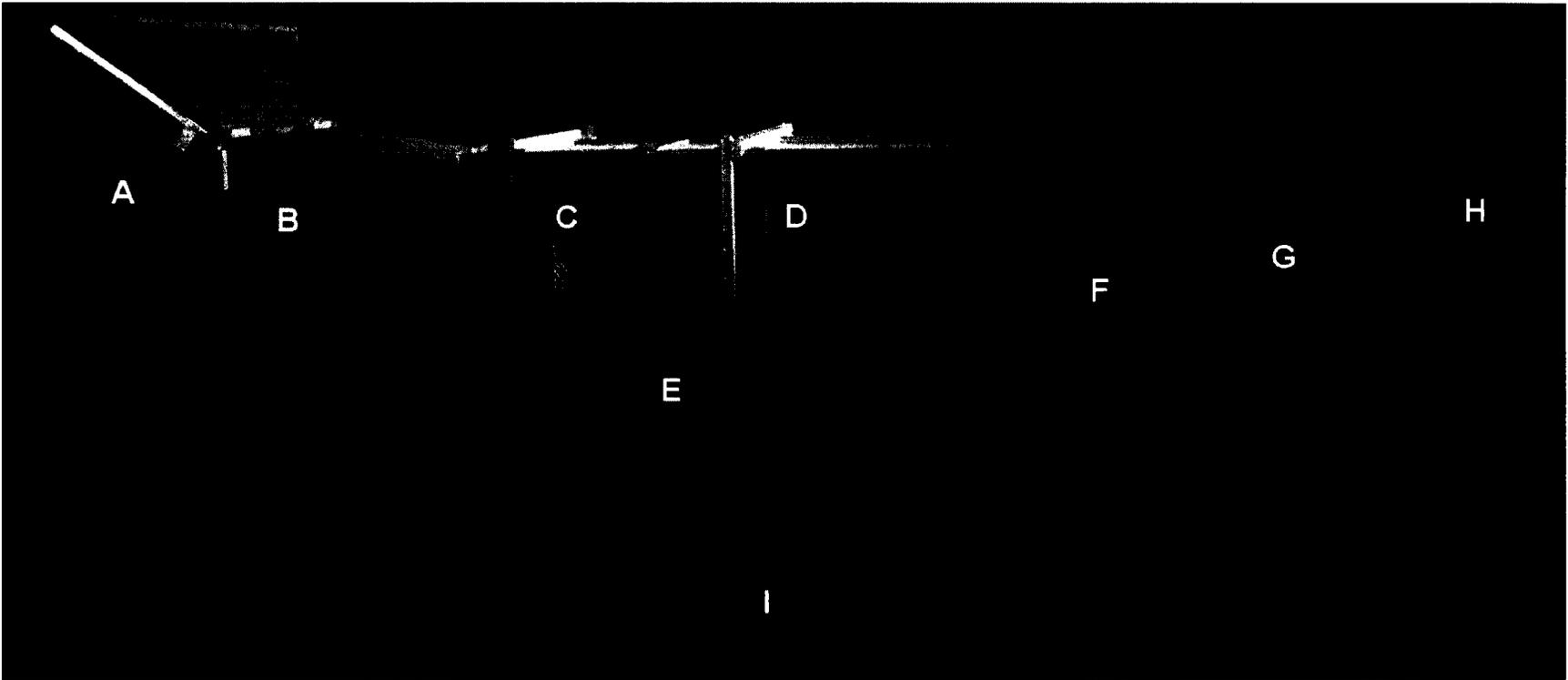


Figure A.1. Wind tunnel in its short configuration. (A) First stage, contraction; (B) second stage, contraction; (C) honeycomb; (D) test section; (E) instrumentation – (left to right) PC for logging output, anemometer readout, proximity readout; (F) expansion; (G) settling chamber; (H) fan; (I) fan control box. Air flow is from left to right.

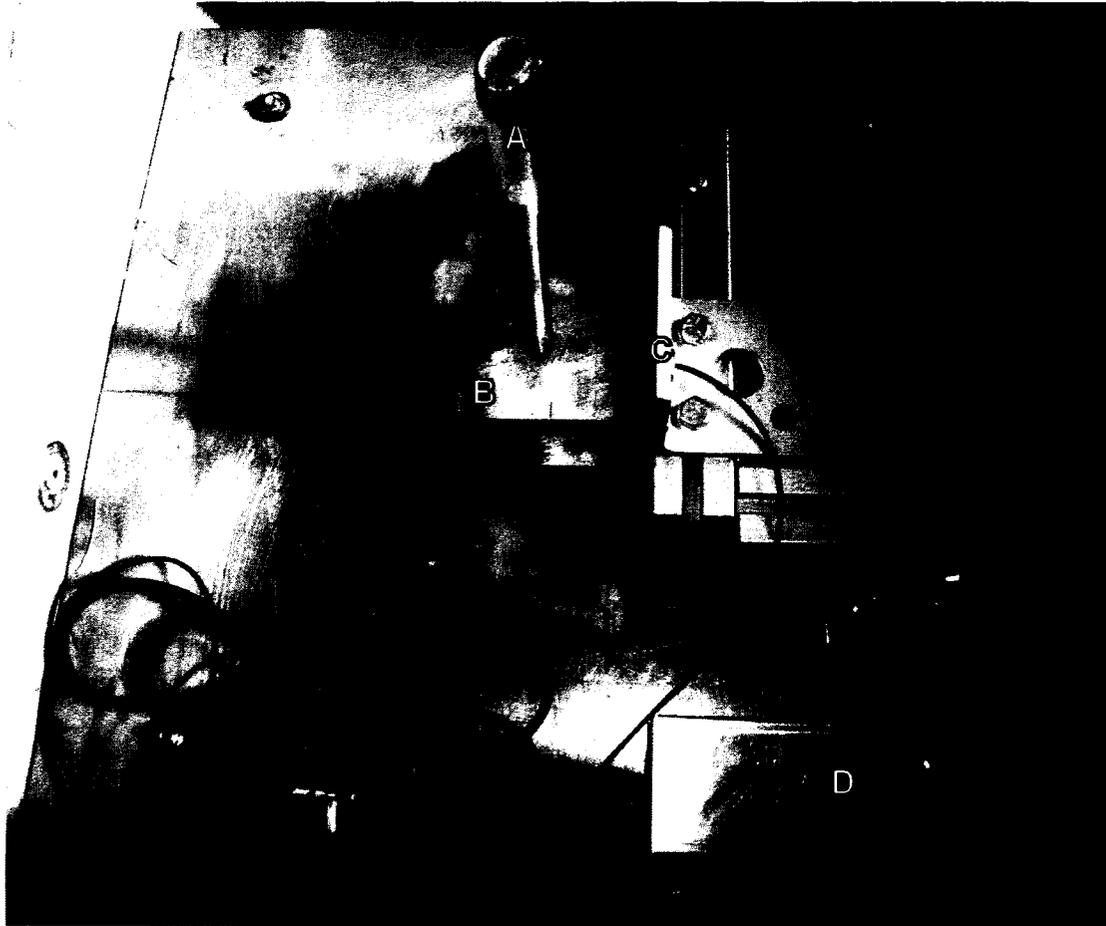


Figure A.2. Proximity sensor and plant mount for measuring force exerted on a plant by wind. (A) Plant mount; (B) spring-mounted metal plate; (C) proximity sensor; (D) DCV output plugs. Air flow is from left to right. The target of the proximity sensor is a steel plate that is at least twice the diameter of the sensor in both dimensions. Everything visible in the image except the top of (A) is below the floor of the wind tunnel and covered by a trapdoor during operation.

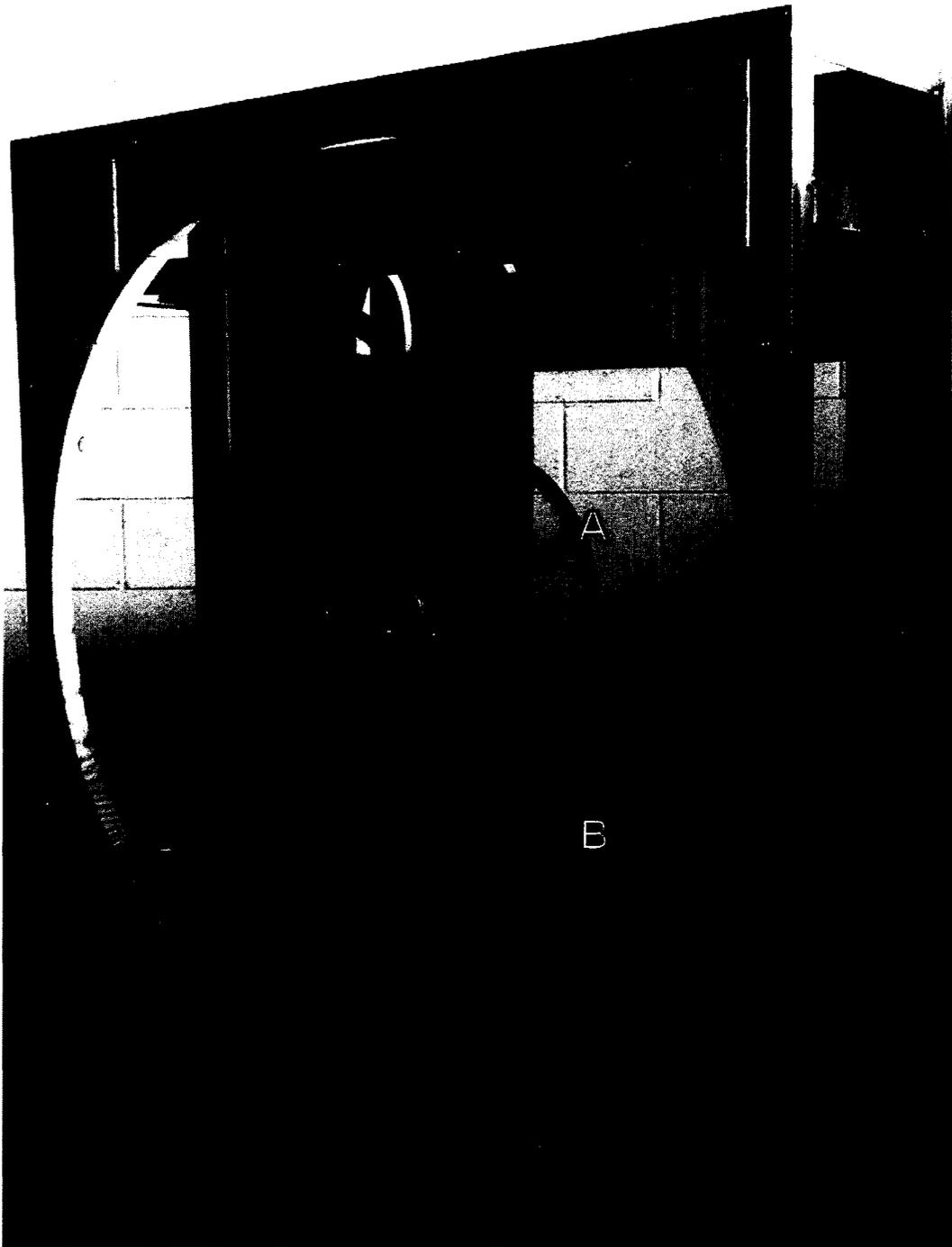


Figure A.3. Welded steel frame for the fan. (A) Eighteen inch fan pulley; (B) DC motor with 1.75" pulley. The approximate 10:1 pulley ratio allowed fine speed control as well as the use of a relatively small drive motor. The motor size allowed the use of a standard 120VAC circuit as the power source.



Figure A.4. Fan section drive components. (A) Six- blade fan capable of moving 31,630 CFM at its maximum rated RPM of 600; (B) 18" fan pulley; (C) DC motor.

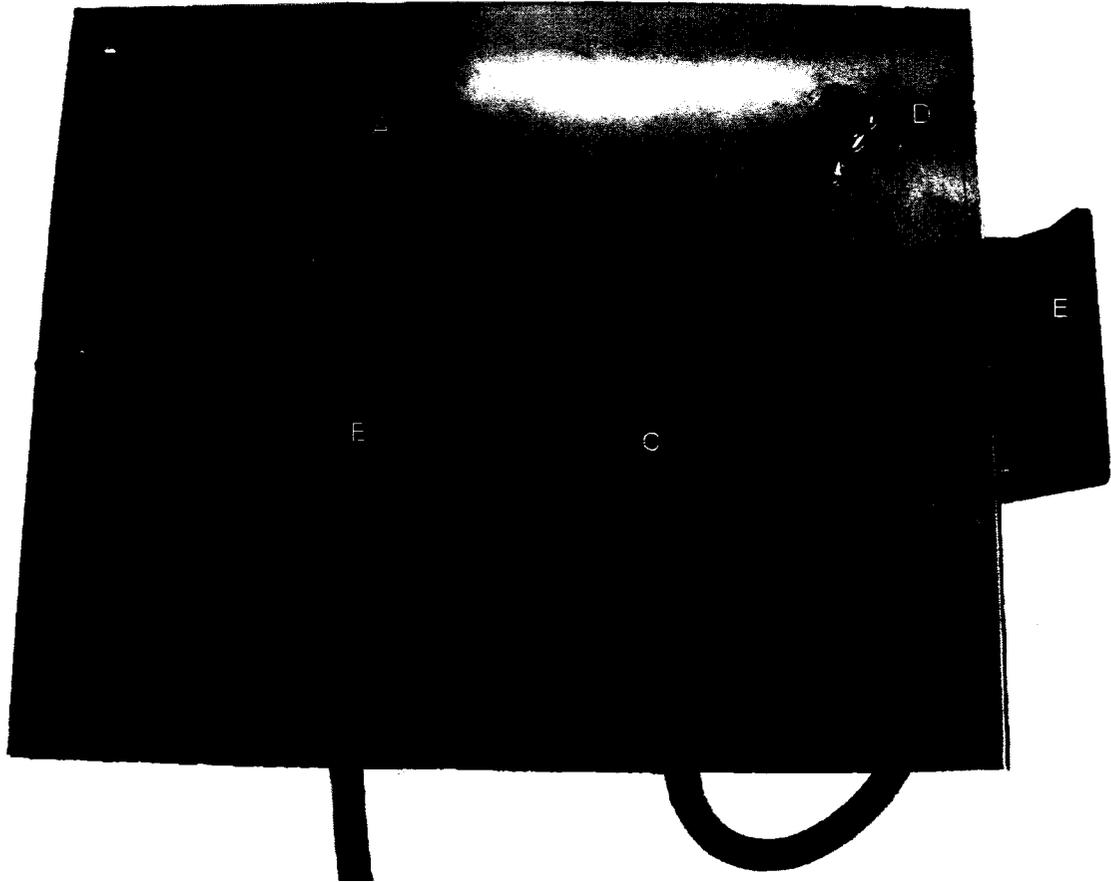


Figure A.5. Wind tunnel fan control box. (A) ammeter; (B) voltmeter; (C) fan speed control; (D) master power switch; (E) cooling fan. The ammeter and voltmeter were necessary to avoid blowing fuses or breakers and to avoid overstressing the motor.

Appendix B: Wind Tunnel User Guide

Setup.

The tunnel should be set up in a protected area with ample room at both ends to minimize air flow restrictions. Performance will be optimal if placed indoors so that ambient airflow is minimal and won't either amplify or restrict tunnel air flow. This will further ensure that an air flow of zero is attainable.

Begin by setting up the main test section (Figure B.1 – B). When this section is satisfactorily placed, lower it by moving the angle-iron levers attached to the casters. This provides a solid base for experiments.

Next, place the contraction section at the end of the main test section with the honeycomb. This is most easily accomplished with one person adjusting its position while looking through the contraction at the honeycomb. When satisfactorily placed, lock the caster (there is only one caster with a lock). Note: a nice addition would be to add a sliding door between the contraction section and the honeycomb. This would add a true zero air flow capability in the test section.

There are three extension tubes for when experiments require longer test sections (Figure B.1 – C, D, E). If one or more of these are to be used, place the false floor (labeled as such) in the main test section. Note: in its current design, the false floor will prohibit the use of the proximity sensor. Hence, if this instrumentation is to be used, the extension tubes cannot be used. This could be remedied by simply cutting a hole of appropriate size in the false floor.

Next, line up the desired number of extension tubes. There are not casters on these sections, but they are lightweight enough to be easily moved. These sections are identical except for the placement of the legs. The legs are offset such that the three tubes can be placed on end and nested together.

Finally, place the fan section at the end. Note: the tubes are smaller than the end of the fan section. The excess area of the fan section can be sealed with duct tape in this configuration.

At the relevant ends of all section there is half-inch thick foam weather stripping to aid in sealing joints. This foam may need to be replaced periodically. Duct tape can also be used to seal the extension tubes as needed.

Plug in the power strip mounted just beneath the door to the main test section and turn it on. This provides power to the proximity sensor as well as outlets for the fan and a computer. **Make sure that the circuit used has at least a 15 amp breaker.**

If the proximity sensor is to be used, plug in the Digital Multimeter (DMM) to the appropriate outlets (Figure A.2 – D, labeled ‘DCV Output’). Turn on the DMM and set it to read DC volts. This output can also be logged to a PC; the software and the interface cord are in the DMM box.

The ammeter sensor (mounted on a telescoping rod) should be inserted through the hole in the top of the main test section – friction will adequately hold it in place and adjusted to the desired height. The output from the ammeter can also be logged to a PC.

However, the user would need to purchase the software and interface cord.

Note: the user should read the directions and specifications for all instrumentation prior to use.

Operation.

The fan is operated by first turning on the main switch (Figure A.5 – D). This turns on the cooling fan and provides power to the controller. **Make sure the control knob (Figure A.5 – C) is turned to the off position (all the way counter-clockwise) before turning on the main power.** Turn on and increase the fan speed by **slowly** turning the control knob clockwise.

Make sure to monitor the ammeter and voltmeter as the control knob is adjusted.

The control box is equipped with a 15 amp time-delay fuse. The time-delay prevents it from being blown by brief surges, but make sure not to exceed 15 amps on the ammeter for more than a second or two. The fuse can be replaced and most hardware stores stock the appropriate fuse. However, care should be used when removing the lid of the control box as there are a number of wires that run from the lid to the control circuit mounted to the bottom of the box. The fan speed is usually restricted first by draw in amperes. However, while it can briefly go up to 130 volts, the motor is not rated to exceed 90 volts for sustained periods.

Storage.

All of the sections can be stored in as little as 11 by 12 feet of floor space provided there is a high enough ceiling and large enough doors. The three extension tubes may be placed on end and nested together. The expansion can also be (carefully!) nested inside the first stage of the contraction. If the tunnel is to be stored for an extended period of time, the batteries should be removed from the anemometer and DMM. The tunnel should not be stored where it will be exposed to the elements. However, it does not need to be stored in a temperature controlled environment.

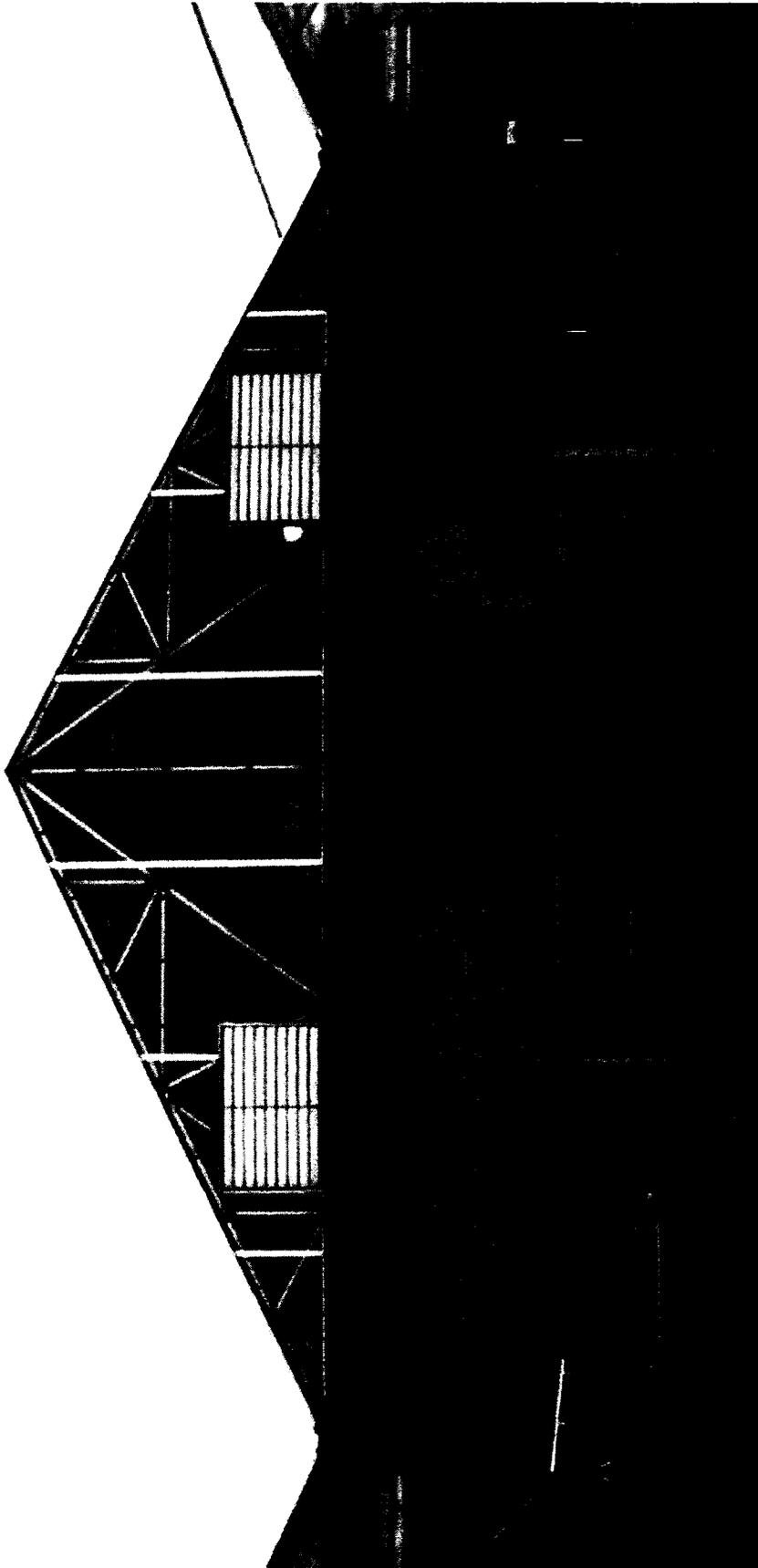


Figure B.1. Wind tunnel in its longest configuration. (A) Contraction section; (B) main test section; (C, D, E) extension tubes; (F) expansion/fan section.

Appendix C: Metadata

Note that metadata were written as independent units so there are redundancies among the different metadata as well as with the methods of Chapter 4.

Wind data

Raster datasets of wind direction and wind speed were generated with the meteorological model MicroMet (Liston and Elder 2006). I used 0.58 and 0.42 for the slope and curvature weights, respectively, as suggested by Liston and Elder (2006) and 30 m for the curvature length. The topographic inputs to MicroMet were USGS, 10 m Digital Elevation models (DEM) converted to ASCII text. The weather inputs to MicroMet were the mean wind direction and the 95th percentile of sustained wind speed measurements. This selection for wind speed was based on two premises: (1) I assumed that, while gusts may be important for breaking stems and initiating tumbling dispersal, sustained wind is more important for movement and (2) that it is wind events or storms rather than the everyday, background wind that are important for movement. I felt that the 95th percentile of sustained wind would be a reasonable representation of major wind events

that would drive dispersal without overly biasing wind calculations by inputting the maximum sustained winds.

MicroMet was configured by Glen Liston to output ASCII text files of wind direction and wind speed which were converted to raster datasets. Note that these data follow the most common convention of reporting wind direction as the compass bearing *from* which the wind is coming.

Sites. Two study sites in Colorado, USA were used in this research. One was on a private ranch near Larkspur, CO (north of Colorado Springs) and the other was on Boulder County Open Space property near Superior, CO (southwest of Boulder). The Larkspur site was approximately 400 m higher in elevation than the Superior site and has more shrub and woodland interspersed within its extent.

Naming convention. The naming convention for datasets generated with MicroMet began with a two-letter abbreviation for the type of data (wd = wind direction; ws = wind speed) immediately followed by an underscore. The first letter after the underscore designated the site (b = Superior; g = Larkspur; these letters reflect ownership of the respective properties rather than geographic proximity to a town used above for descriptive purposes). The rest of the file names reflected the time period over which weather observations were made for the input to MicroMet (Table 1).

Observed Movement

Centaurea diffusa is an invasive weed that disperses via the tumbleweed mechanism.

From October 2006 to April 2007, the tumbling movement of this species was tracked to assess the accuracy of a movement modeling effort.

Sites. Two study sites in Colorado, USA were used in this research. One was on a private ranch near Larkspur, CO (north of Colorado Springs) and the other was on Boulder County Open Space property near Superior, CO (southwest of Boulder). Both sites were heavily infested with *C. diffusa*.

Methods. Individual plants were clipped, marked with blue spraypaint and fluorescent orange survey tape, labeled with unique numbers and released at various points and various dates within the extent of large pastures at each of my field sites. GPS coordinates (Garmin GPSMAP 60CSx) were collected for each release point by averaging 30 points. The sites were searched by foot periodically and the subsequent locations of released plants recorded with the same GPS methodology. Plants found lodged in shrubs or fences such that movement was unlikely to continue were re-released at another location. Otherwise, plants were left where they were found.

These data are presented as line data and are best symbolized with an arrow at ending points. However, doing so is somewhat misleading as locations are only known for the start and endpoints; the true path between those points is unknown.

Naming convention. The first letter in each file name designates the field site where data were collected (b = Superior; g = Larkspur; these letters reflect ownership of the respective properties rather than geographic proximity to a town used above for descriptive purposes). This is followed by the letter v and an underscore for the stated purpose of the data in validating a movement model. The characters surrounded by underscores indicate time period represented by the data (Table 1). The final 3 characters, trk, are simply an abbreviation for track.

Directional Prediction Envelopes

These data are the bounds on a generalized prediction for the movement direction of an invasive tumbleweed (*Centaurea diffusa*).

Sites. Two study sites in Colorado, USA were used in this research. One was on a private ranch near Larkspur, CO (north of Colorado Springs) and the other was on Boulder County Open Space property near Superior, CO (southwest of Boulder). Both sites were heavily infested with *C. diffusa*.

Methods. Raster datasets of wind direction and wind speed were generated with the meteorological model MicroMet (Liston and Elder 2006). I used 0.58 and 0.42 for the slope and curvature weights, respectively, as suggested by Liston and Elder (2006) and 30 m for the curvature length. The topographic inputs to MicroMet were USGS Digital Elevation models (DEM) converted to ASCII text. The weather inputs to MicroMet were the mean wind direction and the 95th percentile of sustained wind speed measurements. This selection for wind speed was based on two premises: (1) I assumed that, while gusts may be important for breaking stems and initiating tumbling dispersal, sustained wind is more important for movement and (2) that it is wind events or storms rather than the everyday, background wind that are important for movement. I felt that the 95th percentile of sustained wind would be a reasonable representation of major wind events that would drive dispersal without overly biasing wind calculations by inputting the maximum sustained winds.

From October, 2006 to April, 2007 data were collected on the movement of individual, marked *C. diffusa* plants. Each apex in these data represents a release point for one or more plants. The lines (of an arbitrarily long 3,000 m) were drawn at the maximum and minimum angles of the MicroMet modeled wind direction within the extent. The idea was that this range represented the range of wind directions the plants might experience.

Naming convention. The first eight characters in the file name are simply an abbreviation for prediction envelope followed by an underscore. The next character designates the site (b = Superior; g = Larkspur; these letters reflect ownership of the respective properties rather than geographic proximity to a town used above for descriptive purposes). The remaining characters denote the time period reflected by the data (Table C.1).

Movement Potential Surfaces

These data are a prediction surface for the purpose of modeling the movement of the invasive tumbleweed, *Centaurea diffusa*. The values are NODATA where movement is predicted not to occur while all other values are wind speed (m/s) *beyond* the minimum necessary for movement.

Sites. Two study sites in Colorado, USA were used in this research. One was on a private ranch near Larkspur, CO (north of Colorado Springs) and the other was on Boulder County Open Space property near Superior, CO (southwest of Boulder). Both sites were heavily infested with *C. diffusa*.

Methods. I developed a conceptually simple, mechanistic model to predict tumbling movement of *C. diffusa*. This model predicts movement based on vegetation, topography, the estimated movement threshold modified by slope and vegetation, and wind speed and direction as modeled by MicroMet (Liston and Elder 2006). In simplest terms, this model calculates whether or not there is sufficient physical force at a given location exerted by wind to overcome the resistance to movement exerted by landcover and slope and projects the direction of travel.

Raster datasets of wind direction and wind speed were generated with the meteorological model MicroMet (Liston and Elder 2006). I used 0.58 and 0.42 for the slope and curvature weights, respectively, as suggested by Liston and Elder (2006) and 30 m for the curvature length. The topographic inputs to MicroMet were USGS, 10 m

Digital Elevation models (DEM) converted to ASCII text. The weather inputs to MicroMet were the mean wind direction and the 95th percentile of sustained wind speed measurements. This selection for wind speed was based on two premises: (1) I assumed that, while gusts may be important for breaking stems and initiating tumbling dispersal, sustained wind is more important for movement and (2) that it is wind events or storms rather than the everyday, background wind that are important for movement. I felt that the 95th percentile of sustained wind would be a reasonable representation of major wind events that would drive dispersal without overly biasing wind calculations by inputting the maximum sustained winds.

Based on my observations, I assumed that shrubs present a barrier to tumbling plants while all other landcover types would allow plant movement if there was sufficient wind in a given cell. Wind speed was adjusted from the weather station observation height to a height of 0.2 m using the log wind profile (Sutton 1953, Monteith 1975, Goudrian 1977, Oke 1987, Stull 1988, Monteith and Unsworth 1990, Geiger et al. 2003):

$$u_z = \frac{u_*}{\kappa} \ln\left(\frac{z}{z_0}\right) \quad [\text{C.1}]$$

Where u_z is the wind speed at height z , u_* is the friction speed, κ is von Karman's constant (≈ 0.41), and z_0 is roughness length (a measure of surface roughness). In tall vegetation such as forests, an additional variable, d (zero plant displacement), is sometimes subtracted from z and is approximately 0.63 of the height of the roughness elements (Monteith 1975, Monteith and Unsworth 1990). However, this only valid if the height at which wind speed is being calculated is at least $d + z_0$ (Sutton 1953). Since the height at which a plant experiences wind is much less than $d + z_0$, particularly in woodland cover types, d is not included here. I assumed a roughness length of 0.001 for

grass, 0.003 for soil, and 1.0 for woodland. These values are the lower end of ranges given by Oke (1987) and are thus conservative in their estimation of the effect of vegetation on wind speed. I chose to use the lower estimates because roughness length depends on wind speed for these vegetation types with higher wind speeds resulting in lower roughness lengths due to a 'flattening' of the vegetation at high wind speeds (Sutton 1953). Friction speed (u_*) is constant only for a given wind profile (Sutton 1953, Monteith 1975, Goudrian 1977, Oke 1987, Stull 1988, Monteith and Unsworth 1990, Geiger et al. 2003), so it was calculated separately for each cell using the observed speed at station height. Values of u_* were used to calculate the wind speed at the height at which most plants experience wind. One half of the average height and canopy diameter of plants from my sites was 0.198 m (SE=0.45). Hence, 0.2 m was an approximate midpoint of both standing and prone plants and was a reasonable approximation for the height at which plants generally experienced wind.

Movement Threshold Estimation. Plants were collected from my field sites as bolting rosettes and transplanted with their field soil into 3.8 L pots. They were reared outdoors with drip irrigation sufficient to prevent wilting until senescence began. Plants were transferred to a greenhouse and allowed to complete senescence without any additional water. After senescence was complete, I broke the stems near the soil surface and used a wind tunnel to estimate the minimum wind speed (m/s) necessary to move a plant.

Plants were placed in the wind tunnel with the stems upwind and wind speed gradually increased until tumbling movement was initiated. The wind speed at that moment was recorded. Wind tunnel air flow was monitored with a hot-film probe, in

conjunction with a constant temperature anemometer (Hotwire anemometer, model 407123, Extech Instruments). This procedure was conducted for all plants on each of two surfaces; soil (fine gravel and sand) and grass. The grass was grown in flats and was also allowed to senesce before trials. Grass height was reasonably uniform at approximately 20 cm.

The estimated movement threshold on soil was used for cover types such as dry lakebeds and roads, and the grass movement threshold was used for all grass and woodland cover types (Table C.2). The woodland cover types such as ponderosa pine (*Pinus ponderosa*) that occur at my field sites are fairly open and typically have an understory component of grass and herbaceous vegetation. Therefore, I assumed that these cover types would not present the physical barrier that shrubs do. However, as wind speed is substantially reduced in woodland, grass and woodlands are not ultimately treated equivalently by the model.

The effect of slope was estimated using the following, well-established physical relationship:

$$F_s = F_l + mg \sin \alpha \quad [\text{C.2}]$$

where F_s is the force necessary to move an object up or down a slope; F_l is the force necessary for movement on a level; m is mass; g is acceleration due to gravity and α is the angle of the slope (positive or negative). This relationship requires that the wind speed threshold estimate be converted to units of force (N). From aerodynamics and wind engineering, the following equation relates the aerodynamic overturning moment to the wind speed and the remaining principal independent variables:

$$M_B = \left(\frac{1}{2} \rho U^2 \right) C_M A \sqrt{A} \quad [\text{C.3}]$$

where M_B is the overturning moment associated with stem breaking, ρ is air mass density, U is wind speed, C_M is the moment coefficient and $A\sqrt{A}$ is volume, while A is a reference area. However, the units of a moment are in terms of force-length (e.g. N-m), so this might not be the most reliable means of calculating the force exerted on an average plant by a given wind speed. However, from Equation C.3 it is reasonable to hypothesize a simple relationship of force with the square of wind speed.

To develop a conversion between wind speed and force, I chose to estimate this relationship empirically with a subset of the plants used to estimate the movement threshold. Seven plants were visually selected from the plants used in estimating movement thresholds that were a representative range of plant sizes and shapes. The test section of the wind tunnel was equipped with a proximity sensor (GageProx 8mm unshielded proximity sensor, Kaman Instruments) calibrated to monitor wind drag effects on a plant. The output from this sensor was logged to a personal computer and sampled at 1-second intervals. Thirty samples per plant were used to calculate the temporal average of the acquired data. Output voltage ranged from 0.000 to 10.000 DCV over a calibration proximity range of 3 mm, thereby giving proximity accuracy to 3 μm . The proximity was the distance between the sensor and a sensor target. The latter was a metal plate spring-mounted and furnished with a mount employed to test (individual) plants. Given that force is directly proportional to change in proximity, this device was calibrated to provide information on wind force exerted on a plant. During calibration, known force was applied to the system. Proximity was measured for wind speeds of 0, 1.9, 3.4, 5.3, and 7.2 m/s conditions and the difference in proximity was converted into force, using the calibration conversion factor. These velocities were chosen for

repeatability and represented approximately the full range achievable with the wind tunnel. Data for individual plants were regressed separately and the average parameter estimates used for converting wind speed to force.

The empirically derived model for the wind-force relationship was:

$$f = \beta_0 + \beta_1 u^2 + \beta_2 u \quad [\text{C.4}]$$

where u is wind speed.

Surfaces representing movement potential for plants were generated using wind data observed at the sites for selected time periods of observed plant movement.

Movement potential was calculated by determining if there was sufficient wind to overcome vegetation type and slope. If movement could occur, the cell value was wind speed beyond the minimum necessary for movement at that cell. To convert values of wind force (N) used for calculating movement potential back to wind speed for more intuitive interpretation, I simply inverted Equation C.4:

$$u = \frac{-\beta_2 + \sqrt{\beta_2^2 - 4(\beta_1)(\beta_0 - f)}}{2(\beta_1)} \quad [\text{C.5}]$$

Otherwise, the cell was assigned a value of NODATA; signifying a barrier to dispersal.

The final surfaces were clipped from 6 by 8 km to the geographic extent of validation data plus a 1 km buffer on all sides. The final extent for the Larkspur site was 3 (east-west) by 3.7 km and 3.75 (east-west) by 2.7 km for the Superior site.

Detailed steps.

1. Run MicroMet and convert results from ASCII text to projected raster datasets

- Convert MicroMet predicted wind direction from source directions to travel directions. The convention for all wind direction data is to report source direction and this is the assumed input for MicroMet. This is accomplished with the following Map Algebra expression (# is used to precede a comment on a line-by-line basis):

```
# convert wind direction from source direction to travel direction; north is zero and east is 90 degrees
con([WD] >= 180, [WD] - 180, [WD] + 180)
```

- Calculate slope based on converted wind direction. Wind directions were sorted into 24 bins for slope calculations. This number was chosen as a compromise between resolution and complexity. The bins were centered on cardinal directions. The following is a sample of the Map Algebra expressions used ([WD] is the wind direction raster):

```
# north
con([WD] > 352.5, (ATan((([shiftS] - [DEM]) / 10)) * 57.29578, 0)
con([WD] <= 7.5, (ATan((([shiftS] - [DEM]) / 10)) * 57.29578, 0)

con([WD] > 7.5 & [WD] <= 22.5, ( ATan ( ( 3 * ( ( [shiftS] - [DEM] ) / 10 ) + 2 * ( ( [shiftSW] - [DEM] ) / (
10 * Sqrt(2) ) ) ) / 5 ) * 57.29578, 0 )

con([WD] > 22.5 & [WD] <= 37.5, (ATan( ( 2 * ( ( [shiftS] - [DEM] ) / 10 ) + 3 * ( ( [shiftSW] - [DEM] ) / (
10 * Sqrt(2) ) ) ) / 5 ) * 57.29578, 0)

# northeast
con([WD] > 37.5 & [WD] <= 52.5, (ATan((([shiftSW] - [DEM]) / (10 * Sqrt(2)))) * 57.29578, 0)

con([WD] > 52.5 & [WD] <= 67.5, (ATan( ( 3 * ( ( [shiftSW] - [DEM] ) / ( 10 * Sqrt(2) ) ) + 2 * ( ( [shiftW]
- [DEM] ) / 10 ) ) / 5 ) * 57.29578, 0)

con([WD] > 67.5 & [WD] <= 82.5, (ATan( ( 2 * ( ( [shiftSW] - [DEM] ) / ( 10 * Sqrt(2) ) ) + 3 * ( ( [shiftW]
- [DEM] ) / 10 ) ) / 5 ) * 57.29578, 0)

# east
con([WD] > 82.5 & [WD] <= 97.5, (ATan((([shiftW] - [DEM]) / 10)) * 57.29578, 0)
```

- Convert MicroMet predicted wind speed to values of force (N) as necessary for Equation C.2 using Equation C.4. Following is the Map Algebra expression used.

$$0.001187111 + 0.006108896 * \text{sqr}([\text{WS}]) + 0.006429602 * [\text{WS}]$$

5. Subtract movement threshold from wind force based on vegetation, slope, and

Equation C.2. The following are the Map Algebra expressions used.

```
# soil (veg = 1)
con([Veg] == 1, [WF] - 0.1138 + 0.01 * 9.8 * Sin(DD_slp), 0)
```

```
# grass (veg = 2)
con([Veg] == 2, [WF] - 0.1794 + 0.01 * 9.8 * Sin(DD_slp), 0)
```

```
# woodland (veg = 3)
con([Veg] == 3, [WF] - 0.1794 + 0.01 * 9.8 * Sin(DD_slp), 0)
```

note that shrub cover is omitted as this cover type is assumed to be a barrier. The following step implicitly results in areas with that cover type being assigned values of NODATA.

6. Sum three resulting grids and convert resulting values \leq zero to NODATA and

back-convert remaining values from wind force (N) to wind speed (m/s) using

Equation C.5 for interpretability of results.

```
# back-convert to wind speed (m/s)
con([remv_neg], (-0.006429602 + Sqrt(Sqr(0.006429602) - 4 * 0.006108896 * (0.001187111 -
[remv_neg]))) / (2 * 0.006108896) )
```

Naming convention. File names for these data begin with a four letter abbreviation for movement potential followed by an underscore (mvpt_). The next character denotes the site (b = Superior; g = Larkspur; these letters reflect ownership of the respective properties rather than geographic proximity to a town used above for descriptive purposes). The following character(s) indicate the time period reflected by the dataset (Table C.1). Datasets with an underscore followed by 'xt' have been clipped to the final extent used for model (reduced to eliminate artificial edge effects).

Spatial Reference Information (all datasets)

All data are projected in UTM Z13N, NAD83. The grain of all raster datasets is 10 m.

The final spatial extent of the Larkspur site was:

Horizontal

In decimal degrees

West: -104.861127

East: -104.826327

North: 39.182155

South: 39.148767

In projected or local coordinates

Left: 512000.000000

Right: 515000.000000

Top: 4337000.000000

Bottom: 4333300.000000

The final spatial extent of the Superior site was:

Horizontal

In decimal degrees

West: -105.207171

East: -105.163221

North: 39.938103

South: 39.913706

In projected or local coordinates

Left: 482300.000000

Right: 486050.000000

Top: 4420900.000000

Bottom: 4418200.000000

Literature Cited

- Geiger, R., R. H. Aron, and P. Todhunter. 2003. The climate near the ground, 6th edition. Rowman and Littlefield Publishers, Inc., Lanham, MD.
- Goudrian, J. 1977. Crop micrometeorology. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Liston, G. E., and K. Elder. 2006. A meteorological distribution system for high-resolution terrestrial modeling (MicroMet). *J. Hydrometeorology* 7:217-234.
- Monteith, J. L. 1975. Vegetation and the atmosphere. Academic Press, London.
- Monteith, J. L., and M. Unsworth. 1990. Principles of Environmental Physics, 2nd edition. Edward Arnold, London.
- Oke, T. R. 1987. Boundary layer climates, 2nd edition. Methuen and Co., New York.
- Stull, R. B. 1988. An introduction to boundary layer climates. Kulwer Academic Publishers, Dordrecht, The Netherlands.
- Sutton, O. G. 1953. Micrometeorology. McGraw-Hill Book Co, London.

Table C.1. Sampling periods for weather data and model validation. Wind direction is reported as the direction from which it came.

Site	Dates	Period	Mean Direction	95%ile Wind Speed (m/s)
Larkspur (g)	10/7 through 11/15	i	215.4	8
	11/15 through 11/20	ii	199.3	9.1
	11/20 through 3/7	iii	210.1	10
	3/7 through 3/28	iv	194	10.4
	3/28 through 4/12	v	215.2	10.4
	10/7 through 11/20	vi	212.5	8.1
	11/15 through 3/7	vii	209.3	9.8
	11/20 through 3/28	viii	208.1	10
	3/7 through 4/12	ix	202.4	10
	10/7 through 3/7	x	209	9.7
	11/15 through 3/28	xi	207.5	10
	11/20 through 4/12	xii	209	10
	10/7 through 3/28	xiii	209	9.7
	11/15 through 4/12	xiv	208.3	10
	10/7 through 4/12	xv	209.6	9.7
Superior (b)	2/16 through 2/17	i	222	26.8
	2/17 through 3/7	ii	221.5	15.7
	3/7 through 4/5	iii	218	22.4
	4/5 through 4/19	iv	260.6	24.6
	2/16 through 3/7	v	222	17.9
	2/17 through 4/5	vi	NA	NA
	3/7 through 4/19	vii	243	23.8
	2/16 through 4/5	viii	NA	NA
	2/17 through 4/19	ix	233.8	22.4
	2/16 through 4/19	x	234.1	22.4

Table C.2. Reclassification from SWreGAP values to generalized values used in modeling restrictions to the tumbling dispersal of *C. diffusa*.

Site	SWreGAP Description	Model Classification
Larkspur	Rocky Mountain Montane Dry-Mesic Mixed Conifer Forest and Woodland	Woodland
	Rocky Mountain Montane Mesic Mixed Conifer Forest and Woodland	Woodland
	Rocky Mountain Ponderosa Pine Woodland	Woodland
	Rocky Mountain Gambel Oak-Mixed Montane Shrubland	Shrub
	Western Great Plains Foothill and Piedmont Grassland	Grass
	Western Great Plains Riparian Woodland and Shrubland	Shrub
	Western Great Plains Floodplain Herbaceous Wetland	Grass
	Open Water	Soil
	Developed, Open Space - Low Intensity	Woodland
	Developed, Medium - High Intensity (Road)	Soil
	Agriculture	Soil
	Invasive Perennial Grassland	Grass

Superior	Western Great Plains Cliff and Outcrop	Soil
	Rocky Mountain Ponderosa Pine Woodland	Woodland
	Rocky Mountain Gambel Oak-Mixed Montane Shrubland	Shrub
	Rocky Mountain Lower Montane-Foothill Shrubland	Shrub
	Inter-Mountain Basins Mixed Salt Desert Scrub	Shrub
	Western Great Plains Foothill and Piedmont Grassland	Grass
	Western Great Plains Shortgrass Prairie	Grass
	Western Great Plains Riparian Woodland and Shrubland	Shrub
	Western Great Plains Floodplain Herbaceous Wetland	Grass
	Open Water	Soil
	Developed, Open Space - Low Intensity	Woodland
	Developed, Medium - High Intensity (Road)	Soil
	Agriculture	Soil
	Recently Burned	Grass
	Invasive Perennial Grassland	Grass

Appendix D: Code

R

Jeff A. Tracey developed this script which proved very useful and accurate in estimating cumulative seed deposition parameters (see Chapter 4). I want to express my immense gratitude for his time and expertise!

```
#
=====
=====
# fit nonlinear regression model to tumbleweed seed dispersal data
# Jeff, John, and Dirk
#
=====
=====

#
=====
=====
# negative log-likelihood of Poisson regression model
# assumes linear decline in rate due to seed loss over distance z
#
=====
=====
poisRegLinNLL <- function(p, dat) {
  # give parameters names (not necessary, but clearer)
  print(p)
  a = p[1]
  b = p[2]
  d.half = p[3]
  # calculate rate at each of the distance covariates
  r = (a - b*dat$z)*(dat$d/(d.half + dat$d))
  # calculate the negative log-likelihood under Poisson dist'n
  v = dat$n*log(r) - r - lfactorial(dat$n)
  #na.v.ind = which(!is.finite(v))
}
```

```

#na.v.cnt = length(na.v.ind)
#print(paste("Num NA values in v =", na.v.cnt), quote=F)
#print(na.v.ind)
nll = -1*sum(v)
# return negative log-likelihood
#print(paste("poisRegLinNLL() returns", nll), quote=F) # FOR
DEBUGGING
return(nll)
}

#
=====
# make data need to plot fitted rate over distance
# d.max in meters
#
=====
poisRegLinPredict <- function(p, d.max=7.620093, n.runs=4,
run.steps=50, num.sims=20) {
  a = p[1]
  b = p[2]
  d.half = p[3]
  # create d and z distance values
  d.vals = rep(seq(0, d.max, length=run.steps), n.runs)
  z.vals = seq(0, d.max*n.runs, length=n.runs*run.steps)
  # calculate rate
  r.loss = (a - b*z.vals)*(d.vals/(d.half + d.vals))
  # make some simulated data
  simN = matrix(0, nrow=num.sims, ncol=n.runs*run.steps)
  for(i in 1:(n.runs*run.steps)) {
    simN[,i] = rpois(num.sims, r.loss[i])
  }
  res = list(d.vals=d.vals, z.vals=z.vals, r.loss=r.loss,
n.sim=simN)
  return(res)
}

#
=====
# read in data, fit the model(s)
#
=====
# read in data: should have fields d, z, and n
obs.dat = read.table("seedsInput.txt", header=T, sep=",")
use.ind = which(obs.dat$d > 0 & obs.dat$z > 0)
obs.dat = obs.dat[use.ind,]

# call the optimization function
# 1. need to give initial parameter estimates
# * for a and b, could look at mean near the middle of each run,
fit line
# * for d.half, we discussed a value between 1 and 2 based on
observing plot

```

```

p = c(2.0, 0.03, 2.0)
fitRes = nlm(poisRegLinNLL, p, hessian=TRUE, dat=obs.dat,
print.level=1)
parFinal = fitRes$estimate
varcov <- try(chol2inv(fitRes$hessian), silent=TRUE); # try to get
inverse of Hessian
if(class(varcov) == "try-error") {
    varcov <- matrix(NA, nrow=length(fitRes$estimate),
ncol=length(fitRes$estimate));
}

# display results
sink("tubleWeedParams01.txt")
print(paste("alpha =", parFinal[1]), quote=F)
print(paste("beta =", parFinal[2]), quote=F)
print(paste("d.half =", parFinal[3]), quote=F)
print("variance-covariance matrix (param. variance on diagonal):",
quote=F)
print(varcov)
sink()

#
=====
=====
# make a plot...
#
=====
=====
newP = parFinal # set this to the fitted parameters
fitVal = poisRegLinPredict(newP)
lineInfo = data.frame(fitVal$d.vals, fitVal$z.vals, fitVal$r.loss)
names(lineInfo) = c("d", "z", "r")
write.table(lineInfo, "lineData01.txt", sep="\t", row.names=F, quote=F)

jpeg("t-weedRegExample02.jpg", height=400, width=600, quality=100)
plot(fitVal$z.vals, fitVal$r.loss, type="l", col="blue", lwd=2,
ylim=c(0, max(fitVal$n.sim)), xlab="distance", ylab="seed loss")
for(i in 1:length(fitVal$z.vals)) {
    points(rep(fitVal$z.vals[i], length(fitVal$n.sim[,i])),
fitVal$n.sim[,i], col="red", pch=20)
}
lines(fitVal$z.vals, fitVal$r.loss, col="blue", lwd=2) # redraw the
line over the points
graphics.off()

jpeg("t-weedRegRes.jpg", height=400, width=600, quality=100)
plot(fitVal$z.vals, fitVal$r.loss, type="l", col="blue", lwd=2,
ylim=c(0, max(obs.dat$n)), xlab="distance", ylab="seed loss")
points(obs.dat$z, obs.dat$n, pch=20, col="red")
lines(fitVal$z.vals, fitVal$r.loss, col="blue", lwd=2) # redraw the
line over the points
graphics.off()

```

SAS bootstrapping macro

This macro was developed by Gary C. White after I had completed the bootstrapping that is reported in Chapter 4 by hand. I wanted a more efficient means for future work and Dr. White was very generous with his time. My profuse thanks to him for his help!

```
*Authors: Gary C. White and Dirk V. Baker;

title "bootstrap analysis of CENDI seed dispersal distances";
option nonotes;
%let NCases=2727;
%let NVars=9;
%let Total=%eval(&NCases*&NVars);
data tunnel;
infile 'C:tunnel_bts_data.csv' delimiter=',';
input N Z S V ZS ZV SV ZSV W;
%macro BOOTSTRAP;
%do Rep=1 %to 1000;
    Data tunnelb;
        Array aData{&NVars, &NCases} Vall-Val&Total;
        Array vars[&NVars] N Z S V ZS ZV SV ZSV W;
        Retain Vall-Val&Total;
        Set tunnel end=last;
        do i=1 to dim(vars);
            aData[i, _n_]=vars[i];
        end;
        if last then do;
            do Case=1 to _n_;
                iCase=int(ranuni(0)*_n_)+1;
                do i=1 to dim(vars);
                    vars[i]=aData[i, iCase];
                end;
                Keep N Z S V ZS ZV SV ZSV W;
                Output;
            end;
        end;
    run;
ods listing close;
ods output Summary=Summary ;
proc means Mean;
    var Z S V ZS ZV SV ZSV;
data Summary;
    set Summary;
    BootstrapRep=&Rep;
run;
proc append base=MasterSummary data=Summary;
proc glm data=tunnelb;
    ods listing close;
```

```

        ods output ParameterEstimates=ParameterEstimates(keep=Parameter
Estimate);
        model N = Z S V ZS ZV SV ZSV / solution;
        weight W;
run;
*ods listing;
data ParameterEstimates;
    set ParameterEstimates;
    BootstrapRep=&Rep;
*proc print data=ParameterEstimates;
run;
proc append base=Master data=ParameterEstimates;
%end;

%mend;
%Bootstrap;
ods listing;
proc print data=Master;
proc print data=MasterSummary;
/*proc means data=Master;
    class Parameter;
    var Estimate;
proc means data=MasterSummary;*/
run;

quit;

```

Model Documentation

The following is the detailed documentation of the models used to create movement potential surfaces for Chapter 5. All were created with ESRI's ArcGIS 9.2

ModelBuilder and are in the order used.

Model Name: Text to Raster NAD83

Description: Converts ASCII text file (output from MicroMet (Liston and Elder 2006)) to raster and defines its projection as UTM Zone 13N, NAD83.

Details: Uses the ArcGIS Text to Raster conversion tool and the Define Projection tool.

Model Name: Shift 8 Directions

Description: Shifts an input DEM in 8 directions for slope calculations in the Get Slope model.

Details: Uses the ArcGIS Shift tool to shift a DEM one cell in each of eight directions.

This allows the calculation of slope based on rise over run. For instance, to calculate the slope in the southerly direction, simply subtract the DEM from the north Shift (ShiftN).

Model Name: Adjust Wind Speed

Description: Adjusts wind speed rasters (from MicroMet) for height and vegetation using the log wind profile model. Assumes observations are made at 2 meters above the ground and height of interest is 0.2 meters. The latter is based on the average of one-half the average height and canopy diameters of diffuse knapweed over 2 years of observations at 2 sites in Colorado. Assumes zero plane displacement (d) to be zero and

roughness length (z_0) to be 0.001 for soil, 0.003 for grass, and 1 for woodland. These are the low end of ranges given by Oke (1987).

Details: This is a two-step process. The first step is to calculate friction velocity (U^*) for the observation height. The second is to use the calculated U^* to calculate the wind velocity at a new height. Finally, all negative values are set to zero.

Map Algebra Syntax:

```
Ustar1 = con([veg] == 1, ([WS] * 0.41) / Ln(2 / 0.001), 0)
```

```
Ustar2 = con([veg] == 2, ([WS] * 0.41) / Ln(2 / 0.003), 0)
```

```
Ustar3 = con([veg] == 3, ([WS] * 0.41) / Ln(2 / 1), 0)
```

```
WS1 == [Ustar1] / 0.41 * Ln(0.2 / 0.001)
```

```
WS2 == [Ustar2] / 0.41 * Ln(0.2 / 0.003)
```

```
WS3 == [Ustar3] / 0.41 * Ln(0.2 / 1)
```

```
adjWS == [WS1] + [WS2] + [WS3]
```

```
con([adjWS] > 0, [adjWS], 0)
```

```
*****
```

Model Name: Convert Wind Direction

Description: Converts directions in a grid from a source ('from') direction (standard for wind) to a travel ('to') direction.

Details: Map Algebra Expression: $\text{con}([\text{WD}] \geq 180, [\text{WD}] - 180, [\text{WD}] + 180)$

```
*****
```

Model Name: Get Slope

Description: This model was designed to create a slope grid based on an input direction.

The inputs are a grid of directions (e.g. wind), DEM, and the same DEM shifted 1 cell in each of the 8 directions (total of 10 input grids). From these, a total of up to 24 direction-dependent slopes are calculated and summed to produce a single output slope grid. The directional bins are centered on the cardinal directions and the number 24 chosen for symmetry and as a compromise between desired resolution and manageability.

Details:

Map Algebra Syntax

```
1a: 352.5      con([WD] > 352.5, (ATan((([shiftS] - [DEM]) / 10)) * 57.29578, 0)
1b: 7.5        con([WD] <= 7.5, (ATan((([shiftS] - [DEM]) / 10)) * 57.29578, 0)

2: 22.5        con([WD] > 7.5 & [WD] <= 22.5, ( ATan ( ( 3 * ( ( [shiftS] - [DEM] ) / 10 ) + 2 * ( (
[shiftSW] - [DEM] ) / ( 10 * Sqrt(2) ) ) ) / 5 ) ) * 57.29578, 0 )

3: 37.5        con([WD] > 22.5 & [WD] <= 37.5, (ATan( ( 2 * ( ( [shiftS] - [DEM] ) / 10 ) + 3 * ( (
[shiftSW] - [DEM] ) / ( 10 * Sqrt(2) ) ) ) / 5 ) ) * 57.29578, 0)

4: 52.5        con([WD] > 37.5 & [WD] <= 52.5, (ATan((([shiftSW] - [DEM]) / (10 * Sqrt(2)))) *
57.29578, 0)

5: 67.5        con([WD] > 52.5 & [WD] <= 67.5, (ATan( ( 3 * ( ( [shiftSW] - [DEM] ) / ( 10 *
Sqrt(2) ) ) + 2 * ( ( [shiftW] - [DEM] ) / 10 ) ) / 5 ) ) * 57.29578, 0)

6: 82.5        con([WD] > 67.5 & [WD] <= 82.5, (ATan( ( 2 * ( ( [shiftSW] - [DEM] ) / ( 10 *
Sqrt(2) ) ) + 3 * ( ( [shiftW] - [DEM] ) / 10 ) ) / 5 ) ) * 57.29578, 0)

7: 97.5        con([WD] > 82.5 & [WD] <= 97.5, (ATan((([shiftW] - [DEM]) / 10)) * 57.29578, 0)

8: 112.5       con([WD] > 97.5 & [WD] <= 112.5, (ATan( ( 3 * ( ( [shiftW] - [DEM] ) / 10 )
+ 2 * ( ( [shiftNW] - [DEM] ) / ( 10 * Sqrt(2) ) ) ) / 5 ) ) * 57.29578, 0)

9: 127.5       con([WD] > 112.5 & [WD] <= 127.5, (ATan( ( 2 * ( ( [shiftW] - [DEM] ) / 10 )
+ 3 * ( ( [shiftNW] - [DEM] ) / ( 10 * Sqrt(2) ) ) ) / 5 ) ) * 57.29578, 0)

10: 142.5      con([WD] > 127.5 & [WD] <= 142.5, (ATan((([shiftNW] - [DEM]) / (10 * Sqrt(2)))) *
57.29578, 0)

11: 157.5      con([WD] > 142.5 & [WD] <= 157.5, (ATan( ( 3 * ( ( [shiftNW] - [DEM] ) / ( 10 *
Sqrt(2) ) ) + 2 * ( ( [shiftN] - [DEM] ) / 10 ) ) / 5 ) ) * 57.29578, 0)
```

12: 172.5 $\text{con}([\text{WD}] > 157.5 \ \& \ [\text{WD}] \leq 172.5, (\text{ATan}((2 * (([\text{shiftNW}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) + 3 * (([\text{shiftN}] - [\text{DEM}]) / 10)) / 5) * 57.29578, 0)$

13: 187.5 $\text{con}([\text{WD}] > 172.5 \ \& \ [\text{WD}] \leq 187.5, (\text{ATan}(((\text{shiftN}] - [\text{DEM}]) / 10)) * 57.29578, 0)$

14: 202.5 $\text{con}([\text{WD}] > 187.5 \ \& \ [\text{WD}] \leq 202.5, (\text{ATan}((3 * (([\text{shiftN}] - [\text{DEM}]) / 10) + 2 * (([\text{shiftNE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) / 5) * 57.29578, 0)$

15: 217.5 $\text{con}([\text{WD}] > 202.5 \ \& \ [\text{WD}] \leq 217.5, (\text{ATan}((2 * (([\text{shiftN}] - [\text{DEM}]) / 10) + 3 * (([\text{shiftNE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) / 5) * 57.29578, 0)$

16: 232.5 $\text{con}([\text{WD}] > 217.5 \ \& \ [\text{WD}] \leq 232.5, (\text{ATan}(((\text{shiftNE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) * 57.29578, 0)$

17: 247.5 $\text{con}([\text{WD}] > 232.5 \ \& \ [\text{WD}] \leq 247.5, (\text{ATan}((3 * (([\text{shiftNE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) + 2 * (([\text{shiftE}] - [\text{DEM}]) / 10)) / 5) * 57.29578, 0)$

18: 262.5 $\text{con}([\text{WD}] > 247.5 \ \& \ [\text{WD}] \leq 262.5, (\text{ATan}((2 * (([\text{shiftNE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) + 3 * (([\text{shiftE}] - [\text{DEM}]) / 10)) / 5) * 57.29578, 0)$

19: 277.5 $\text{con}([\text{WD}] > 262.5 \ \& \ [\text{WD}] \leq 277.5, (\text{ATan}(((\text{shiftE}] - [\text{DEM}]) / 10)) * 57.29578, 0)$

20: 292.5 $\text{con}([\text{WD}] > 277.5 \ \& \ [\text{WD}] \leq 292.5, (\text{ATan}((3 * (([\text{shiftE}] - [\text{DEM}]) / 10) + 2 * (([\text{shiftSE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) / 5) * 57.29578, 0)$

21: 307.5 $\text{con}([\text{WD}] > 292.5 \ \& \ [\text{WD}] \leq 307.5, (\text{ATan}((2 * (([\text{shiftE}] - [\text{DEM}]) / 10) + 3 * (([\text{shiftSE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) / 5) * 57.29578, 0)$

22: 322.5 $\text{con}([\text{WD}] > 307.5 \ \& \ [\text{WD}] \leq 322.5, (\text{ATan}(((\text{shiftSE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) * 57.29578, 0)$

23: 337.5 $\text{con}([\text{WD}] > 322.5 \ \& \ [\text{WD}] \leq 337.5, (\text{ATan}((3 * (([\text{shiftSE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) + 2 * (([\text{shiftS}] - [\text{DEM}]) / 10)) / 5) * 57.29578, 0)$

24: 352.5 $\text{con}([\text{WD}] > 337.5 \ \& \ [\text{WD}] \leq 352.5, (\text{ATan}((2 * (([\text{shiftSE}] - [\text{DEM}]) / (10 * \text{Sqrt}(2)))) + 3 * (([\text{shiftS}] - [\text{DEM}]) / 10)) / 5) * 57.29578, 0)$

Model Name: Check Veg & Slope

Description: This model uses the output from the GetSlope model to determine whether a plant will move based on vegetation, slope and wind speed. Output is a grid where cell values are NODATA if wind speed is insufficient to move a plant (due to vegetation or slope). All other values are the wind speed BEYOND the minimum necessary for movement.

Details:

Map Algebra Syntax

wind force =

$0.001187111 + 0.006108896 * \text{sqr}([\text{WS}]) + 0.006429602 * [\text{WS}]$

soil threshold of 3.8 m/s = 0.1083 N; grass threshold of 4.2 m/s = 0.1323 N

avg plant weight = 0.01 kg

if shrub, plants will not move - **taken care of with other statements (else = 0)**

if soil, subtract soil movement threshold from wind force, else zero

$\text{con}([\text{Veg}] == 1, [\text{WF}] - 0.1138 + 0.01 * 9.8 * \text{Sin}(\text{DD_slp}), 0)$

if grass, subtract grass movement threshold from wind force, else zero

$\text{con}([\text{Veg}] == 2, [\text{WF}] - 0.136 + 0.01 * 9.8 * \text{Sin}(\text{DD_slp}), 0)$

if woodland, subtract grass movement threshold from wind force, else zero

$\text{con}([\text{Veg}] == 3, [\text{WF}] - 0.136 + 0.01 * 9.8 * \text{Sin}(\text{DD_slp}), 0)$

this assumes that the movement threshold in the understory of woodland is the same as that for grassland. the woodlands in the study extents are ponderosa pine, so this seems to be a reasonable assumption. note that wind speed will be modified for veg type, so while the threshold will be the same in woodland and grass, the wind speed will be reduced in woodland areas.

then sum, remove negative and zero values, and convert back to wind speed

$\text{con}([\text{move}] > 0, [\text{move}])$

wind speed =

$\text{con}([\text{remv_neg}], (-0.006429602 + \text{Sqrt}(\text{Sqr}(0.006429602) - 4 * 0.006108896 * (0.001187111 - [\text{remv_neg}]))) / (2 * 0.006108896)$

Literature Cited

- Liston, G. E., and K. Elder. 2006. A meteorological distribution system for high-resolution terrestrial modeling (MicroMet). *J. Hydrometeorology* 7:217-234.
- Oke, T. R. 1987. *Boundary layer climates*, 2nd edition. Methuen and Co., New York.