Modes of Crown Vetch Invasion and Persistence

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ABSTRACT.—Plant invasions have been hypothesized to proceed at the local scale (i.e., individual patch or stand) according to one of several distinct spatial patterns. However, few studies have attempted to reconstruct the patterns of perennial herbaceous plant invasions at local scales due to difficulty in determining the age of individuals. We used herb chronology to determine the ages of roots within several crown vetch patches in order to characterize the spatial age structure of these patches. Additionally, we examined both sexual and vegetative crown vetch reproduction, with regard to potential impacts on local spread and persistence, through seed bank sampling and greenhouse experiments. We found little distinct spatial age structuring in crown vetch patches, perhaps due to a lack of older roots caused by rapid ramet turnover within patches. We also found no support for the hypothesis, proposed by several land managers, that crown vetch builds up a large seed bank. However, we did find that even small fragments of crown vetch plants are capable of vegetative regeneration, which may be important in explaining this species’ persistence in spite of control measures.

Nomenclature: crown vetch, Coronilla varia L.

As the spread of exotic organisms has generated increasing environmental concern (Vitousek et al., 1996), researchers have worked to document the patterns of past and present invasions (Pysek et al., 1998) and to generate models capable of predicting future ones (Hastings, 1996). These patterns, and likely the processes causing them, have proven to be highly scale dependent (Collingham et al., 2000; Levin, 1992).

It has been possible to reconstruct patterns of invasion at large geographic scales from herbarium records and other sources (Mack, 1981; Weber, 1998). The rate at which many invaders spread can often be accurately modeled at regional scales using simple reaction-diffusion models that assume dispersal and movement are random (Skellam, 1951; Andow et al., 1990; van den Bosch et al., 1992). However, when applied at more localized scales these models have yielded mixed results. Frappier et al. (2003) found that a diffusion model accurately described the spread of a stand of buckthorn (Rhamnus frangula L.) in New Hampshire, but Lonsdale (1993) found that simple diffusion models were inadequate when examining the spread of Mimosa pigra L. from a wetland in Australia. Both of these studies focused on invading woody plants in situations where the progress of the invasion could be reconstructed by aging stem cross sections or observing aerial photographs. Few studies have attempted to reconstruct the patterns of perennial herbaceous plant invasions at local scales, i.e., individual patch or stand, due to difficulty in determining the age of individuals (Dietz, 2002).

If the spatial spread of invasives across a landscape can be predicted accurately by models that assume movement is random, then the models are useful without further complication (Andow et al., 1990). However, movement is clearly not random. Plant dispersal and recruitment are greatly affected by micro-site variation (Kadmon and Shmida, 1990) and neighbor effects (Barton, 1993). Understanding the movement of invaders at a finer scale may help us understand the processes that govern invasions. Clonal plants may be particularly useful study organisms in examining localized patterns of invasion, as they have the ability to respond to local conditions by selectively placing ramets in favorable sites (Evans and Cain, 1995; Van Kleunen and Fischer, 2001).

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Lovett Doust (1981) proposed two possible, contrasting, invasion patterns for clonal species. She described species that would advance as tightly packed fronts, a “phalanx pattern,” as one extreme, and species that would spread out into the surrounding vegetation to minimize intraspecific contact, a “guerilla pattern,” as another. Wilson and Lee (1989) expanded the concept of invasion patterns beyond clonal species to include all plant invasions and added the term “infiltration invasion” to describe a pattern where both short and long distance dispersal occur simultaneously. These patterns could potentially occur at either the scale of individual populations or at much larger landscape scales. Identifying by which, if any, of these patterns an individual population has expanded could provide valuable insight into the processes that prevent or allow a species to spread locally (Dietz, 2002). Additionally, if the pattern by which a population is expanding is close to the phalanx or infiltration pattern, it should be possible to estimate the rate of spread of the population from the spatial-age structure (Dietz, 2002).

One of the major factors affecting patterns of population expansion is mode of recruitment. Therefore, determining the predominant mode of reproduction driving population expansion would be useful in understanding observed patterns. This information should also be invaluable in developing means to control the expansion of problematic populations (Gaskin, 2006).

This paper details a series of observational studies and controlled experiments aimed at furthering an understanding of the dynamics of crown vetch (Coronilla varia L.) invasions. In one study we used herb chronology, a recently developed technique for aging herbaceous perennials (Dietz and Ullmann, 1997), to age individual crown vetch plants. We tried several sampling patterns in different patches of crown vetch in order to describe the patterns by which the patches had spread. We also made detailed maps of the borders of individual patches within a site, and remade the maps 1 y later to observe changes in patch boundaries through time. We also sampled the seed bank in and around established crown vetch patches in order to gain perspective on the role of recruitment from seed in the persistence of crown vetch patches. Additionally, we examined the ability of crown vetch stem fragments to root out and survive in order to determine if above ground asexual reproduction could possibly explain some of crown vetch’s ability to resist attempted control measures.

**STUDY SYSTEM**

**THE PLANT**

Crown vetch is a herbaceous perennial legume native to the Mediterranean region. Its trailing stems form dense patches in which very few other species are found. Crown vetch spreads asexually by rhizomes and also by seed. According to the USDA’s plant distribution maps crown vetch is now widespread in the United States, being found in all lower 48 states except North Dakota (USDA, 2007). It has been widely used as a ground cover and for erosion control, and was heavily planted along roadsides between the 1950s and 1980s. However, crown vetch has fallen out of favor for this use, as its effectiveness in erosion control has come into question (USDA, 2002). Crown vetch also competes with more desirable native vegetation (Symstad, 2004; Walck et al., 1999) and can spread away from roadsides and into natural areas (Solecki, 1997). It is difficult to eradicate once established, and prairie reconstruction near or on roadsides can be made difficult or impossible in areas with large crown vetch populations (Shirley, 1994).

**STUDY SITES**

Field work to examine the spatial structure of root ages in crown vetch patches and the distribution of crown vetch seed in the soil seed bank was conducted at a site (42.08°N,
93.94°W) in Boone County, Iowa, and at Iowa State University’s western research farm (42.07°N, 95.84°W) in Monona County, Iowa.

**Boone.**—The Boone site was approximately a half-acre of un-maintained land adjacent to the Des Moines River and the city of Boone’s water purification plant. Vegetation at the site was a diverse mix of native and introduced species. While introduced forage grasses such as *Bromus inermis* Leyss. and *Poa pratensis* L. were prevalent, there were also many prairie grasses such as *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, *Schizachyrium scoparium* (Michx.) Nash, and *Panicum virgatum* L. at the site. The forb community included some native genera including *Silphium* L., *Verbena* L., *Solidago* L. and *Helianthus* L., as well as a wide variety of weeds and introduced species such as *Cirsium arvense* (L.) Scop., *Rosa multiflora* Thunb., *Lotus corniculatus* L., and *Ambrosia* L. The site also contained extensive patches of crown vetch (Fig. 1). It is unlikely that crown vetch was seeded directly into the site, but it was seeded along a county road that borders the site. These roadside populations are the most likely original source of propagules for the patches now invading the site.

**Western Research Farm.**—Iowa State’s western research farm is located in the loess hills region of Iowa. The crown vetch patches used in seed bank sampling were in a pasture located adjacent to a roadside ditch containing crown vetch. Prior to 2002, the pasture was dominated by smooth brome (*Bromus inermis* Leyss.). In 2002 the area was treated with herbicide, plowed under and planted with prairie species as part of a restoration study. Many weeds came into the pasture after it was planted, but crown vetch was not one of the early invaders and by the end of 2003 was still present only in trace amounts. However, in 2004 crown vetch became a major problem. By May 2005, dense patches of crown vetch had formed so that it comprised 46% of the vegetative cover in the restoration experiment. Smooth brome had also become quite prevalent, and these invaders forced the abandonment of the restoration experiment (B. Wilsey, unpubl.).

**METHODS**

**SPATIAL-AGE STRUCTURE**

We characterized the spatial-age structure of three crown vetch patches at the Boone site. We hypothesized that roots of similar ages might be clustered together in relatively distinct regions of the patches, and that locating and delineating these regions would provide insight into the pattern of spread that had led to the current patch dimensions. As we had no reasonable way of forming *a priori* hypotheses about the relative sizes or locations of these regions within patches, we tried different sampling methods in each patch in order to obtain an idea of the type of sampling design that would be most effective.

The smallest patch sampled (patch 1) measured roughly 3 × 3.5 m. Seventy-three 0.25 m² quadrats were sampled within this patch. Quadrats were placed directly adjacent to one another, for complete coverage of about 2/3 of the total patch. All roots were dug up within each quadrat. The roots were aged by counting annual growth rings in cross sections of the root, using the methodology of Dietz and Ullman (1997). After aging all of the roots from several quadrats it became clear that larger, thicker roots were always older than smaller, thinner roots. Subsequently, only the largest roots from each quadrat were aged.

The second crown vetch patch (patch 2) sampled was roughly twice as large as the first. A 6 m transect was run across the center of the patch. Five transects were run across the patch perpendicular to the 6 m main transect, crossing it at 1 m intervals. All transects were sampled every 0.5 m. The sampling procedure consisted of removing one shovel full of soil and extracting all crown vetch roots from it. The largest of these roots were then aged.
Fig. 1.—Ages of all crown vetch roots sampled in three separate patches in Boone County, Iowa. The bar graphs show the age distribution of all sampled roots. In patch one, each box represents one 0.25 m$^2$ quadrat. The number shown in each quadrat is the age of the oldest root found within that quadrat. The two empty boxes are quadrats that contained no crown vetch. In patch 2 each line segment represents 0.5 m. In patch 3 each line segment represents 1 m.
The third patch (patch 3) sampled was quite large, roughly 300 m². A 22 m long transect was run across the center of the patch, and a second 20 m long transect was run perpendicular to this transect so that it crossed at the midpoint in the center of the patch. The sampling procedure was the same as for the second patch, except that the sampling interval was 1 m instead of 0.5 m.

We used linear regression to test for a relationship between distance from patch edge and root age in patches 2 and 3. A strong, negative relationship would have been indicative of expansion in a phalanx type pattern, while a positive or weak relationship would have several possible explanations. This test was not performed on patch 1 because exact distances from all roots to the patch edge could not be determined from collected data. We also conducted spatial autocorrelation analysis to examine the spatial structure of root ages in all patches. The objective of these analyses was to examine the patterns of patch expansion, not maintenance; therefore, all analyses included only the oldest root from each sampling point or quadrat.

PATCH BOUNDARY MAPPING

We used a Trimble GeoXT GPS unit with sub-meter accuracy to map the boundaries of all crown vetch patches at the Boone site on 31 August 2004, and again on 29 August 2005. On each of these days we walked through the site to locate all crown vetch patches. At each patch, we slowly walked around the patch outline while recording our path with the GPS unit. These data were recorded as shape files and then imported into ArcView 9.0. In ArcView, we calculated the area of each shape file. These areas were summed in order to obtain the total area covered by crown vetch patches in each year. Our goal was to examine year-to-year variation in total patch size in order to determine if crown vetch was actively expanding within the site.

SEED BANK

We examined the distribution of crown vetch seeds in the persistent soil seed bank at the Boone site and at the Western Research Farm. On 19 May 2005 at the Boone site, one 41 m long transect was placed through a large patch of crown vetch and out into an area with smaller scattered patches. We sampled at 22 points along this transect. All sampled points were at least 0.5 m apart, and points were selected so that samples were taken within and on the borders of the large and smaller patches of crown vetch, as well as in areas with other vegetation. At each sampling point two 2.5 cm diameter soil cores were taken to a depth of 15 cm, for a total of 44 soil cores. These cores were separated into four layers, the surface layer from 0–2 cm deep, and subsequent layers from 2–6, 6–10 and 10–15 cm deep. These were then bagged and taken directly to an Iowa State greenhouse. Each of the 176 samples (44 cores × 4 layers/core) was spread out in a 4 in pot on top of sterilized potting soil. All pots were kept watered and seed germination was recorded weekly. All seedlings were removed when they could be identified to the generic level. Seedlings that became large enough to inhibit the germination of other seeds in the same pot, but that could not yet be identified, were transplanted into separate pots and allowed to continue growing. These seedlings were kept until they could be positively identified, or at least until we could be certain that they were not crown vetch. We ran the experiment for 17 wk.

The procedure followed at the Western Research Farm pasture was quite similar to the one used at the Boone site, except for the layout of the transects. On 21 June 2005, a 4 m transect was run through a patch of crown vetch. At the 1 and 3 m points along this transect, 3 m long side transects were placed at right angles to the main transect across the patch and out into the adjacent grassland. Each transect was sampled at 0.5 m intervals, with two soil
cores being removed at each sampling point. Soil cores were taken to a depth of 10 cm, and divided into three layers 0–2, 2–6 and 6–10 cm deep. A total of 42 soil cores were taken. Each layer from each core was placed in its own pot for a total of 126 pots, and the same procedure described above was followed to determine the number and composition of the viable propagule supply in the soil.

ABOVE GROUND VEGETATIVE REPRODUCTION

Because we found no evidence to support the hypothesis that crown vetch builds up a large seed bank (see results), and because mowing has been shown to be ineffective in crown vetch control (Symstad, 2002), we examined the ability of crown vetch to regenerate from vegetative fragments. We clipped plants at ground level and brought them to the lab. Plant sections in the following categories were cut from the plants: leaflet only, 5–10 cm section of leaf, 2–10 cm long section of stem without a node and 2–10 cm long section of stem with a node. These sections were then placed in pots on the surface of packed potting soil. Three sections, all of the same type, were placed in each pot. Ten pots were given each section type, for a total of 40 pots. These pots were divided into two sets of twenty pots (five pots per section type). One set was watered two to three times per week until the soil was well saturated, the other set was only watered once per week. All pots were on the same table in the greenhouse, but the low and high water treatments were slightly separated in order to avoid incidental watering of the low water treatment. All pots were monitored for one month.

RESULTS

SPATIAL-AGE STRUCTURE

We aged a total of 287 roots from the three crown vetch patches. The majority of these (66%) were only 2 or 3 yr old. The root ages from each patch, and the spatial distribution of the oldest roots are shown in figure 1. There was a significant relationship between distance from the edge of a patch and root age, with younger roots tending to occur closer to the edge. Although the r-squared values (0.17 in patch 3 and 0.21 in patch 2) for this relationship were weak, it does suggest that the patches are expanding. The spatial autocorrelation analysis (Fig. 2) confirms a weak tendency, observable in the diagrams in figure 1, for roots of similar age to occur close to one another. However, all significant spatial auto-correlation quickly disappears at larger distances (Fig. 2). The lack of significant auto-correlation over large portions of the patches, along with the predominance of similarly aged (2–3 yr old) roots throughout the patches, make it difficult to reconstruct a specific pattern of expansion from the collected data.

PATCH BOUNDARY MAPPING

The total area of all crown vetch patches at the Boone site was 3060 m$^2$ in 2004. One year later, this area had increased to 3650 m$^2$ (Fig. 3). This increase was due to the appearance of several new small patches, as well as the expansion of existing patches. However, not all of the patches expanded between 2004 and 2005. Some of them contracted, and others shifted location slightly by shrinking on one side while expanding on another. The latter effect could be due to a slight systematic error in the coordinate system obtained from the gps readings between years.

SEED BANK

The viable seed bank of all species at the Boone site contained an estimated 13,150 seeds/m$^2$, while the western research farm site seed bank had an estimated 9200 seeds/m$^2$. Both of
these viable seed densities are within the range reported for Great Plains grasslands by Lippert and Hopkins (1950). No crown vetch seedlings emerged from any of the soil samples at either site.

**VEGETATIVE REPRODUCTION**

In the high water treatment, all 15 of the stem sections that contained a node survived and produced new growth by sending up shoots from the node. Some of this new growth was visible as early as 3 d after the experiment began. None of the stem sections without nodes or the leaf sections produced any new growth, but they were still green at the end of the month.

In the low water treatment, several of the stem sections that contained nodes produced new growth, but none of them survived past three weeks. All of the plant sections in the low water treatment were clearly dead by the end of the month.

**DISCUSSION**

There are several patterns by which clonal species have been hypothesized to invade (Lovett Doust, 1981). If crown vetch patches spread in distinct patterns, understanding
these patterns would be very useful in developing methods for controlling this species. However, we were unable to detect any such patterns in the spatial age structure of crown vetch patches. We found some weak spatial autocorrelation at very short distances, meaning that roots of similar age were more likely than would be expected by chance to be found close to one another, but this autocorrelation disappeared very quickly as distance...
increased. Dietz (2002) found strong spatial-age structure in a patch of spotted knapweed (*Centaurea maculosa* Lam.) when he first sampled in 1999. However, when the patch was re-sampled in 2003 it had not expanded beyond the 1999 boundaries and this structure had disappeared (Dietz, 2004). The crown vetch patch boundary mapping we did in 2004 and repeated in 2005 showed that the total area of all crown vetch patches at the Boone site had increased. There did not appear to be a consistent pattern of increase, a few new patches had appeared, and some old patches had expanded while a few had shrunk slightly or shifted. Some of this increase may have been due to sampling error, as it is possible that we did not find every small patch present at the site in 2004. However, it seems unlikely that sampling error could explain all of the increase, especially since some of the larger patches had clearly expanded in size. If the older crown vetch patches have reached some sort of dynamic equilibrium with their surroundings and only expand and contract in response to annual variation in local conditions, then natural population turnover as older individuals within the patch die and are replaced could destroy any spatial-age structure that may have been present as the patches were initially expanding. This would imply that models of invasive spread based on simple patterns or random movement and the rate of population increase may give accurate predictions initially (Andow *et al.* 1990), but that these predictions may become less accurate as the invasion progresses and interactions between new invaders, established members of the invasive population and the surrounding habitat increase. However, the lack of distinct spatial patterns in root ages in these crown vetch patches may simply result from the fact that the majority of roots sampled (66%) were only 2–3 yr old. Ramet turnover within crown vetch populations may simply be too fast for much detectable spatial-age structuring to develop.

Crown vetch is quite difficult to eradicate once established. One explanation frequently given for the resilience of crown vetch is that it is thought to build up a large and persistent seed bank (The Nature Conservancy, 2003). This belief is likely based on the fact that the plants flower and produce seed for nearly the entire growing season. It is usually possible to find both newly opened flowers and mature fruits right next to each other within a crown vetch patch. However, in a study examining interactions between patches of crown vetch and tall fescue along a roadside embankment, Luken (1987) noted that successful recruitment from seed was rare in established crown vetch patches. To our knowledge, our seed-bank sampling represents the first attempt to actually collect data on crown vetch in the seed bank. We were unable to find any viable crown vetch seed in soil samples taken in and around two established crown vetch patches. This result may surprise some land managers, but it is perhaps not unusual given the low rates of sexual reproduction by many clonal species (Harper, 1977; Erikkson, 1989). We did find extensive systems of underground rhizomes in the patches we sampled, indicating a great deal of vegetative reproduction was taking place. Through our greenhouse study, we also documented crown vetch’s ability to propagate from fragments of the above-ground stems. Although it is not clear to what extent this actually takes place in the field, it could be the mechanism behind other experimental results showing that mowing is ineffective as a crown vetch control method (Symstad, 2002).

While many crown vetch invasions are probably initiated by seed, as it has been reported to invade sites not directly adjacent to plantings (The Nature Conservancy, 2003), asexual reproduction appears to be much more important than sexual reproduction in explaining the persistence and resilience of established patches. In addition to the extensive rhizome systems found under crown vetch patches, any aboveground stem section that contains a node is capable of generating a new plant—provided adequate moisture is present. Keeping crown vetch patches mowed may help prevent the production of seed that could disperse to
start new invasions, but is unlikely to help eradicate existing patches. Additionally, because very small stem fragments are capable of regeneration, it is highly unlikely that any contact herbicide could kill enough of the stems to prevent a patch from coming back, and even herbicides that translocate throughout the plant may not reach all the plants in a given patch. Repeated control measures in combination with close monitoring will be needed to remove crown vetch from areas where it is undesirable.

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Literature Cited


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