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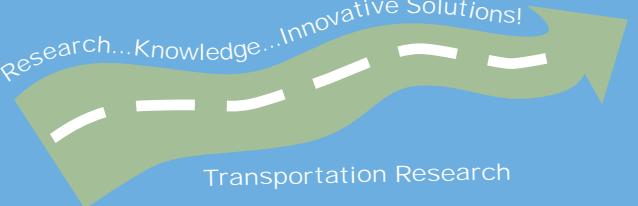
Production and Wind Dispersal of Canada Thistle
(*Cirsium arvense* L.) Achenes

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| 1. Report No. MN/RC 2008-39 | 2. | 3. Recipients Accession No. | |
| 4. Title and Subtitle Production and Wind Dispersal of Canada Thistle (<i>Cirsium arvense</i> L.) Achenes | | 5. Report Date September 2008 | |
| 7. Author(s) R.L. Becker, M.J. Haar, B.D. Kinkaid, L.D. Klossner, and F. Forcella | | 6. | |
| 9. Performing Organization Name and Address Department of Agronomy and Plant Genetics University of Minnesota 1991 Upper Buford Circle 411 Borlaug Hall St. Paul, Minnesota 55108 | | 8. Performing Organization Report No. | |
| 12. Sponsoring Organization Name and Address Minnesota Department of Transportation 395 John Ireland Boulevard, Mail Stop 330 St. Paul, Minnesota 55155 | | 10. Project/Task/Work Unit No. | |
| | | 11. Contract (C) or Grant (G) No. (c) 81655 (wo) 172 | |
| 13. Type of Report and Period Covered Final Report | | 14. Sponsoring Agency Code | |
| 15. Supplementary Notes http://www.lrrb.org/PDF/200839.pdf | | | |
| 16. Abstract (Limit: 200 words) Quantity, quality and dispersal distance of wind-blown achenes and pappi were determined during the peak time of dispersal over twelve site-years in Minnesota during 2006 and 2007. Approximately twice as many pappi than achenes were trapped. Wind blown pappi tend to travel near the ground. Most achenes fell near the parent plants and their population density declined exponentially with increasing distance. Over 80% of pappi collected did not have an achene attached. Concomitantly, seed production in Canada thistle was monitored for 8 site-years in Minnesota. Averaged across years and locations, female Canada thistle shoots that flowered produced an average of 38% empty, 17% shrunken, and 44% normal achenes. Male shoots produce about half the number of seedheads compared to female shoots. A low level of hermaphroditic expression was observed in male shoots. Though seed production by female Canada thistle is extremely variable, when sufficient pollen is available, Canada thistle clearly has the potential to generate significant contributions to seedbanks to maintain invasive stands. However, dispersal by wind is for the most part, local. Long distance dispersal of significant numbers of healthy achenes would be a rare event. | | | |
| 17. Document Analysis/Descriptors Achenes, Canada thistle, <i>Cirsium arvense</i> , dispersal, pappi, production, seed, trap, wind | | 18. Availability Statement No restrictions. Document available from: National Technical Information Services, Springfield, Virginia 22161 | |
| 19. Security Class (this report) Unclassified | 20. Security Class (this page) Unclassified | 21. No. of Pages 50 | 22. Price |

Production and Wind Dispersal of Canada Thistle (*Cirsium arvense* L.) Achenes

Final Report

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September 2008

Published by:

Minnesota Department of Transportation
Research Services Section
395 John Ireland Boulevard, Mail Stop 330
St. Paul, Minnesota 55118

This report represents the results of research conducted by the authors and does not necessarily represent the views or policies of the Minnesota Department of Transportation and/or the Center for Transportation Studies. This report does not contain a standard or specified technique.

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ACKNOWLEDGEMENTS

We would like to thank Minnesota Department of Transportation (Mn/DOT) and The Center for Transportation Studies for partial funding of this work. We also thank Drs. Luke Skinner, Minnesota Department of Natural Resources; Donald Wyse, University of Minnesota; and Tina Markeson, Dan Warzala, and the late Robert Jacobson, Mn/DOT, for their helpful guidance and input as members of a technical advisory panel, and especially to Robert Jacobson for his advocacy supporting this work. We would also like to thank Dean Petersen, USDA ARS North Central Soil Conservation Research Lab, Morris MN, for his assistance in managing the Morris trap site; Lizabeth Stahl and Ryan Miller, University of Minnesota Extension; for their assistance in managing trap sites in Welcome and Elysian, respectively; and Drs. Jeanie Katovich and Laura van Riper and students Gina Kawsowski and Andrea Hannan for their assistance in trap maintenance and data collection. We thank Britta Boyum, Matt Carlson, and Andre' Miranda for their perseverance in counting and sorting achenes and Doug Miller for data analysis and site prep. Finally, we thank landowners Richard Perrine and Brad Carlson for access to their Conservation Reserve Program native prairies.

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EXECUTIVE SUMMARY

The potential for Canada thistle to spread by wind-blown achenes and for production of achenes was evaluated. Quantity, quality and dispersal distance of wind-blown achenes and pappi were measured during the peak time of achene dispersal at twelve site-years in Minnesota during 2006 and 2007. Achenes and pappi were collected on traps constructed of wire mesh, coated with adhesive and arranged at set distances and heights around a source patch of Canada thistle measuring 0.9 m in diameter. An estimate of productivity from these 0.9 m diameter Canada thistle stands during the one week sampling period was 1,054 normal achenes, 163 empty achenes, 140 shrunken achenes and 3,972 pappi. Approximately twice as many pappi as achenes were produced. Wind influenced the direction of dispersal, but the contribution of wind to the distance of Canada thistle dispersal appears to be small and wind blown pappi tend to travel near the ground. Most achenes fell near the parent plants and the population density declined exponentially with increasing distance. Over 80% of pappi collected between 1.5 and 6.1 m from the source did not have an achene attached. Using two sampling strategies the average population density at the margin of a Canada thistle stand was 141.5 and 109.1 normal achenes per m² at a distance of 3.0 m the average population density was 20.1 and 15.2 normal achenes per m².

Achene production in Canada thistle was monitored for 8 site-years in Minnesota. Development of flowers and production of viable achenes differed among sampling dates, between years, and among sites. Achenes were classified as nonviable (empty achene pericarp), achenes of questionable viability and vigor (shrunken achenes), and achenes assumed to have the potential to produce vigorous, viable seedlings (fully filled, normal achenes). Averaged across years and locations, female Canada thistle shoots that flowered produced an average of 26.0 flowers, and 829.6 achenes per shoot. Of these 829.6 achenes 318.9 were nonviable, 142.5 were of questionable viability and vigor, and 368.3 were normal, plump achenes. Expressed as percentages of achenes produced, 38% were empty, 17% shrunken, and 44% normal. An individual flower on a female shoot produced, on average, 12.3, 5.5, and 14.2 empty, shrunken and normal achenes, respectively. Both the low and high extremes of achene production per shoot at individual sites occurred in 2006. When averaged across sites, 2006 exceeded 2007 production of seedheads and total achene production by a factor of 1.6 x and 2.8 x, respectively. Male shoots produce about half the number of seedheads compared to female shoots, averaging 13.5 flowers per shoot. Of note, a low level of hermaphroditic expression was observed in male shoots with an average of 252.2 empty, 1.7 shrunken and 0.6 normal achenes produced per male shoot (99.1, 0.7 and 0.2%, respectively). Though achene production by female Canada thistle is extremely variable, when sufficient pollen is available, Canada thistle clearly has the potential to generate significant contributions to seedbanks to maintain invasive stands. Improved management strategies based on better timing and implementation of recommended best practice for control of Canada thistle are possible with a better understanding of achene dispersal and production.

Based on the achene flight work (Haar et al. CTS Flight Study), and this mass balance work, movement of Canada thistle achenes was local. Only 3.7% of the pappi reaching the 6.1 m perimeter of the trap array carried a normal achene in the achene flight study. Based on the mass balance work, about 44% of achenes produce by an individual flower were normal with 14.3 normal achenes produced per flower on average, and 368.3 normal achenes produce per emerged flowering female shoot on average. Using data from the combined studies, an estimated 29 normal achenes per

emerged flowering female shoot would travel 6.1 m (8.0% of the average 368 produced per emerged shoot the reached the 6.1 trap perimeter). Yet, if landscape-scale Canada thistle populations are high, even though a small portion of achene moved relatively short distances, the potential for movement on a landscape scale is significant. Our trap design did not allow estimation of the distance pappi with achenes attached that reached the 6.1 m perimeter might have traveled if they had not been trapped. Conceivably, achenes could be carried great distances in severe storm events, common during pappi release in this region. Having said that, considering Canada thistle is common in most of Minnesota and has been for many years, we propose that the risk of new infestations of thistle establishing via pappi flight is small compared to the challenges of implementing management of established populations when pappi flight is underway to attempt to prevent achene movement. Once pappi have begun to disperse is not the time to implement management.

Once first blooms are visible, there is a small window where mowing can effectively prevent achene production. Derscheid and Schultz (1960) defined the window as up to 7 to 9 days after blooms appear in research in South Dakota, with peak production of achenes occurring 8 to 11 days after blooms appear and with up to 80% germination of these new achenes. Mowing may help reduce achene dispersal if pappi flight has begun, but should be done when pappi are wet dew and involucre are closed in the early morning to minimize flight during mowing. Pappi will still release from downed shoots and fragmented seedheads after mowing, but are released from a lower height, closer to entrapping vegetation surfaces (personal observation). Additionally, a significant proportion of seed will be threshed from the seedhead, detached from pappi, and left in place with fragmenting mowers (rotary mowers or flail choppers) compared to sickle mowers. Herbicide application is not recommended during the time of pappi flight as control will be inconsistent and efficacy low. At the same time, non-target forbs may be at a growth stage conducive to severe damage or plant death while little may be gained on Canada thistle management. Resources allocated towards long-term control of Canada thistle (labor, money, and environmental impact of mechanical or herbicidal control) in ecosystems where it is widespread and has been historically present, would be better utilized toward optimizing control of established patches than in emergency management of pappi dispersal.

The elimination of established Canada thistle requires the destruction of its extensive root system. Destruction of the root system with a single herbicide treatment, clipping, mowing, rouging or tillage operation is seldom achieved. However, depletion of food reserves through repeated tillage, timely mowing or pulling can diminish or eliminate an infestation. Adding timely application of herbicide to these practices can reduce the time and labor required to eliminate a stand. Mechanical control (mowing, shallow tillage to severe shoots, hand rouging) should be performed when carbohydrate reserves are at their lowest and repeated at monthly intervals two or three times during the remainder of the season. The best timing for mechanical control of Canada thistle would be to clip, till, or hand rouge when buds have developed and the first thistle flowers are beginning to show color, but before viable Canada thistle achenes develop to comply with the Minnesota Noxious Weed Law. Programs that removed Canada thistle shoot growth (including fall regrowth) for two to three years with tillage (Hodgson, J. M., 1971) or after 4 years of close mowing (Schreiber, M., 1967) usually result in Canada thistle elimination.

Unlike mechanical control, herbicide application would be best delayed until late-summer or early-fall when herbicide will translocate most effectively to the roots and to quiescent root buds. Canada thistle regrowth remains active until late fall even following light

frosts and will absorb and translocate herbicide very efficiently. Desirable spring ephemerals may gain additional tolerance to herbicides with little vegetation physiologically active at the time of fall applications. If late maturing desirable forbs are present and of concern, herbicide should be applied in late-spring when thistle are in the bud stage and the late emerging forbs are in early growth stages or not yet emerged. As with mechanical control, two or three applications of herbicide in sequential years are usually required to eliminate an established stand.

In summary, where Canada thistle is widely distributed, the risk of spread of Canada thistle via wind dispersal is overstated based on high numbers of pappi in flight, considering over 80% do not carry viable achenes, and especially in Minnesota, considering the existence of widespread, preexisting seedbanks. Heimann and Cussans (1996) noted that although it is thought that achene dispersal accounts for a relatively small amount of spread, new infestations are likely the result of seedling establishment. In areas of isolated, localized infestations where Canada thistle is not yet widely distributed, extraordinary measures should be undertaken to prevent development of pappi capable of wind dispersal of viable achenes. Ideally these isolated populations would be known, and management undertaken before achene production and flight become an issue with appropriate spring or fall management programs.

CHAPTER 1. WIND DISPERSAL OF CANADA THISTLE (*CIRSIUM ARVENSE* L.) ACHENES

INTRODUCTION

Canada thistle was introduced to North America from Europe around the beginning of the 18th century (Moore, 1975). It is now the most frequently listed noxious weed among the states of the United States and the provinces of Canada (Skinner et al., 2000). Clearly, Canada thistle dispersal is effective. In Minnesota, where this study was conducted, Canada thistle is listed as a noxious weed and seed (ORS, 2007) and is the state's most prevalent and persistent broadleaf weed, found in all crops, pastures and natural areas (Durgan, 1998). Control is mandatory for state agencies and private land-owners. The sight of Canada thistle inflorescences in bloom and pappi floating across the landscape often trigger calls for enforcement of weed laws. These complaints are based on the premise that wind-blown achenes are an important means of dispersal and invasion of new sites. However, it is not clear to what extent this premise is valid and a false premise could lead to mismanagement. Pappus flight occurs at a time that is not optimal for cultural or chemical control. Herbicide applications made when achenes are mature are less efficacious to non-effective and may perversely damage desirable non-target native forbs and disturb habitat for wildlife such as nesting waterfowl or pheasants at that point in the season. Current management practices to comply with noxious weed laws recommended by University of Minnesota State Extension Weed Specialist when flowering has begun would be to mow before achenes mature followed by a fall application of herbicide. Fall herbicide application or spring bud-stage application of the appropriate herbicide would preclude the need to prevent achene flight (Roger Becker, personal communication).

A review of the literature revealed that, like many weed species, Canada thistle would benefit from more study of fecundity (Norris, 2007). Previous studies indicate that productivity of Canada thistle achenes is variable and influenced by resource availability, degree of pollination (Lalonde and Roitberg, 1989) and possibly genotype (Hodgson, 1964). Achenes are viable 10 days after flowers open (Derscheid and Schultz, 1960). However, many flowers do not develop into achenes. Bostock and Benton, (1979) reported an average of 61 flowers in a capitulum, of which 39.3% developed into achenes, while Hayden (1934) reported on average, approximately half of the 60 to 75 flowers in each capitulum bore seed. The average number of achenes per capitulum reported in the literature varied from fewer than 1 (Amor and Harris, 1974), 26.2 (Bostock and Benton, 1979), to a high of 46 (Hayden, 1934). Hayden (1934) found the number of achenes produced per capitulum ranged from 1 to 104, while Derscheid and Schultz, (1960) found a narrower range of 15 to 82 achenes per capitulum. Furthermore, not all achenes are viable. Derscheid and Shultz (1960) reported 20 to 91% of achenes as viable while Hayden (1934) found that 95% of achenes germinated.

Compared to other members of the Asteraceae, the pappus of Canada thistle is relatively large and the achene relatively lightweight (Sheldon and Burrows, 1972). These characteristics should enable the achene-pappus units of Canada thistle to spend relatively more time airborne and disperse greater distances. Based on terminal velocity of the achene-pappus units, the maximum dispersal distance for Canada thistle has been estimated to be 11.35 m at a wind speed of 16.41 kph (Sheldon and Burrows, 1972). Although not a great distance, the estimate exceeded that of 17 species of Asteraceae. Field studies of similar species, musk thistle (*Carduus nutans* L.) and bull thistle (*Cirsium vulgare* Savi.), indicate that achene dispersal is largely local. At wind speeds of 20.4 kph, less than 1% of harvested musk thistle achenes traveled more than 99.7 m on a paved surface and over 80% of achenes were deposited within 39.9 m of release (Smith and Kok, 1984). Only 10% of bull thistle achenes traveled 32.0 m and 65% of achenes fell within 2.0 m of the parent plant (Klinkhamer and de

Jong, 1993). We note that because the pappi and achene of Canada thistle separate easily, the actual distance of achene dispersal may be less than predicted. Canada thistle is among the species of Asteraceae described by Shmida (1985) of which the achenes and pappi are deciduous. Anecdotal observations of wind-blown pappi without achenes by the authors and a reference to the same phenomenon in Bakker (1960) led the authors to develop the present study to better determine the contribution of wind-blown achenes to the dispersal of Canada thistle. Our objective was to improve understanding of the role wind dispersal plays in the spread and persistence of Canada thistle by measuring the quantity, quality, and dispersal distance of wind-blown Canada thistle achenes under field conditions. Potential benefits of this knowledge include improved management recommendations, provision of accurate information to land managers and the public about the role of wind dispersal in invasion, re-evaluation of current enforcement guidelines, and reduced negative impact of management on native forbs and wildlife.

METHODS AND MATERIALS

Two trap designs were used to characterize wind dispersal of Canada thistle achenes, as we were uncertain at the initiation of the study whether either would work. A relatively open spiral design and a cylindrical cage enclosure design were used, both constructed around an isolated 0.9 m diameter source stand of Canada thistle at the center of the trapping array. Spiral traps were set at Elysian, Morris, St. Paul and Welcome, MN in 2006, and at Elysian, Morris, Waseca and Welcome MN in 2007. Cage traps were set at Lamberton and at Rosemount MN in 2006 and in 2007.

Individual traps that were set perpendicular to the ground to collect achenes and pappi moving through the air were termed ‘flight’ traps. A second set of traps were set parallel to the ground to collect achenes and pappi as they fell were termed ‘rain’ traps. Traps were made of steel wire mesh cloth (1.5 mm diameter wire with 6.4 mm spacing for flight traps, and with 3.2 mm spacing for rain traps) acquired from TWP, Inc, 2831 Tenth St., Berkeley CA 94710, and coated with polyisobutylene adhesive, purchased from The Tanglefoot Company, Grand Rapids, MI. Pre-testing was conducted in 2006 to find wire mesh cloth gap dimensions and polyisobutylene application to best trap pappi without getting coated mesh openings too fine creating an air dam where pappi would vortex around the traps under low velocity, laminar flow conditions. The 6.4 mm mesh met these criteria. A 3.2 mesh for rain traps left openings small enough after the adhesive was applied to allow drainage, yet would catch falling achenes.

Due to the parachute design of pappi, the broad tops of pappi typically impacted flight traps first, with achenes, if present, held perpendicular to and away from the vertical trap surface. Seed rain traps were placed at the base of flight traps to catch achenes that detached and fell from flight traps. With time, capillary movement of adhesive engulfed pappi and achenes, if still attached, and neither could easily be detached. Pappi that lightly attached from low impact forces under low wind velocities could detach before being engulfed, however, especially when winds shifted to the opposite direction and significantly so if wind speeds escalated after shifting direction during storm events. For this reason, it was decided that trapping would be allowed to occur for approximately 1 week before data collection to minimize losses due to pappi detachment. Some sites were counted at longer intervals or were counted a second time depending on how pappi flight progressed following trap activation, but the trapping interval never exceeded 2 weeks. Because this monitoring protocol resulted in a snapshot in time during seed movement, a companion set of studies were established to monitor achene production

throughout the season to help inform seed dispersal characterized in this study (publication in progress).

To set the spiral traps, diameter lines were marked to divide a 6.1 m circle into 1/8^{ths}. Traps were spaced evenly around the circumferences and staggered to avoid interference. A rain trap was placed parallel to, and at the base of each flight trap interior to the circumference line to catch achenes that may detach after pappi impacted flight traps. These flight and rain trap sets were arranged with eight flight and rain trap sets placed equidistant around each circumference at 1.5, 3.0, and 4.5 m, and 16 traps placed equidistant around the circumference at 6.1 m from the center of the Canada thistle source stand. Only rain traps were placed at 0.5 m as this was adjacent to the edge of the source patch shoots. Flight traps this close to the source patch would interfere with pappi flight to traps further away from the source. Traps were numbered with marking paint sequentially clockwise with number one set due north of the source patch at 1.5 and 6.1 m, and trap number one at 3.0 and 4.5 m offset clockwise 1/3 and 2/3 the distance to the next 1/8th marker line along the circumference, respectively. The result of this arrangement was a spiral pattern (Figure 1).

The bottom of flight traps were set to the height of the bottom of the majority of source Canada thistle inflorescences and stapled to wooden laths (1.2 m x 3.8 cm in x 1.9 cm) or attached by nylon self-locking cable ties to 10 mm electric fence posts (at 1.5 through 4.5 m circumferences) or to steel fence posts (at 6.1 m circumference). The size of traps increased with distance from the center of the Canada thistle stand (Figure 2). Flight traps measured 0.3 by 0.6 m, 0.5 by 0.6 m, 0.6 m², and 1.2 by 0.8 m at distances 1.5, 3.0, 4.5 and 6.1 m, respectively. Rain traps measured 0.15 m², 0.3 m², 0.3 by 0.5 m, 0.3 by 0.6 m and 0.3 by 0.8 m at distances 0.5, 1.5, 3.0, 4.5 and 6.1 m, respectively. To reduce predation rain traps were set 15 cm above ground stapled to two wooden stakes (29.2 cm x 3.8 cm x 1.9 cm). Vegetation within the trapping area was mowed to approximately 15 cm in height prior to trap activation. All flowering Canada thistle that could be found were also mowed within a 0.42 km of the trap site to avoid contamination.

The second trapping scheme used a cylindrical cage design to achieve a higher degree of enclosure than the spiral design, and thus, more complete trapping of pappi released from the source (Figure 3). A cylinder measuring 2.4 m in height and 6.1 m in diameter was constructed of 6 welded wire livestock panels set around a source stand of Canada thistle. Panels were made from 5.2 mm diameter steel rods and measured 1.3 m in height and 4.9 m in length. Two panels were stacked for a total height of 2.4 m. Panels were supported by two steel fence posts, one bolted on top of the other and set to 2.4 m in height above the soil surface. Electric fence wire was used to attach panels to posts and wire mesh cloth to the panels. The entire cylinder wall was covered by wire mesh; in effect the cylinder wall became a flight trap. To allow pollinator access, wire mesh was not attached and adhesive not applied until sample collection began when pappi flight was underway. At that point, 3 strips of 6.4 mm mesh wire cloth 6 m long and 1.2 m wide were evenly spaced and suspended across the top of the cylinder, dividing the area into 1/6^{ths}. A pole supported the wire mesh at the center. Rain traps were set as previously described for spiral traps, but at 0.5, 1 and 3 m from the center of the thistle source stand and were set on the 1/8th diameter lines without a staggering spiral since no flight traps were set above rain traps to avoid obstructing pappi flight to the cylinder wall trap. The source stand of thistle was maintained at 0.9 m in diameter, as in the spiral design. To manage weeds within the cylinder, trifluralin was applied at a rate of 2.2 kg a.i./ha to bare ground within a 7.6 m radius of the new

thistle patch, then raked by hand to incorporate. The area from 7.5 to 10.7 m in radius was planted to winter wheat and the surrounding fields were planted to soybean, oat or were in grass.

Research sites for both trap designs were chosen to avoid contamination by non-source achenes and to avoid trees and buildings that would interfere with wind. Because cylindrical cages were much more difficult to construct than spirals, Canada thistle stands were established at locations where cylinders could be built and Canada thistle was planted to establish the source population. Sixty Canada thistle root sections with buds were collected from at least 6 different locations. Lateral root fragments were cut into segments measuring 10 to 20 cm in length, and planted in a 0.9 m diameter hole dug 15 cm deep. Root stock was evenly distributed, soil replaced, then lightly packed and watered. Natural Canada thistle patches were used at spiral sites except at St. Paul in 2006; where, to have a spiral trap close to campus, the target population was planted as described for the cage sites. At Lamberton the same stand was used for the caged site in both years. In 2007, Canada thistle plants at the Rosemount cage and St. Paul spiral trap sites became diseased so the traps were reestablished in oat fields at Rosemount and Waseca for the cage and spiral trap sites, respectively, when *in situ* thistle populations were flowering. At trap reestablishment, thistle was mowed to leave a 0.9 source patch. Surrounding thistle and oat was mowed to avoid interference or contamination.

Canada thistle is dioecious, so care was taken to include at least one male shoot in each source stand. At caged sites, the walls of the cylinders were divided into two bands. A lower band extended from ground level to 1.2 m above the soil surface and an upper band from 1.2 to 2.4 m. Each band was then subdivided with marking paint into 8 equal sections measuring 1.4 m². Traps were numbered sequentially clockwise with marking paint similar to the spiral sites with trap number one set due north in each rain or wall trap circumference.

Traps were activated (polyisobutylene applied) when dispersal began. The signal for the beginning of dispersal was that the involucre bracts of several female shoots were open or ready to open. Polyisobutylene adhesive gel was mixed 1:1 with mineral spirits then applied to traps by hand using a paint brush, paint rollers, or compressed air atomizing sprayers. Overall, paint brushes were most effective. The strategy for sampling was to collect for a one week during the peak period of dispersal. Pappi on each flight and rain trap and section of cylinder wall or ceiling were counted within one to two weeks after activation. Pappi were classified as with or without an achene attached and achenes were further classified as nonviable (empty pericarp), of questionable viability and vigor (shrunken) or those assumed to have the potential to produce vigorous viable seedlings (fully filled and normal). Empty achenes appeared thin and shriveled and are thought to result from lack of pollination or abortion (Lalonde and Roitberg, 1989; 1994) or were found as empty pericarps. A few empty achenes were attributed to feeding by finches (*Carduelis spp.*), or the Canada thistle bud weevil (*Larinus planus* F.).

Achene viability was evaluated using tetrazolium (Grabe, 1970). Samples of 25 randomly selected achenes were replicated for each achene type. Achenes were imbibed in darkness at 21°C for 20 to 24 hrs on filter paper (Whatman® no. 1) moistened with 1 ml of sterile deionized water in petri dishes (100 mm diameter and 15 mm in height) sealed with parafilm. Imbibed achenes were cut using a scalpel and placed cut side down on filter paper moistened with 1 ml of 0.1% 2,3,5 tetrazolium chloride solution (w/w) in petri dishes and returned to imbibition conditions for 20 to 24 hrs; then staining was evaluated under a microscope. Empty achenes did not contain embryos, so were not tested. Achenes captured on traps were not tested because of potential effects of polyisobutylene on viability. Instead, tests were conducted with achenes collected at nearby locations at the time of sample collection.

Pappi sometimes overlapped on traps, making it difficult to determine which achene and pappus composed a unit. It was assumed that all achenes trapped at distances greater than 0.5 m from the source had traveled attached to a pappus although it was not always possible to identify which pappus. The number of pappi released without an achene was derived from the difference between the number of total pappi and the number of achenes. At the time of harvest the number of inflorescences in the source stand was counted and a visual estimate was made of the percentage of inflorescences contributing to dispersal. Inflorescences having ripe pappi expended or partially expended were considered to have contributed to dispersal. Achene deposition over the ground surface area extending 3.0 m from the center of the Canada thistle patch was estimated by extrapolation from rain trap samples to the complete 360-degree area at each distance.

SAS general linear model was used to analyze data. Each site and year combination was considered a replicate of the study. Data were combined for each flight trap and corresponding rain trap at its base. Rain and flight traps at each distance were treated as sub-samples and averaged before analysis. Before analysis data were subjected to the Shapiro-Wilk test to determine if the distribution of error differed from normal and Levene's test was used to evaluate homogeneity of variance. When data did not satisfy these assumptions for ANOVA, data were transformed to logarithms before analysis. Paired t-tests were used to compare treatment means and after analysis means were back-transformed to original units.

Achene and pappi dispersal was mapped. Each rain and flight trap was assigned a Cartesian coordinate point relative to the center of the Canada thistle stand, which served as the origin. The number of achenes and pappi collected were assigned to the point. Based on these values ArcGIS 9.2, Environmental Systems Research Institute (www.esri.com) software was used to generate contour maps of achene and pappi population density. The natural neighbor interpolation method was used to produce a raster surface of predicted values. The effect of wind on direction and distance of achene and pappi dispersal was evaluated by calculating an average vector of wind direction and speed for the period of sample collection then comparing this vector to the pattern of dispersal observed in the contour graphs. Weather data was obtained online from the Source Weather Underground[®] (www.wunderground.com). Weather station data provided a daily average wind direction and a daily wind run was also calculated from weather station data. Average daily wind speed was multiplied by 24 hrs to provide a daily wind run value. Because the arrangement of the traps was circular in shape, a unit circle was used to calculate wind direction and wind run vectors. The dimensions of the spiral trap, 6.1 m radius, corresponded to one unit of one on the unit circle. For each day the average wind direction expressed in standard degrees was assigned a corresponding point on the unit circle. For example wind directly from the west would be expressed as 270° in standard degrees and be assigned x and y coordinates -1, -1 on the unit circle. The x and y coordinates of the point on the unit circle were multiplied by the daily wind run to calculate the initial point of a wind run and direction spatial vector while the origin of the unit circle was used as the terminal vector point. Daily vectors for the sample collection period were averaged to arrive at an overall vector for direction and wind run for the entire sample collection period. The angle of the vector in standard degrees was arrived at by taking the inverse sine and cosine of the x and y coordinates of the point where the average vector intersects with the unit circle.

RESULTS AND DISCUSSION

Population density of shrunken and normal achenes and total numbers of pappi differed among sample distances from the source (Table 1). The population density of normal achenes was heaviest at 0.5 m from the center of the source (traps adjacent to the Canada thistle stand). An average of 230.8 normal, 92.8 shrunken and 119.8 empty achenes per m² were collected at 0.5 m from source. Fewer pappi, 118.4 per m², than achenes were collected at this distance. The population density of achenes decreased with exponentially distance. An exponential decrease is not surprising because the area of dispersal increases with the square of the distance from the source. Significant numbers of achenes not attached to a pappus simply fell from the source plants during or shortly after pappi release. The population densities of normal achenes were higher at 0.5 m than at 3.0, 4.5 and 6.1 m and were higher at 1.5 m than at 4.5 and 6.1 m from the center of the source. The same pattern was observed for shrunken achenes. Relatively few empty achenes were trapped and their population density did not differ among samples distances. Total pappi population includes pappi attached to achenes and pappi without an attached achene. The highest population density of total pappi was collected 1.5 m away from the source. At greater distances the population density was lower. Population density of pappi was also lower close to the source plants at 0.5 m as expected, since rain traps were set without a corresponding vertical flight trap to avoid interference with source pappi release. At 0.5 m, with only rain traps present, more achenes than pappi were collected, with a significant number of achenes simply falling from the source plants without an attached pappus.

Between 82.7 and 88.8% of the total pappi collected in the spiral trap design did not have an attached achene (Table 2). The percentage of pappi with a normal achene ranged from 8.0 to 12.6 and pappi with a shrunken or an empty achene attached ranged from 1.5 to 3.3 and 1.3 to 1.8%, respectively. The fact that over 80% of pappi are not attached to an achene at a distance of 1.5 m from the source indicates that pappi left the inflorescences without an attached achene or that the achene and pappi separated immediately after release. Numerically, there was a trend for the percentage of free pappi to increase and the percentage of pappi with normal achenes to decrease with distance from the source; though these differences were not significant ($P \geq 0.05$). Because the quality of achenes did not change significantly with distance and the population density of normal achenes decreased exponentially with distance, we conclude that the primary cause of differences in population density among sample distances is dilution. As distance from the source increased, the population of achenes and pappi is distributed over a larger area. Achenes and pappi drop out of the population over distance, but this change appears small compared to the change in area. The high percentage of pappi without an attached achene is evidence of the deciduous nature of the Canada thistle pappus. It is difficult to understand the ecological advantage or the value of producing a pappus that easily separates from its achene. Schmida (1985) has referred to the phenomenon of deciduous pappi as a paradox. Perhaps, long-distance dispersal of achenes or seed is less important to perennial species such as Canada thistle than it is for annuals (Anderson, 1992). The reproductive strategy of Canada thistle may be to keep achenes near the local favorable site. Others have suggested that the function of the pappus is to protect achenes from dampness rather than aid in dispersal (Dandeno 1905; Sheldon and Burrows 1973).

In the cylindrical cage trapping system, the highest achene population density was also collected near the source plants on rain traps on the ground, or floor of the cylinder (Table 3). The population density of empty or shrunken achenes at 0.5 m distance was greater than that collected at 1.5 m distance and greater distances. A greater population density of normal achenes

was collected on the ground at 0.5 m and 1.5 m distances than were collected on the walls or ceiling of the trap. The population densities of pappi and normal achenes collected on the ceiling and upper portion of the cylinder wall were fewer than that collected on the ground at 0.5 m or the lower portion of the wall indicating that both pappi and achene-pappus units traveled relatively near to the ground. At 0.5 m distance the population density of normal achenes was greater than the population density of pappi or empty or shrunken achenes. On the ceiling and walls of the cylinder the population density of pappi is greater than of any achene type. At the intermediate distances of 1.5 and 3.0 m, the population of pappi is greater than that for empty or shrunken achenes, but not greater than normal achenes. Cylinder trap data was used to estimate productivity of Canada thistle stands. This data was preferred because the more complete sampling strategy should result in a more accurate estimate. In spiral traps pappi and achenes could float between, above, or below flight traps in the spirals. In the cylinders the only route of escape was through portions of the ceiling. Data from rain traps were extrapolated to the entire 360-degree area within 3.0 m radius and added to the numbers of pappi and achenes collected on the wall and ceiling of cylinders. The estimate for the 0.9 m diameter stand of Canada thistle was 2803.3 pappi, 1054.4 normal achenes, 140.2 shrunken achenes and 163.1 empty achenes (Table 4). Data from cylinder traps indicate that 51.6 % of pappi produced by the Canada thistle stand did not have an attached achene. The difference between the 51.6% of pappi lacking an achene from cylinder traps and the over 80% of the pappi without an achene in spiral data is not a conflict. Data from 0.5 m distance was heaviest in achenes and lowest in pappi numbers, including this data is important for the estimate of overall productivity for a thistle stand. Flight traps in spiral trapping systems sampled quality over distance and because most achenes fell near the parent plants approximately 80% of pappi at distances greater than 0.5 m are without an attached achene. Tetrazolium tests indicated that 88% of normal and 50% of shrunken achenes were viable.

Data were collected for both spiral and cylinder traps during a one week period under a range of environments at several locations, over two growth cycles that encompassed relatively low to high plant competition. Application of results to larger areas or longer time periods will depend on the density of inflorescences and degree of maturity. At the end of the one week period an average of 64.5% of source shoots were judged to be post dispersal or in the process of dispersing achenes and pappi and an average of 99.4 inflorescences contributed to the productivity of the Canada thistle source stand.

Contour graphs illustrate the influence of wind on the distance and direction of pappi and achene dispersal (Figures 4A through 4R). Comparisons between the population distributions of achenes and pappi for a site and year indicate that the distribution of pappi was greater in distance and area. This observation is consistent among sites except St. Paul, where distribution of both achenes and pappi was low. Contour graphs illustrate the observation that achenes do not travel far from the parent plants. Most achenes fell to the ground at the margin of the source patch with relatively little influence of wind on dispersal. At each site the heaviest population of pappi was near the source plants and concentration decreased with increasing distance. Distribution of pappi was not even and direction of dispersal was influenced by wind. At some sites the relationship between average wind vector and the direction of pappi is readily discernable. At Elysian in 2007, for example, the distribution of pappi is heaviest to the southwest of the source plants and the average wind direction and speed for the sample period was from the northeast at 33 km/day. At other sites such as Waseca 2007 or Welcome 2006 the highest density of pappi is found downwind for the average wind direction with low population

density upwind. At other sites there are clearly two high density areas reflecting changes in wind direction. Wind of course is variable by nature and an average wind direction and wind run conceals this variation. Another complication to understanding the role of wind in dispersal of Canada thistle is that although wind may be present it will not affect dispersal if pappi are not ripe and environmental conditions are not conducive to release. The strength of the wind expressed as wind run appears to have less influence on dispersal than wind direction. The shortest average wind run was 33 km/day observed at Elysian in 2007. Comparison to other sites with higher average wind runs does not reveal a strong relationship between wind run and dispersal distance or area. The study was not designed to make more than general correlation between the direction and strength of wind and dispersal of Canada thistle. More frequent and detailed measurements of wind and readiness of achenes for dispersal would be necessary and may be the subjects of further study.

Certainly a lack of long-distance wind dispersal is not a hindrance to the dispersal of Canada thistle as a species. While local dispersal may be due to wind blown achenes and vegetative reproduction, as Ada Hayden noted in 1934, long-distance dispersal and introduction of Canada thistle to new locations is primarily by human agents. Prolific vegetative reproduction may compensate for inefficient pappus and achene dispersal. Our findings advance understanding of the reproductive potential and the scale and extent of wind dispersal in Canada thistle. Information about achene movement has the potential to improve management strategies through better timing and implementation of recommended best practice for control of Canada thistle. Many factors influence achene productivity and wind dispersal among them release height, settling velocity, wind velocity, humidity, local topography, local vegetation genotype, fertility and pollinators (Anderson, 1991). All could be the subjects of further study. A key result is that 7 % of pappi (88 % viable of the 8.0 of pappi with a normal achene) that reached the 6.1 m perimeter of the spiral trapping array contained a normal viable achene. Perceptions by land managers are that most or all of Canada thistle pappi in flight contain achenes capable of establishing new infestations. We propose that in regions like Minnesota where Canada thistle is already common, placing higher priority and resource allocation on management to prevent pappi flight over that of controlling established populations may be counter productive.

The techniques described in this paper and equations describing seed transport (Figure 5) could be used to study wind dispersal in other species. In addition to Canada thistle achenes, the traps collected insects and other wind dispersed achenes such as dandelion (*Taraxacum officinale* Weber ex F.H. Wigg.) and sowthistle (*Sonchus spp.*). Fortunately, the size and shape of the achenes and pappi were distinguishable from Canada thistle. From our experience in this study, one weakness of our spiral design was we could not measure long-distance transport during storm or unusual wind events. For example, strong winds in excess of 53 km/h occurred at the Waseca spiral trap site 2 and 4 days after activating the traps, from the southwest and northwest, respectively. This typical, shifting wind directions resulted in a bimodal trapping of pappi and achenes. With sustained strong winds, pappi were released in clusters of entangled pappi with seed entrapped whether attached or not. These pappi clusters are relatively heavy and seemed to become entrapped in surface vegetation or traps within the 6.1 m bounds of our design. The occasional pappi could be seen rising on updrafts created by surface shear turbulence however, and moving out of visual contact. Many pappi appeared to lack an attached achene, in part due to the relatively violent release from the seedhead and considering the deciduous nature of Canada thistle pappi. A few pappi had an achene attached however, providing a risk of spread over long distances via wind dispersal. The odds are against these relatively low numbers of achenes being

able to germinate and establish a new colony once they land, but on a landscape scale, still of consequence. Expanding the trapping array to better estimate dispersal on a larger scale would be confounded from contamination from non-source Canada thistle in a state like Minnesota where its presence is pervasive. The spatial distribution of achene dispersal and the seasonal achene production will be explored further in subsequent manuscripts and build on this study.

Table 1. Population densities of empty, shrunken, normal achenes and pappi collected on rain and flight traps within a 6.1 m radius around a source of Canada thistle achenes that measured 0.9 m in diameter. Samples were collected at four distances from the source at four spiral sites in Minnesota in 2006 and repeated in 2007. Total pappi population density includes pappi that were attached and not attached to achenes. Means have been back-transformed to original units after analysis of log transformed data.

| Distance from source (m) | Achene type | | | Total Pappi |
|-----------------------------|-------------------|----------|---------|----------------|
| | Empty | Shrunken | Normal | |
| | (m ²) | | | |
| 1.5 | 3.2 a | 9.2 a | 45.3 a | 317.1 a |
| 3.0 | 2.2 a | 3.9 ab | 17.1 ab | 135.0 ab |
| 4.5 | 1.8 a | 1.6 b | 11.5 b | 99.5 b |
| 6.1 | 1.1 a | 1.4 b | 8.4 b | 57.9 b |

Means in a column differ according to paired t-tests (P=0.05).

Table 2. Mean percentage of pappi collected with an attached empty, shrunken or normal achene or without an attached achene within a 6.1 m radius around a source of Canada thistle achenes which measured 0.9 m in diameter. Samples were collected at four distances from the source at four spiral trap sites in Minnesota in 2006 and repeated in 2007.

| | Pappi by achene type | | | |
|----------------------|----------------------|----------|--------|-----------|
| Distance from source | Empty | Shrunken | Normal | No achene |
| (m) | % | | | |
| 1.5 | 1.3 | 3.4 | 12.6 | 82.7 |
| 3.0 | 1.6 | 2.3 | 11.8 | 84.3 |
| 4.5 | 1.8 | 1.5 | 8.5 | 88.2 |
| 6.1 | 1.7 | 1.5 | 8.0 | 88.8 |

Means did not differ by achene type according to paired t-tests (P=0.05).

Table 3. The mean number of empty, shrunken, normal and total achenes collected on the ceiling, walls or floor within a 3 m radius around a source of Canada thistle achenes that measured 0.9 m in diameter in cage cylinder traps at two sites in Minnesota in 2006 and 2007. After analysis of log transformed data means were back transformed to original units.

| | Achene type | | | Total |
|---------------------------------------|-------------------|------------|-------------|-------------|
| | Empty | Shrunken | Normal | Pappi |
| Trap position | (m ²) | | | |
| Floor rain, 0.5 m distance | 13.7 a (b) | 24.8 a (b) | 109.1 a (a) | 28.0 a (b) |
| Floor rain, 1.5 m distance | 0.7 b (b) | 1.0 b (b) | 6.4 b (a) | 21.3 ab (a) |
| Floor rain, 3.0 m distance | 1.7 b (b) | 1.7 b (b) | 10.7 b (ab) | 16.7 ab (a) |
| Wall flight, lower band, 3 m distance | 0.2 b (b) | 0.2 b (b) | 3.3 bc (b) | 39.7 a (a) |
| Wall flight, upper band, 3 m distance | 0.1 b (b) | 0.0 b (b) | 0.2 c (b) | 6.0 b (a) |
| Ceiling flight | 0.0 b (b) | 0.0 b (b) | 0.0 c (b) | 0.6 c (a) |

Means in a column followed by the same letter and means in a row followed by the same letter in parentheses are not different according to paired t-tests (P=0.05).

Table 4. Mean and standard error for the number of empty, shrunken, normal and pappi collected on the ceiling, walls and floor collected in one week within a 3 m radius around a source of Canada thistle achenes that measured 0.9 m in diameter in cage cylinder traps at two sites in Minnesota in 2006 and in 2007.

| Pappi by achene type | Mean (S.E.) | % of Total Pappi |
|----------------------|-----------------|------------------|
| Empty achene | 163.1 (131.8) | 5.8 |
| Shrunken achene | 140.2 (58.6) | 5.0 |
| Normal achene | 1054.4 (399.9) | 37.6 |
| Pappi without achene | 1445.6 (1249.3) | 51.6 |
| Total | 2803.3 (1362.3) | 100.0 |

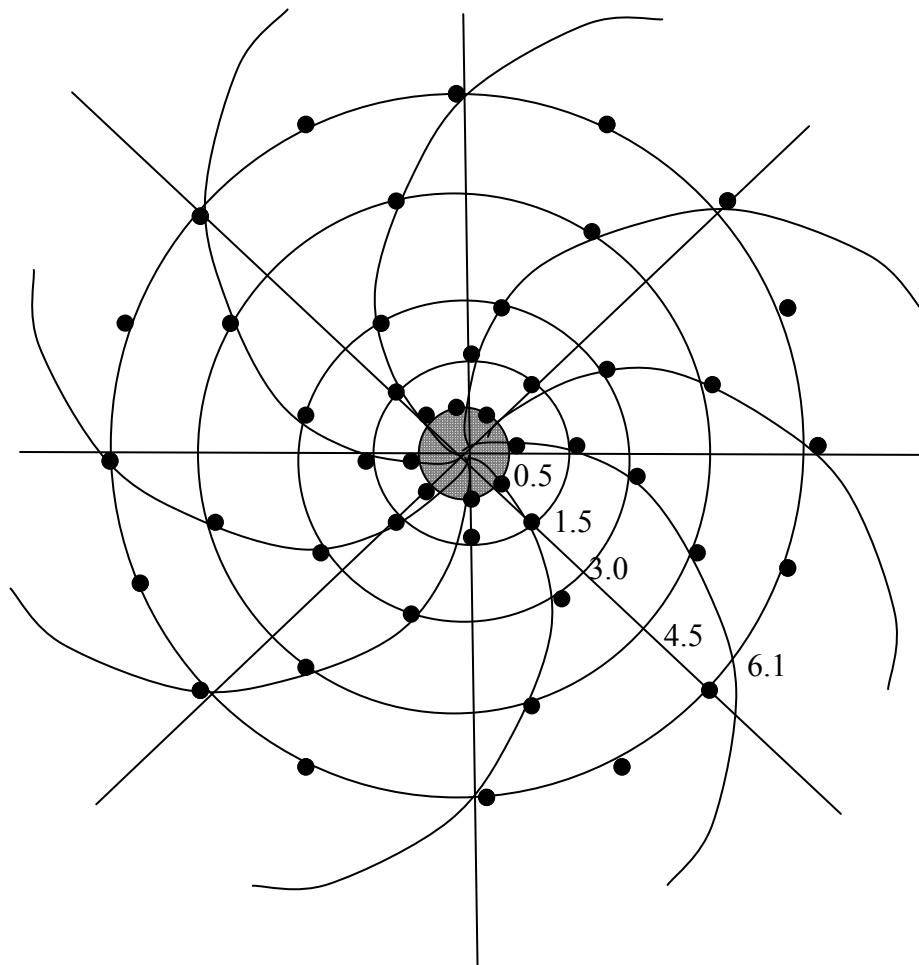


Figure 1. Schematic diagram of spiral open trapping scheme. The position of seed rain and flight traps are represented by dots. Flight and rain traps were placed at 1.5, 3.0, 4.5, and 6.1 m from the center of a 0.9 m diameter source patch of Canada thistle. Rain traps were placed at 0.5 m without a corresponding flight trap to avoid blocking pappi flight from the source. Flight traps were arranged in a spiral to reduce interference as pappi moved out from the source. The 0.9 m source patch is the shaded portion at the center of the trapping array.



Figure 2. Spiral trap dimensions and layout. One spiral is shown.

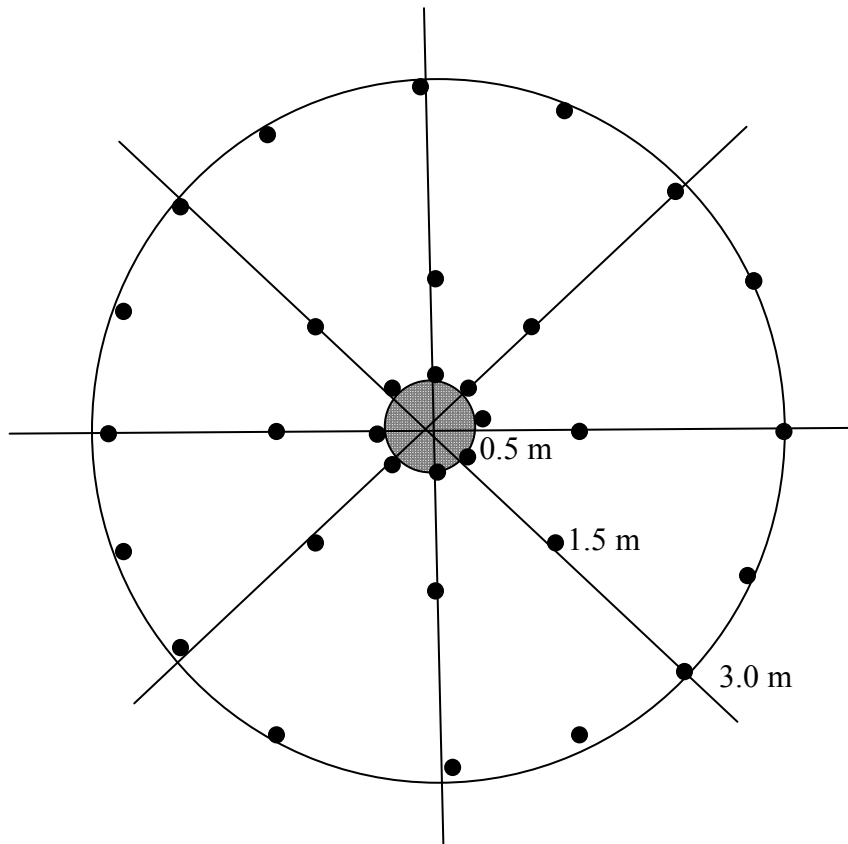
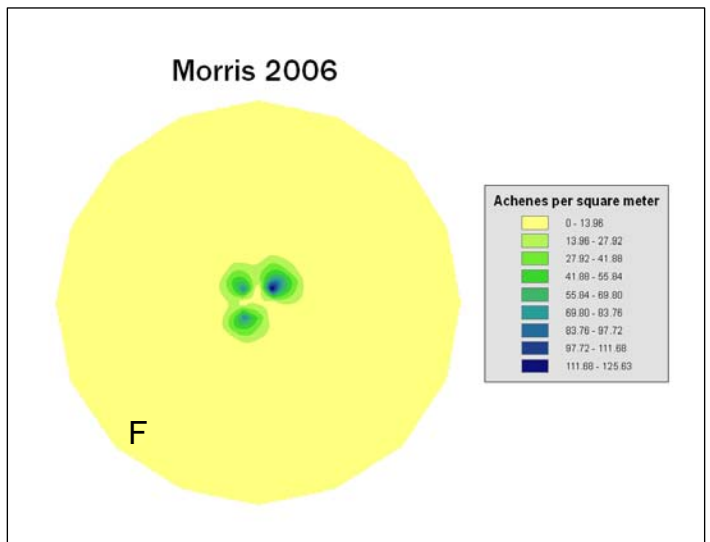
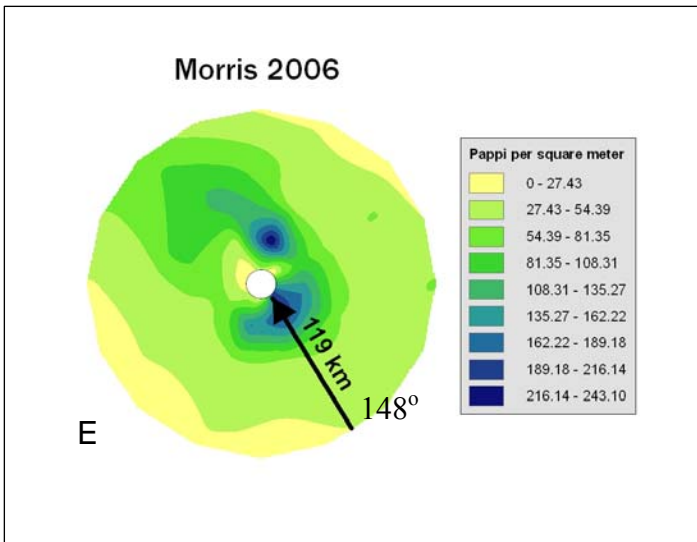
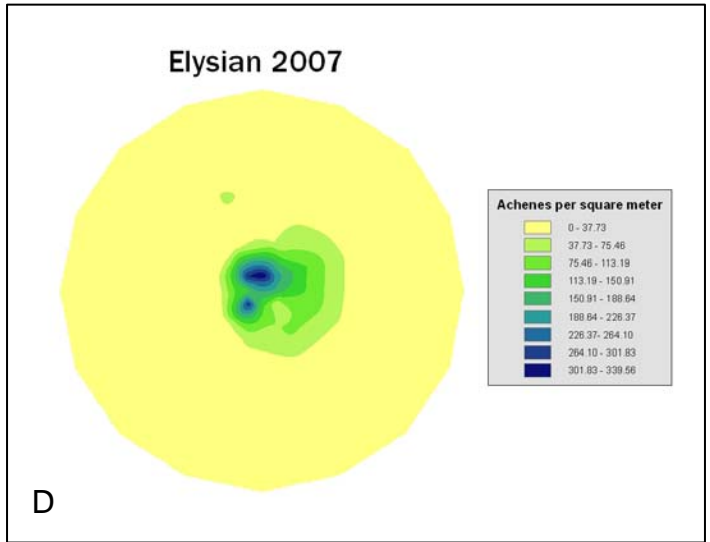
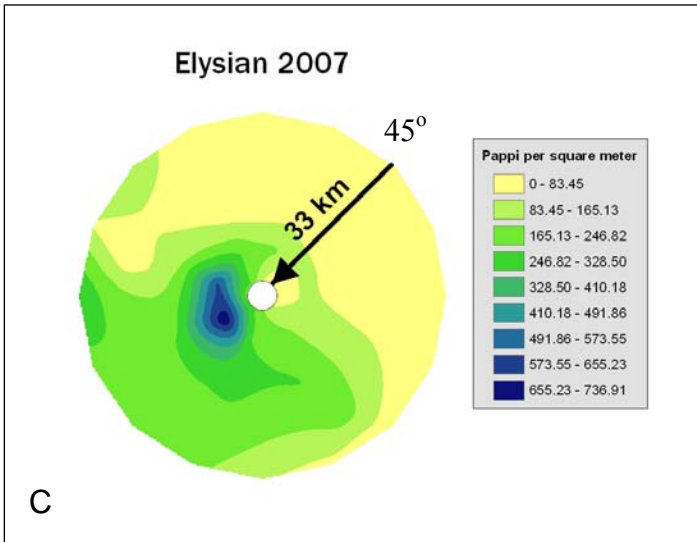
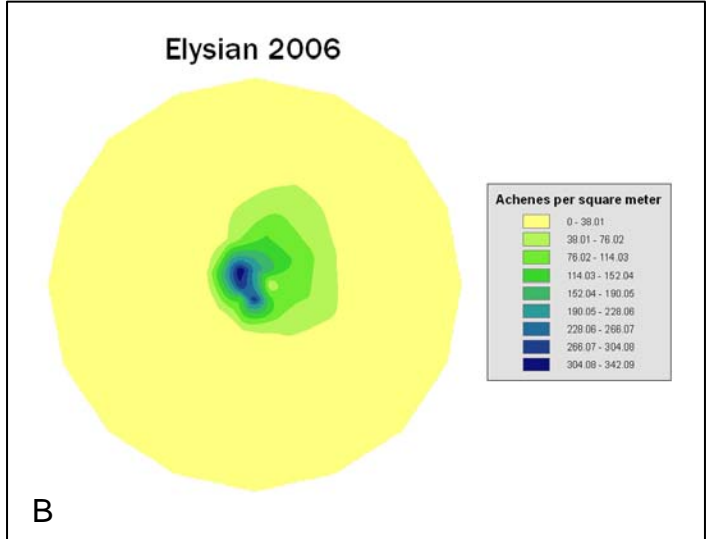
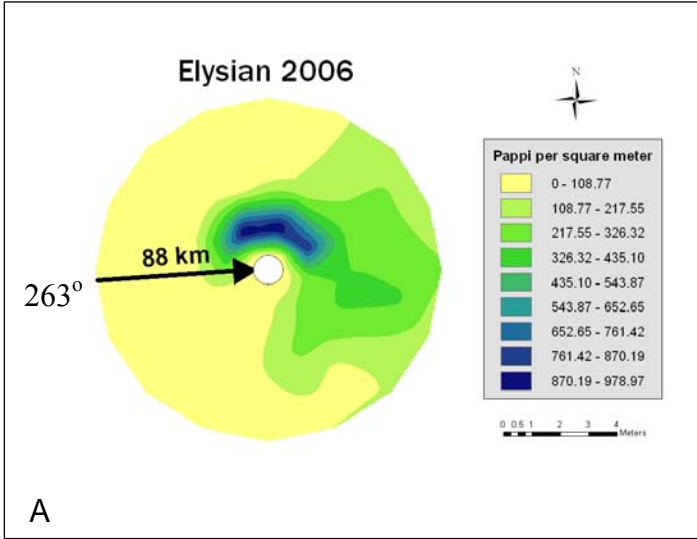
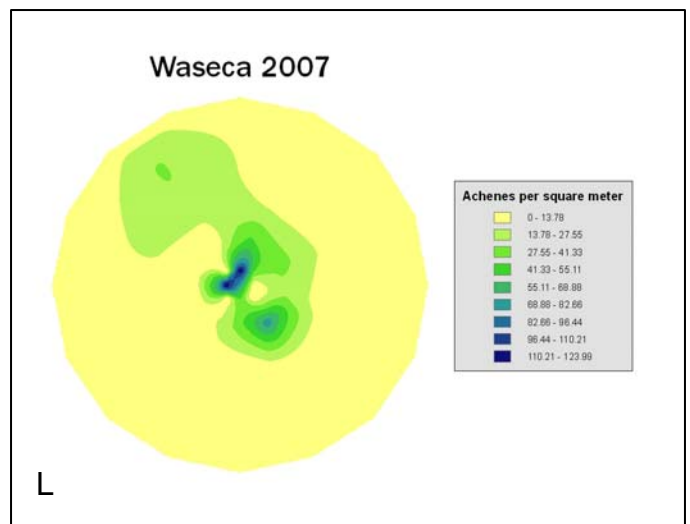
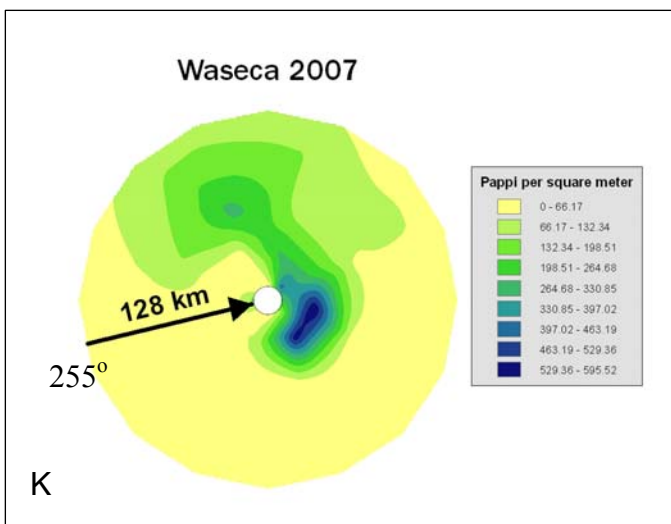
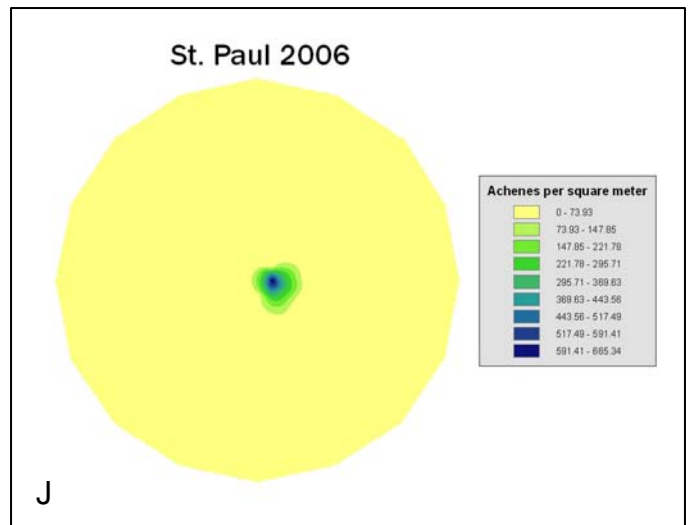
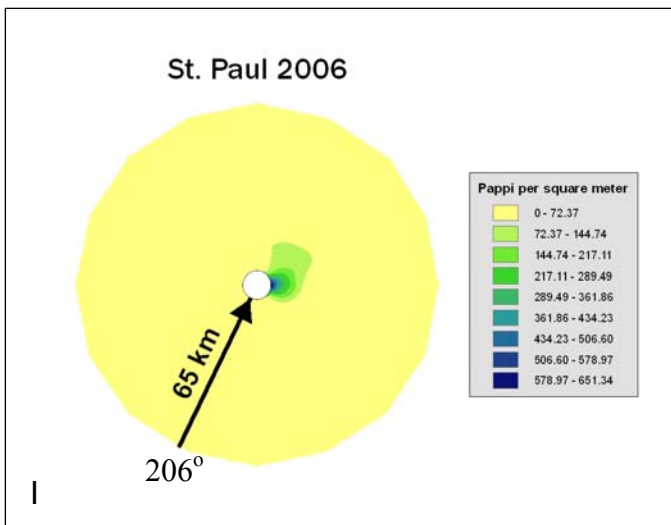
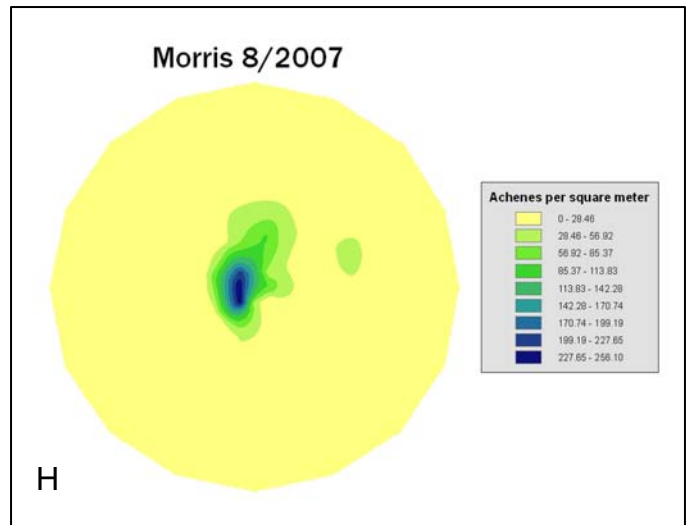
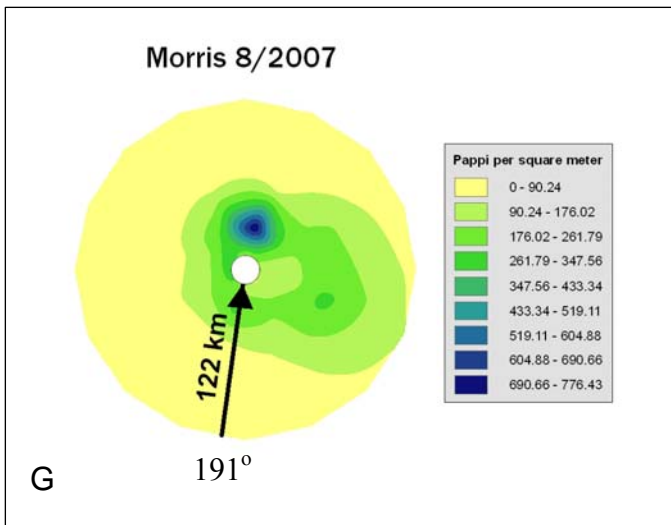


Figure 3. Schematic diagram of cylindrical cage trapping scheme. The position of seed rain traps are represented by dots. Flight traps were the entire cylinder wall 2,4 m in height in a radius of 3.0 m from the center of a 0.9 m diameter source patch of Canada thistle. The source patch is the shaded portion at the center of the trapping array.





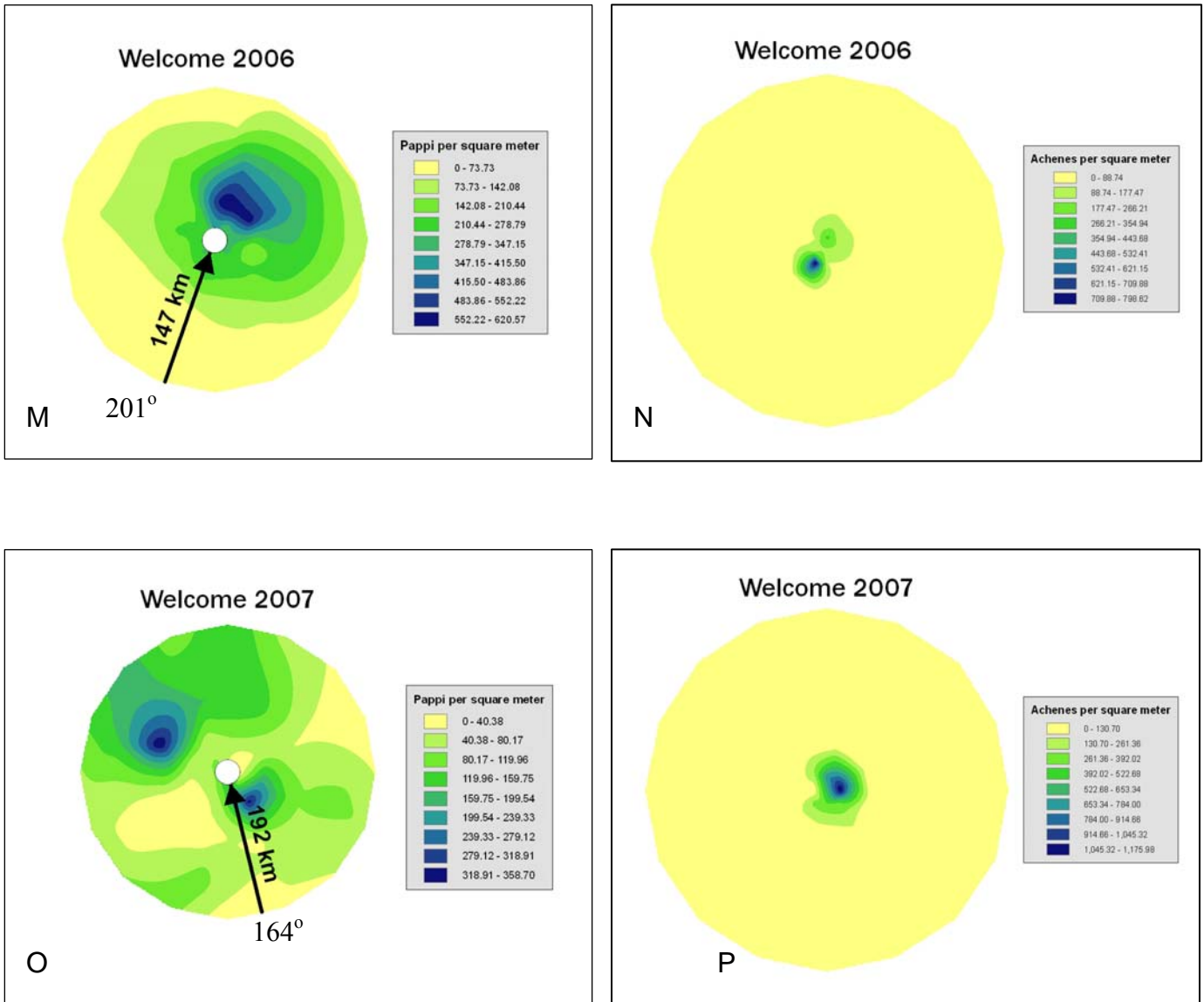


Figure 4. Contour graphs of the predicted achene and pappi population density in a 6.1 m area around a source stand of Canada thistle measuring 0.9 m in diameter which is depicted on the graphs by a white circle. Data for achenes and pappi were collected at four Minnesota locations in two years. The arrow and angle in degrees on graphs of pappi population data depict the average direction of wind for the sample period the value above the area is the average daily wind run per day of the sample collection period.

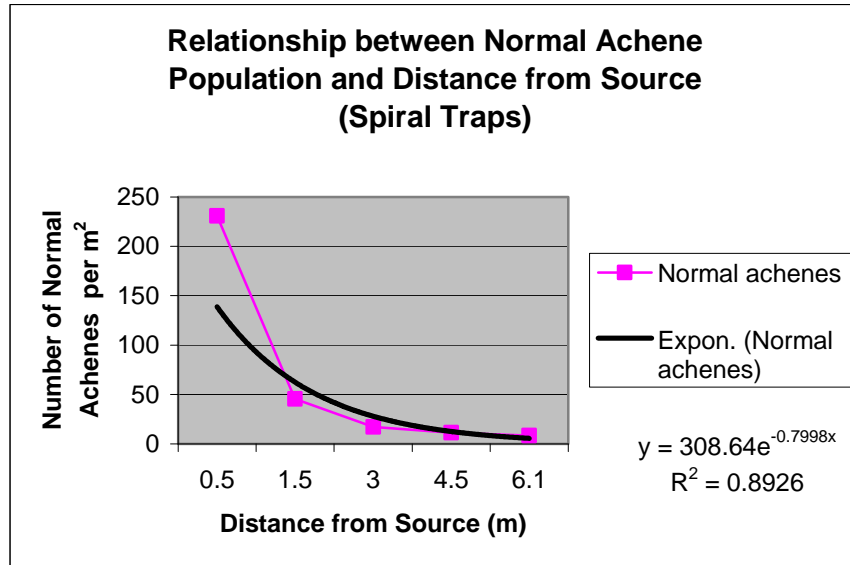


Figure 5. Relationship between normal achene population and distance from a source stand of Canada thistle measuring 0.9 m in diameter for the spiral trapping studies, at four Minnesota locations in two years.

CHAPTER 2. ACHENE PRODUCTION IN CANADA THISTLE (*CIRSIUM ARVENSE*)

INTRODUCTION

Canada thistle is indigenous to Europe, northern Africa and western Asia and was introduced into North America during the colonial period (Moore, 1975). It is now the most frequently listed noxious weed among the states in the United States and in the provinces of Canada (Skinner et al., 2000). In Minnesota, where these studies were conducted Canada thistle is listed as a noxious weed and seed (ORS, 2007). It is the most prevalent and persistent broadleaf weed in Minnesota, found in all crops in pastures, waste areas and natural areas (Durgan, 1998). Canada thistle is a dioecious plant and spreads vegetatively through the production of secondary shoots which emerge from root buds (McAlister and Haderlie, 1985). An excellent review of the biology of Canada thistle flowering and achene production was published by Donald (1994), in which he described the following: an individual shoot produces numerous seedheads in a compound corymb, with terminal and axillary flowers 2 to 2.5 cm in diameter, each composed of disk florets. Florets are contained in an involucre 1 to 2 cm high with numerous overlapping spineless bracts. Pistillate (female) heads are oblong, tapering to the tip of involucre. Staminate (male) heads are ovate, to almost cylindrical in shape. Holm et al. 1977 noted that pappi are plumose (branching) and easily separate from the achene (deciduous). Achene develop and mature from the outer ring of florets in a seedhead, inward (citing Hayden, 1934) and are 2.5 to 4 mm in length (citing Holm et al. 1977).

Observations have focused on measuring the number of achene produced on an inflorescence or shoot basis and were summarized across studies by Donald (1994). Hansen (1918) reported that typically, only a small portion of achene produced were viable, with some shoots producing no achenes at all. It is unclear the degree to which he distinguished between male and female flowers which may have informed this statement. Hill (1983) suspected that similar achene production reports by Hansen (1921) were based on 'an erroneous conclusion emanating from the dioecious condition where male populations spread by vegetative means', suggesting that Hansen had mistakenly monitored male clonal patches of Canada thistle. Lloyd and Myall (1976) noted some male flowers occasionally set a few achenes, and females do not produce pollen. Since some male florets occasionally produced achenes, Hodgson (1968) classified Canada thistle as imperfectly dioecious. Kay (1985) later fully characterized achene production in hermaphroditic males.

Production of Canada thistle achenes varies and is influenced by resource availability, degree of pollination (Lalonde and Roitberg, 1989) and perhaps genotype (Hodgson, 1964). Many florets produce no achenes. Of 61 florets in a seedhead of a female shoot, 39.3% produced achenes (Bostock and Benton, 1979). Hayden (1934) noted approximately half of 60 to 75 florets in each seedhead bore achenes. Productivity measured as the number of achenes per seedhead has been reported to be as low as 1 (Amor and Harris, 1974), 26.2 (Bostock and Benton, 1979) and 46 (Hayden, 1934). Achene production per seedhead was reported ranging from 1 to 104 (Hayden, 1934) and 15 to 83 achenes (Derscheid and Schultz, 1960). Hayden (1934) reported an average of 21 seedheads per shoot (my calculation from her data), about 50% of the approximately 100 florets in a seedhead produced achenes, with an avg. 46 achenes produced per flower. (and 966 achenes per shoot, my calculation from her data). Average achene production per emerged shoot was reported to be 1,530 achenes (Hay, 1937), 600 (Bostock and Benton, 1979). Bakker (1960) observed an individual shoot that produced more than 5,000 achenes. He characterized wild populations in the field in England noting 61.2 florets/ovules per seedhead which produced 26.6 achenes per seedhead and documented 26.2 dispersed after predation, 23.2 capitula per stem, for 600 achenes dispersed per stem. In greenhouse studies, 74% of the plants produced flowers (Lalonde and Roitberg, 1989), pappi

were fully developed approx. one week after pollination, and seedheads with involucre bracts enclosing the achenes and pappus dried and opened at 2 to 3 weeks after pollination (Lalonde and Roitberg, 1989).

Not all achenes produced are viable. Dersheid and Shultz (1960) reported 20 to 91% of achenes were viable in South Dakota while (Hayden, 1934) found that 95% of achenes germinated in Iowa. Lalonde and Roitberg, (1994) noted that fertilized achenes that aborted developed a sclerotized pericarp (termed empty achenes in our study) while unfertilized ovules did not. Number of aborted ovules did not differ between flower types or pollination rates in the greenhouse (Lalonde and Roitberg, 1989) or the field trials (Lalonde and Roitberg, 1994). In field trials, Lalonde and Roitberg, (1994) defined the pollen constraint on female achene production, noting decreased achene production with increased distance to males, and also with decreased male shoot population densities at a give distance. They found that less pollen available increased flowering time (approx. 1.5 days) before withering. The length of time of presence of open flowers and withering flowers remained constant. Container grown achene weights including plume averaged 1.820 mg, and embryos 0.670 mg (Bostock and Benton, 1979). Achene weight varied over time, but with no seasonal pattern in the field (Lalonde and Roitberg, 1994), contrary to their previous greenhouse experiment where a strong seasonal decrease in achene mass occurred (Lalonde and Roitberg, 1989).

Lalonde and Roitberg, (1994) used cold-treatment at 4 C for 10 days to break dormancy, then germinated on filter paper in the dark at 30 C and grew the transplanted seedlings in the greenhouse to determine sex ratios of progeny. They found a strong bias towards production of females. Population studies have shown Canada thistle sex ratios range from 1:1 (Lloyd and Myall, 1976) to 3:1 females to males (Bakker, 1960; Kay, 1985). Lalonde and Roitberg, (1994) postulate that the high ratio of female achenes produced may be expected in light of the findings of Detmers, (1927) and Amor and Harris (1974) that ‘colonization of an isolated locale by one or two individuals may be the rule, rather than exception for *C. thistle*’.

Control of Canada thistle is mandatory for state agencies and private land-owners, and is often promulgated to prevent spread of achenes and based on the premise that achene production and wind-blown achenes are important means of Canada thistle dispersal. Canada thistle inflorescences in bloom and pappi floating across the landscape often trigger calls for enforcement of weed laws and in response expenditure of labor and money on management with potential negative consequences for the environment. Better understanding of achene production will inform and provide perspective and scale to the importance of achene production to the public and land managers and serve as the basis for best management practices. In an effort to better understand the contribution of achenes to the dispersal and persistence of Canada thistle, we carried out the following study to characterize quantity and quality of achenes produced by Canada thistle in Minnesota. These collections were conducted in parallel with achene dispersal studies (Haar et al., CTS flight study) to enhance the characterization of Canada thistle achene dispersal. Additionally, this study will improve our knowledge of achene production in response to Minnesota climate, and build on the existing literature on the fecundity of Canada thistle. Better information on achene production in Minnesota will also help develop integrated weed management strategies, guide use of resources, and inform the public and land managers about the importance and proper timing of management decisions such as determining when mowing and herbicide applications are most effective.

METHODS AND MATERIALS

We surveyed Canada thistle populations throughout Minnesota to determine achene production potential in the field. Canada thistle populations were monitored extensively and at Maplewood, Rosemount, St. Paul, and Elysian MN with weekly or sub-weekly collections of seedheads in 2006 and again in 2007. Sites were monitored from flower initiation until achene

production ceased. In 2006, five additional sites were sampled. Based on the difficulty in processing and sorting achenes collected from the four main collection sites in 2006, we decreased the monitoring scope in 2007 to just repeating the four sites extensively monitored in 2006. Additionally, the initial 2006 results indicated that limiting sampling in 2007 to these four sites would adequately characterize achene production potential.

All sites were established in vigorous stands of Canada thistle. The Rosemount site established following a bromegrass pasture renovation to a native warm season prairie in 2004. The remaining sites were known to be at least six years in age as of 2006 and were all warm season prairies. The health and vigor of the stands based on visual surveys of shoot population densities, shoot height, and flower production were estimated as Rosemont = Elysian > Maplewood > St. Paul. Shoots heights when flowering listed from tallest to shortest ranged from Rosemont : 90 to 180 cm, Elysian : 120 to 150 cm, Maplewood : 90 to 150 cm, to St. Paul : 45 to 60 cm in height.

To establish the collection sites, Canada thistle shoots were randomly selected at bud- to first flower-stage within a 15 m diameter patch at each site. Each site contained males for pollination. If a randomly selected shoot did not have buds visible, it was bypassed until 10 fecund female shoots and 2 to 10 male shoots were identified. Shoots were identified by placing a nylon tag at the base of the targeted shoot with self-locking nylon cable ties. Shoot numbers were assigned and the gender indicated on tags. Shoots were monitored for flower development and achene development and individual seedheads harvested accordingly. Achenes were targeted for harvest when the pappi were becoming loose or free as the involucre bracts opened and appeared ready for achene release (termed 'fluffed'). Achene collection progressed until achene production stopped and any remaining buds and flowers ceased development or aborted. Individual seedheads were harvested, placed in paper sacks noting location, date, shoot number, number of seedheads harvested, and stage of development of seedheads harvested. Seedheads stage of development at harvest ranged from pre-fluff with brown involucres, early fluff, full fluff, partially expended fluff, and expended fluff depending on various factors. Some seedheads were harvested early when damaged by insects, American gold finches (*Carduelis tristis*), white-tailed deer (*Odocoileus virginianus*), or storm damage. At the other end of the spectrum, occasionally some pappi flight had occurred in the interim between sampling. This was particularly true when hot, dry weather followed a cold wet period where involucres could go from tightly closed to open with pappi release in one day.

Samples were stored dry at room temperature in the lab until processing. During the winter, individual seedheads were examined under a dissecting scope, and achenes counted and categorized by number of empty pericarps (nonviable), shrunken achenes (of questionable viability and vigor), and normal, plump achenes (assumed to be viable and with the potential to support a vigorous seedling. These achene types are shown in Figures 6, 7 and 8. Achenes were then placed in coin envelopes and stored at 5°C for future research. Shrunken and normal achene weights were obtained for the 2007 St. Paul, Maplewood and Rosemount collections.

Achene productivity data were quite variable among shoots, among sites and between years. Paired t-tests, ($P=0.05$) were used to compare means within achene type across year and location, and to compare between years. For terminology in this manuscript, we used achenes, florets and seedhead as a mature flower. (Achene, a one seeded fruit that does not open to release the seed, the type produced by Canada thistle, will be used instead of the inclusive term seed, flower is the collective disk florets comprising a seedhead, seedhead refers to an individual inflorescence contained within an involucre, also referred to as a capitulum by some, or simply a flower by most). The term shoot refers to the collective main terminal and axillary shoots

emerging from the soil surface at one point. No attempt was made to determine if individual shoots comprised an interconnected clonal plant.

RESULTS AND DISCUSSION

Canada thistle is a long day plant and does not flower when the photoperiod is less than 8 to 12 hours (Link and Kommedahl, 1958). In our study in Minnesota, flowering began in late June (15 to 15.5 hours of daylight), was most abundant in July, and continued flowering until frost (September). During the fall, populations of Canada thistle consisted of different growth stages as secondary shoots can emerge at this time and develop into rosettes (also termed regrowth) or bolted shoots which produce flowers. Throughout the growing season, we counted and classified a total of 66,366 achenes, monitoring 80 female shoots and 17 male shoots (data not shown). For the four locations monitored during 2006 and 2007, averaged across years and locations, one female Canada thistle shoot produced an average of 26.0 flowers, and 829.6 achenes (Table 1). Of the 829.6 achenes, 318.9 were empty, 142.5 were shrunken, and 368.3 were 'normal'. The average per seedhead was 12.3, 5.5, and 14.2 empty, shrunken and normal achenes, respectively (Table 2). Only shoots with buds visible at the time of tagging were monitored. Since some shoots do not flower, our numbers overestimate achene produced per shoot as each population also included non-flowering shoots. Bostock and Benton (1979) described the challenges of estimating achene production in vegetatively interconnected populations. They noted achene production varied by shoot height, notably with smaller shoots on the periphery of patches producing no achenes at all. We made no attempt to characterize the dynamics of nonflowering shoots in our study.

Canada thistle ecotypes were defined by (Hodgson, 1964 and 1970) and Canada thistle has been shown to differ in numerous traits (Burt and Muzik, 1968; Frank and Tworkoski, 1993; Hodgson, 1964, 1970, and 1973; Hodgson and Moore, 1972; Hunter and Smith, 1972 and Turner et al, 1981). Achene production by Canada thistle varied considerably as reviewed by Donald (1994). This variability was evident in our study. This genetic diversity reflected in the studies cited likely contributed to the variability of achene produced in our study, though we made no attempt to determine if ecotypes existed.

Average number of flowers produced per female shoot ranged from a low of 5.8 to a high of 53.3 at the St. Paul site 2006, and Rosemount site 2006, respectively, (Table 1). Average total achene production ranged from a seasonal low of 77.9 to a high of 2424.4 achenes per shoot, and occurred at these same site-years. Achene production per shoot by type ranged from an average low of 33.1 (St. Paul 2006) to a high of 1006.7 (Rosemount 2006) for empty achenes, shrunken achenes from a low of 8.5 (Elysian 2006) to a high of 568.8 (Maplewood 2006), and normal achenes from an average low of 33.9 (Maplewood 2007) to a high of 1122.0 (Rosemount 2006). The highest annual production of normal achenes for a single shoot (not averages), 1856, occurred at Elysian 2006 and the fewest normal achenes produced, 0, occurred in 6 of 80 shoots although they did flower (data not shown). Rosemount data for 2007 is shown as an example of achene production by individual shoots in Figures 1 through 4 and seasonal average flower and normal achene production is shown in Figure 5 by site and year. Clearly Canada thistle can produce a large amount of achenes, but production varies widely during the season, from shoot to shoot, from year to year, and by location. Numerically, five of the six lows and highs of achene production by type of achene occurred in 2006. Despite most of the lows occurring in 2006, averaged across sites, 2006 exceeded 2007 in production of flowers and of all types of achenes by a factor of 1.6 and 2.8, respectively.

Additionally, a one-time sampling was taken of 10 flowering shoots in an area that was mowed early July adjacent to the main collection site at Rosemount in 2006. This fall regrowth

produced an average of 13.1 seedheads per shoot that in turn produced an average of 14.4 shrunken and 11.7 normal achenes per seedhead, totaling an average of 188.8 shrunken and 158.5 normal achenes per shoot. Compared to average production during a full-season, fall regrowth produced 0.5 x the number of flowers per shoot, a similar number of normal achenes (0.82 x), and approx. 2.5 x the number of shrunken achenes per flower. Fall regrowth produced a similar number of normal achenes per seedhead compared to full season growth, but because the numbers of flowers were considerably fewer, achene production per shoot was notably decreased (0.43 x the number of normal achenes per shoot). Fall regrowth shoots were roughly ½ the height of full season growth in the adjacent sampling area, duration of flowering more compressed and maturity of terminal and axillary flowers more uniform. Though reduced in numbers, fall regrowth clearly can be a significant source of achenes.

Averaged across sites and years, of the achenes produced on full-season growth, 38% were nonviable empty pericarps, 17% were shrunken achenes of questionable viability and vigor and 44% were normal achenes (Table 3). Perhaps more important, seedling vigor correlated with achene type would have to be determined to more accurately characterize the potential for spread via achene dispersal. Shrunken achenes, though viable, may not produce seedlings as vigorous as those arising from normal achenes, achenes with higher starch reserves. Seedlings originating from shrunken achenes would likely suffer higher seedling mortality.

Male shoots produced an average 13.5 flowers per shoot, about half the number of flowers produced by female shoots. Of note, an average of 1.7 shrunken and 0.6 normal achenes were found per male shoot. Individual male flowers averaged 18.72, 0.12, and 0.04 empty, shrunken and normal achenes, respectively. In a survey of Canada thistle in southern Britain, Kay (1985) found 15% of clones had polleniferous ‘male’ flowers (hermaphrodites) with 10 to 65 achenes produced per capitulum and 11% subhermaphrodite with 2 to 10 achenes produced per capitulum. Compared to achene produced on females, achenes were lighter, with lower germination but achenes that did germinate had similar vigor in Kay’s studies. Our term empty achene coat refers to development of an empty pericarp, but with no embryo or starch accumulation similar to what Lalonde and Roitberg, (1989) termed ‘aborted achenes, ovaries that displayed pericarp development but did not contain a healthy embryo’. We assumed we would find only empty achenes in male flowers in our study due in part to the limited number of male flowers sampled, although some clearly developed achenes.

Lalonde and Roitberg, (1989) found that in the greenhouse, achene weight did not differ in 1^o flowers between high and low pollination rates, but 2^o and 3^o flowers produced lighter achenes at high pollination rates due to limits of resource allocation. They indicated 2^o and 3^o flowers developed later than 1^o flowers, and may tend towards lighter achenes. In our work, flowers were bulked by date of sampling and by shoot so weight by flower position could not be determined. Initial collections were noted and bagged as terminal (1^o) or 2^o and 3^o flowers, but the uniformity and rate of seedhead maturation quickly overwhelmed our capabilities to classify achenes by each flower position while monitoring multiple sites. In our field sites, the time interval between maturation of the terminal flower (occasionally with two flowers sharing the terminal position) and first maturation of axillary flowers followed by only a few days, and often there was no distinction between rates of maturation. Achene weights were approx. 1.5 times higher for achenes deemed normal compared to shrunken achenes (Table 4), as expected by definition of our achene type classification criteria. Length of flowering period ranged from 8 to 12 weeks among sites, though the majority of achene production occurred within the 8 week period flowering period reported in an earlier field study near Vancouver B.C. (Lalonde and Roitberg, 1994).

Flower petals typically withered once florets were fertilized, then pappi turned white and elongated. After pappi extended 1 to 2 cm beyond the end of the involucre bracts, the involucre

bracts lost their green color, turned brown, and opened allowing release of pappi and occasionally pappi with achenes. The rate of development of flowers and of viable achenes once the flower color was lost differed considerably among sampling dates, between years, and among sites. Notable also was the development of some flowers with shortened pappi about half the length of 'normal' pappi that were not easily detached from the involucre bracts. This was most common in both years, but was most pronounced in 2007, where some flowers appeared to have been fertilized and pappi started to elongate but acquiesced to what appeared to be a quiescent state for days or even weeks. This may have been the result of localized periods of moisture stress in 2007 which in turn stressed flower and achene production. End of season production in late-August or September appeared to have a higher occurrence of this type of flower development, with some flowers often never fully developing or maturing.

Some flower buds failed to develop florets, dried and aborted. As the season progressed, verticillium wilt plugged vascular flow in the peduncle attaching an individual seedhead or attaching the terminal and axillary seedheads in their entirety on some shoots, resulting in an accelerated, premature dry down and opening of infested flowers and arrested achene development. This occurred on fewer than 2% of shoots monitored. There were minor losses with deer feeding, goldfinch feeding, or stems that were broken during windstorms but this was minor in scope and did not significantly impact the monitoring program.

Lalonde and Roitberg, (1994) noted insect larvae feeding by *Orellia ruficauda* in their fecundity studies. In our study some seedheads were infested with the seed feeding fly (*Terellia ruficauda*), or the seedhead weevil (*Larinus planus* F.). As the collections progressed, often these flowers could be identified by deformed involucre bracts shortened on one side of the flower resulting in a slight curve in both the bract and the pappi as pappi elongated. Adults of both insects were found as achenes were processed later during the winter months and were noted. Typically no achenes were collected from flowers infested by the seed feeding fly. Seedheads infested by the seedhead weevil often did not open normally. Damage by these biological control insects affected less than 0.5% of the flowers monitored and did not significantly alter the outcome of the study. Though achene production by female Canada thistle is extremely variable, when sufficient pollen is available, Canada thistle clearly has the potential to generate significant contributions to seedbanks to maintain invasive stands. Improved management strategies based on better timing and implementation of recommended best practice for control of Canada thistle are possible with a better understanding of achene dispersal and production.

Table 1. Average number of Canada thistle achenes produced per flowering shoot at 4 sites, in 2006 and 2007 in Minnesota.

| | | Average No. per Shoot | | | | | | | | | |
|-----------|------|-----------------------|---------------|------------------|----------------|---------------|------------------|---------------|------------------|----------------|---------------|
| | | Female | | | | | Male | | | | |
| Location | Year | No. flowers/buds | Empty Achenes | Shrunken Achenes | Normal Achenes | Total Achenes | No. flowers/buds | Empty Achenes | Shrunken Achenes | Normal Achenes | Total Achenes |
| Elysian | 2006 | 40.7 b | 557.0 b | 8.5 c | 1008.5 a | 1574.0 b | 15.0 | 453.0 | 0.0 | 0.0 | 453.0 |
| | 2007 | 22.6 c | 122.5 d | 54.2 c | 351.9 b | 528.6 cd | 14.5 | 405.0 | 11.5 | 3.5 | 420.0 |
| Maplewood | 2006 | 30.3 bc | 182.2 d | 568.8 a | 84.9 cd | 835.9 c | -- | -- | -- | -- | -- |
| | 2007 | 24.3 c | 375.8 c | 35.2 c | 33.9 d | 444.9 d | -- | -- | -- | -- | -- |
| Rosemount | 2006 | 53.3 a | 1006.7 a | 295.7 b | 1122.0 a | 2424.4 a | -- | -- | -- | -- | -- |
| | 2007 | 23.0 c | 181.9 d | 87.5 c | 240.6 bc | 510.0 cd | 36.5 | 811.0 | 0.0 | 0.0 | 811.0 |
| St. Paul | 2006 | 5.8 d | 33.1 d | 9.8 c | 35.0 d | 77.9 e | 5.6 | 21.3 | 0.0 | 0.0 | 21.3 |
| | 2007 | 7.9 d | 91.6 d | 79.9 c | 69.4 cd | 240.9 de | 23.5 | 378.5 | 3.0 | 1.5 | 383.0 |
| By Year | 2006 | 32.5 A | 444.8 A | 220.7 A | 562.6 A | 1228.1 A | 7.3 | 99.8 | 0.0 | 0.0 | 99.8 |
| | 2007 | 19.5 B | 193.0 B | 64.2 B | 174.0 B | 431.1 B | 24.8 | 531.5 | 4.8 | 1.7 | 538.0 |
| Overall | | 26.0 | 318.9 | 142.5 | 368.3 | 829.6 | 13.5 | 252.2 | 1.7 | 0.6 | 254.5 |

Canada thistle populations were > 5 years in age, except for the Rosemount population which established during a renovation in 2004. Means in a column (within location or within year) followed by the same letter are not different according to paired t-tests (P=0.05).

Table 2. Average number of Canada thistle achenes produced per seedhead at 4 sites, in 2006 and 2007 in Minnesota.

| | | Average No. per Flower | | | | | | | |
|-----------|------|------------------------|------------------|----------------|---------------|---------------|------------------|----------------|---------------|
| | | Female | | | | Male | | | |
| Location | Year | Empty Achenes | Shrunken Achenes | Normal Achenes | Total Achenes | Empty Achenes | Shrunken Achenes | Normal Achenes | Total Achenes |
| Elysian | 2006 | 13.7 ab | 0.2 d | 24.8 a | 38.7 ab | 30.2 | 0.0 | 0.0 | 30.2 |
| | 2007 | 5.4 d | 2.4 cd | 15.6 b | 23.4 cde | 27.9 | 0.8 | 0.2 | 29.0 |
| Maplewood | 2006 | 6.0 d | 18.8 a | 2.8 de | 27.6 bcd | -- | -- | -- | -- |
| | 2007 | 15.5 ab | 1.4 cd | 1.4 e | 18.3 de | -- | -- | -- | -- |
| Rosemount | 2006 | 18.9 a | 5.5 c | 21.1 a | 45.5 a | -- | -- | -- | -- |
| | 2007 | 7.9 cd | 3.8 cd | 10.5 bc | 22.2 cde | 22.2 | 0.0 | 0.0 | 22.2 |
| St. Paul | 2006 | 5.7 d | 1.7 cd | 6.0 cde | 13.4 e | 3.8 | 0.0 | 0.0 | 3.8 |
| | 2007 | 11.6 bc | 10.1 b | 8.8 cd | 30.5 bc | 16.1 | 0.1 | 0.1 | 16.3 |
| By Year | 2006 | 13.7 A | 6.8 A | 17.3 A | 37.8 A | 13.7 | 0.0 | 0.0 | 13.7 |
| | 2007 | 9.9 A | 3.3 A | 8.9 B | 22.2 B | 21.4 | 0.2 | 0.1 | 21.7 |
| Overall | | 12.3 | 5.5 | 14.2 | 31.9 | 18.7 | 0.1 | 0.0 | 18.9 |

Canada thistle populations were > 5 years in age, except for the Rosemount population which established during a renovation in 2004. Means in a column (within location or within year) followed by the same letter are not different according to paired t-tests (P=0.05).

Table 3. Percentage of Canada thistle achenes produced by achene type at 4 sites, in 2006 and 2007 in Minnesota.

| Location | Year | Percentages | | | | | |
|-----------|------|--------------|------------------|----------------|---------------|------------------|----------------|
| | | Female | | | Male | | |
| | | Empty Achene | Shrunken Achenes | Normal Achenes | Empty Achenes | Shrunken Achenes | Normal Achenes |
| Elysian | 2006 | 35.4 | 0.5 | 64.1 | 100.0 | 0.0 | 0.0 |
| | 2007 | 23.2 | 10.3 | 66.6 | 96.4 | 2.7 | 0.8 |
| Maplewood | 2006 | 21.8 | 68.0 | 10.2 | | | |
| | 2007 | 84.5 | 7.9 | 7.6 | | | |
| Rosemount | 2006 | 41.5 | 12.2 | 46.3 | | | |
| | 2007 | 35.7 | 17.2 | 47.2 | 100.0 | 0.0 | 0.0 |
| St. Paul | 2006 | 42.5 | 12.6 | 44.9 | 100.0 | 0.0 | 0.0 |
| | 2007 | 38.0 | 33.2 | 28.8 | 98.8 | 0.8 | 0.4 |
| By Year | 2006 | 36.2 | 18.0 | 45.8 | 100.0 | 0.0 | 0.0 |
| | 2007 | 44.8 | 14.9 | 40.4 | 98.8 | 0.9 | 0.3 |
| Overall | | 38.4 | 17.2 | 44.4 | 99.1 | 0.7 | 0.2 |

Canada thistle populations were > 5 years in age, except for the Rosemount population which established during a renovation in 2004

Table 4. Average weight of shrunken and normal Canada thistle achenes collected from female shoots at 3 sites in 2007 in Minnesota.

| Location | Shrunken Achenes | Normal Achenes |
|------------------------|-------------------------|-----------------------|
| | ----- mg ----- | |
| Maplewood | 0.797 | 1.227 |
| Rosemount | 0.612 | 0.918 |
| St. Paul | 0.517 | 0.791 |
| Overall average | 0.642 | 0.979 |

Number of Flowers per Shoot

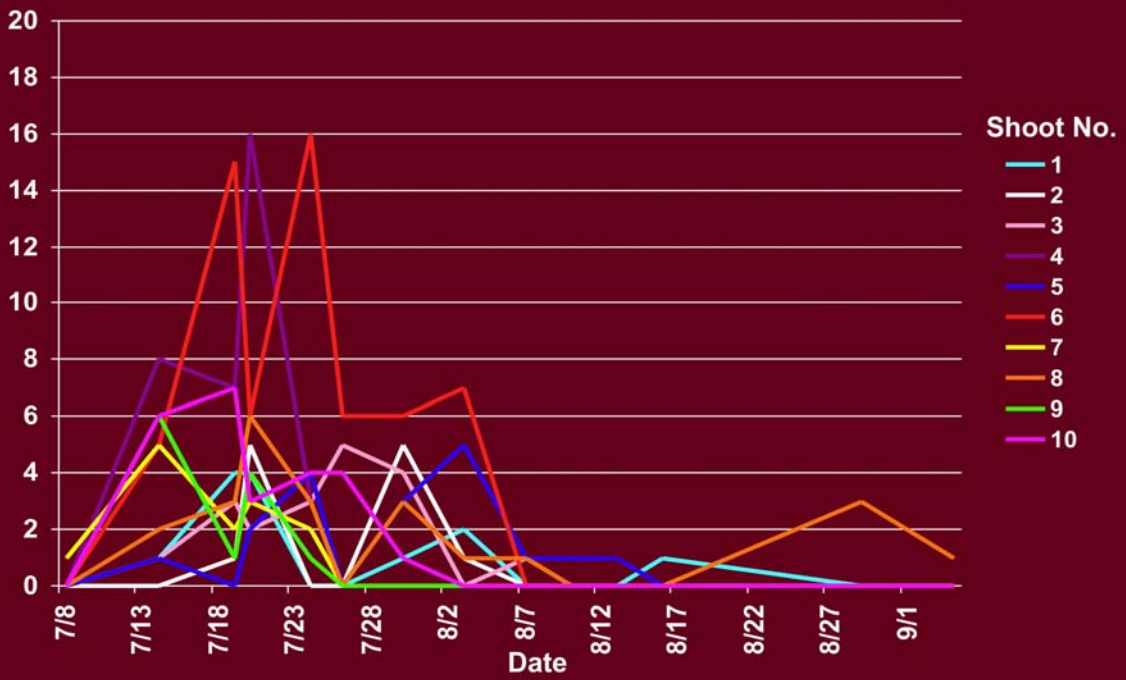


Figure 1. Number of Canada thistle flowers per shoot collected at maturity by sampling date from 10 plants, Rosemount, MN, 2007.

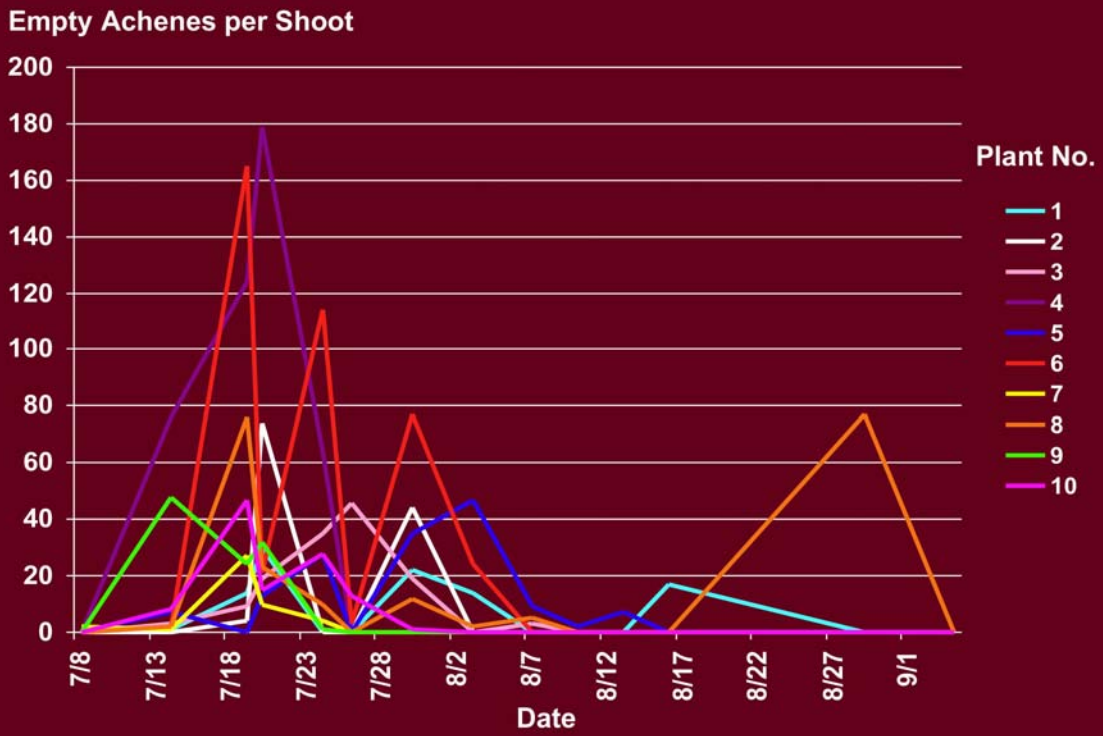


Figure 2. Number of empty Canada thistle achenes collected per shoot by sampling date, Rosemount, MN 2007.

Shrunken Achenes per Shoot

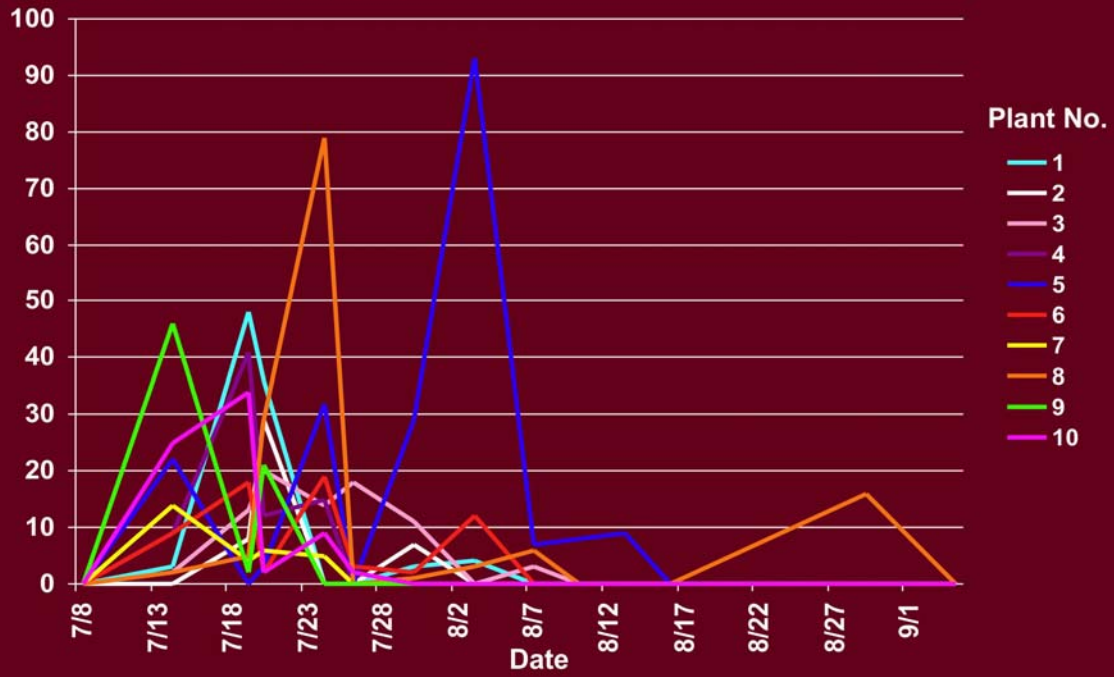


Figure 3. Number of empty Canada thistle achenes collected per shoot by sampling date, Rosemount, MN 2007.

Normal Achenes per Shoot

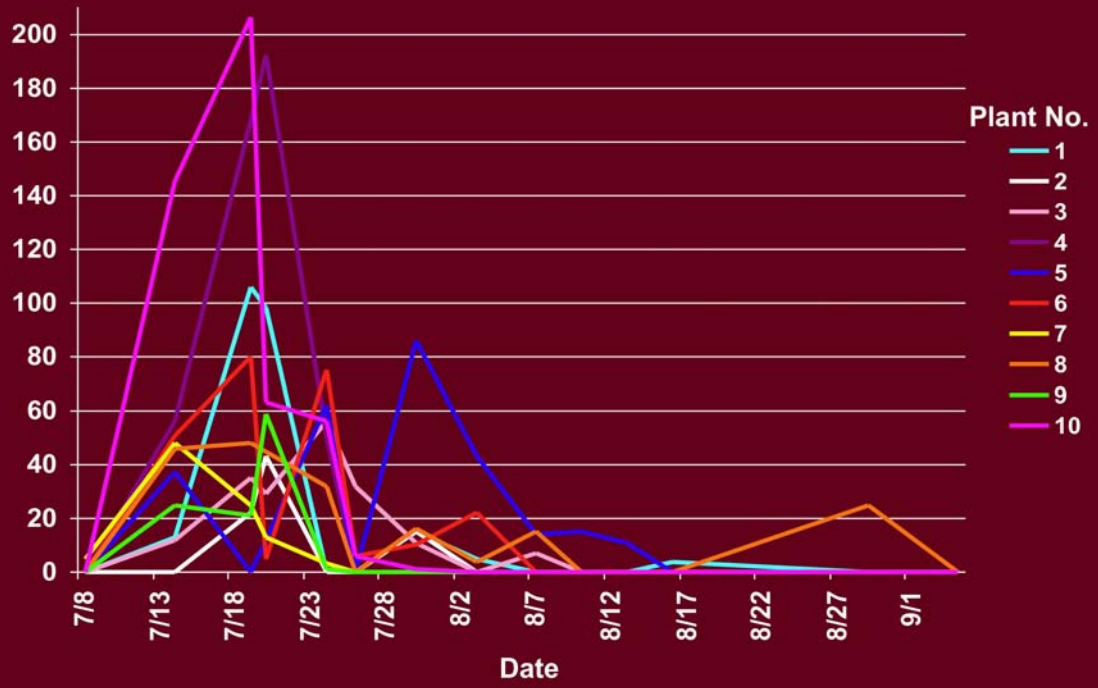
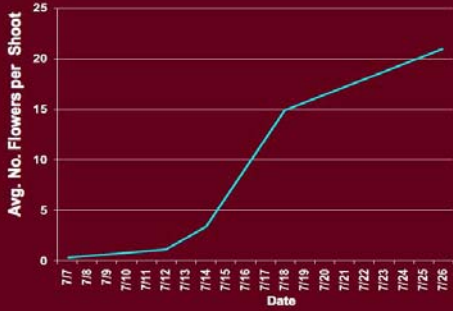
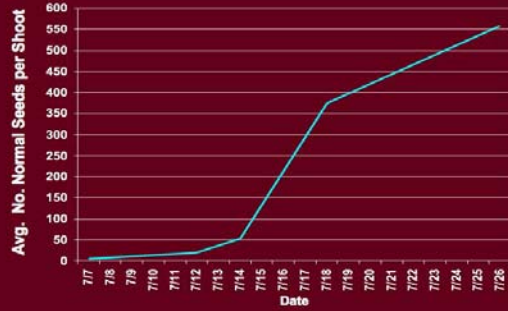


Figure 4. Number of normal Canada thistle achenes collected per shoot by sampling date, Rosemount, MN 2007.

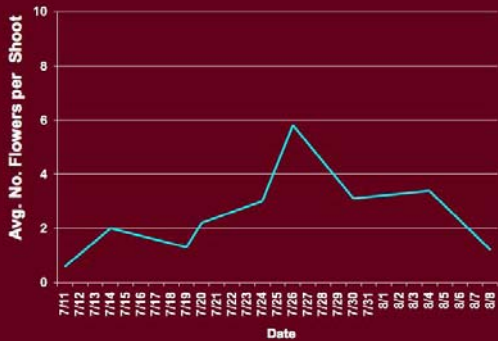
**Canada Thistle Seed Production
Elysian 2006**



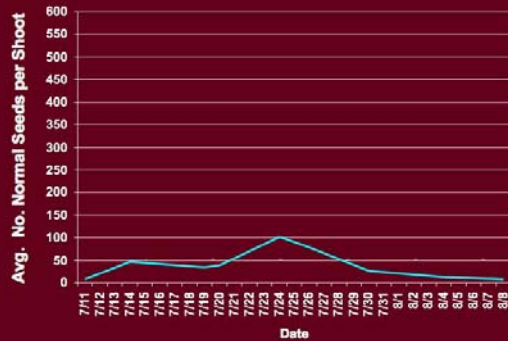
**Canada Thistle Seed Production
Elysian 2006**



**Canada Thistle Seed Production
Elysian 2007**



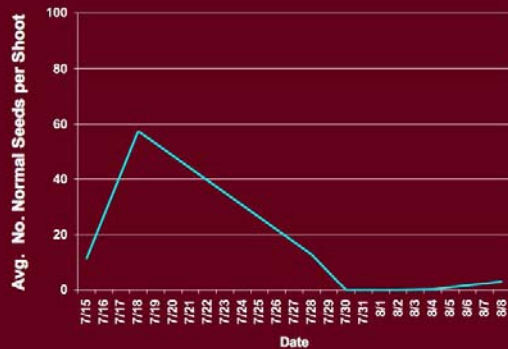
**Canada Thistle Seed Production
Elysian 2007**



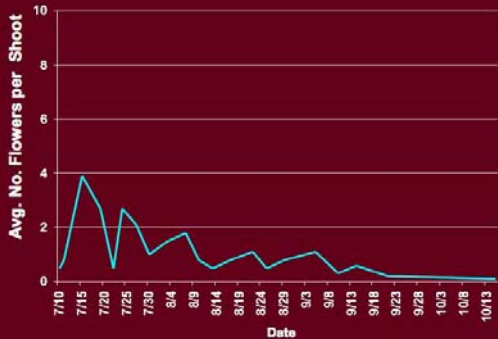
**Canada Thistle Seed Production
Maplewood 2006**



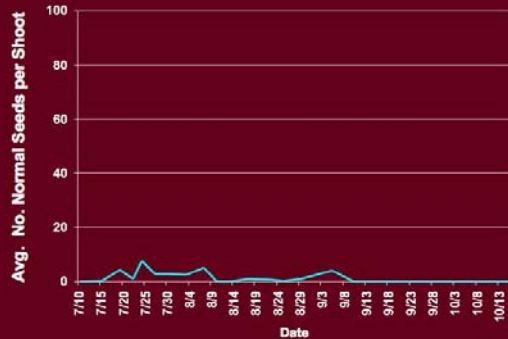
**Canada Thistle Seed Production
Maplewood 2006**



**Canada Thistle Seed Production
Maplewood 2007**



**Canada Thistle Seed Production
Maplewood 2007**



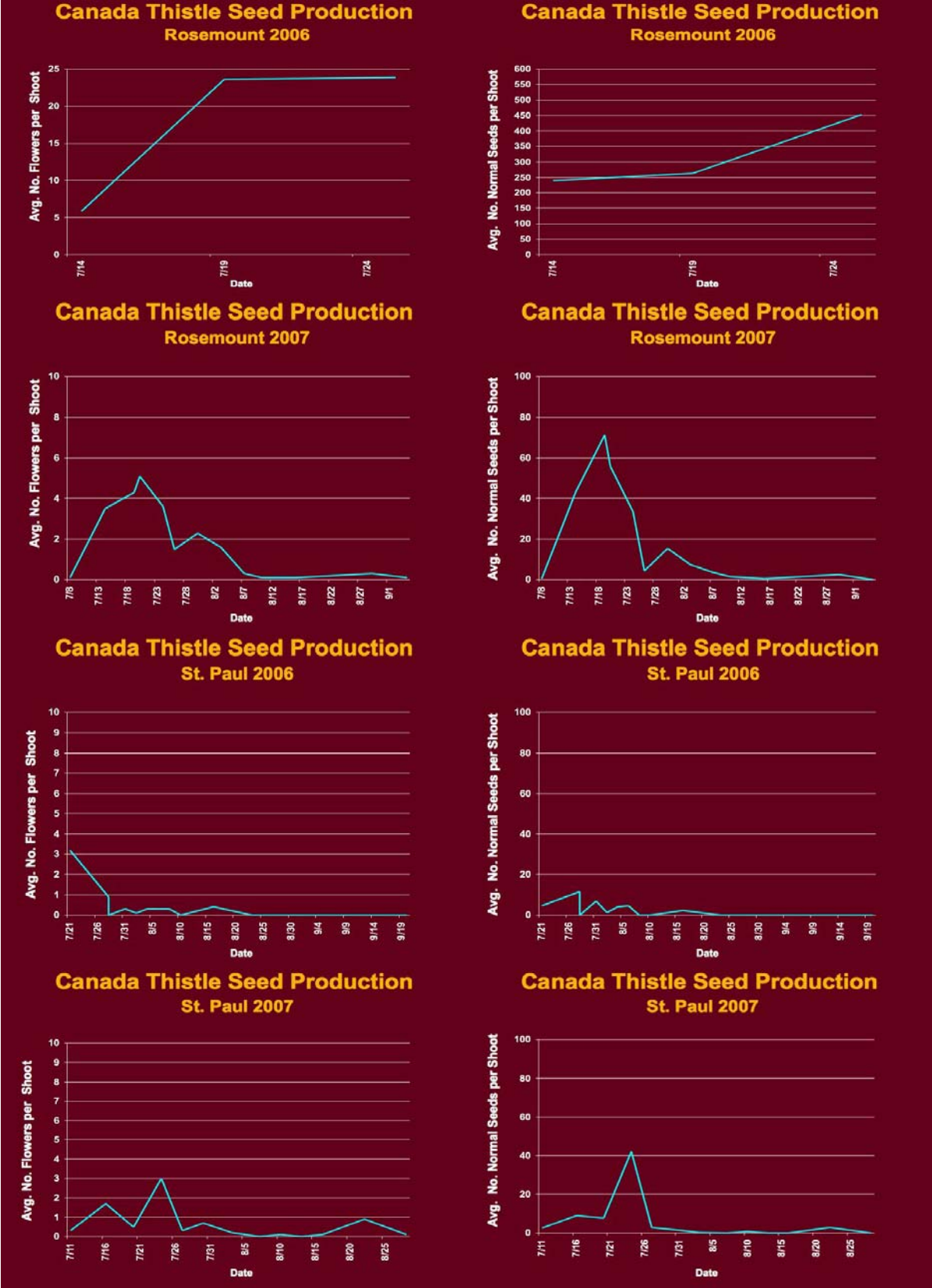


Figure 5. Average number of Canada thistle flowers and achenes produced per female shoot, over two years and four sites in 2006 and 2007, MN.



Figure 6. Empty Achenes. Maplewood site, collected 9-5-07, plant 5F at the fluff stage.



Figure 7. Shrunken Achenes. Maplewood site, collected 9-5-07, plant 5F at the fluff stage.



Figure 8. Normal Achenes. Maplewood site, collected 9-5-07, plant 5F at the fluff stage.

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