EFFECTIVENESS OF SUMMER MOWING FOR WEED CONTROL IN PLANTINGS OF NATIVE C_4 PRAIRIE GRASSES

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ABSTRACT

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Land managers often face seemingly conflicting needs to use land for species conservation or to produce economically valuable goods. Diverse prairie plantings harvested for biomass offer an opportunity to achieve both goals. Persistence of these disturbance-adapted prairie communities requires management strategies that promote desirable native plant diversity and reduce abundance of undesirable weedy species. This is sometimes achieved through prescribed burning or mowing, though mowing effects have not been well studied. To address this knowledge gap, I compared two summer mowing treatments to a no-mowing control in experimental prairies on both loamy and sandy soils for two years. The communities examined contained mature (4- and 5-yr-old) prairie grasses (*Andropogon gerardii* Vitman, big bluestem, and *Schizachyrium scoparium* Michx., little bluestem), as well as young colonizers of both desirable and weedy species. Overall, I found that June mowing reduced weed biomass and seed production on loamy soil. Biomass of native grass colonizers was greatest in mowed blocks, suggesting that mowing stimulated native colonization. However, these benefits of mowing came at the cost of some reduction in the size and reproductive output of mature prairie grasses. June and July mowing substantially reduced size and flowering of native grasses without additional weed control benefits. I therefore suggest that June mowing could be a useful component of adaptive management in tallgrass prairie in the Great Lakes region, with careful consideration of effects on summer-nesting bird species, but I advise against mowing in both June and July.

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Distribution of North American tallgrass prairie: Past and present

Prairies historically dominated much of the North American Great Plains region and large portions of the Midwestern United States. Estimates suggest that prior to European settlement these North American prairies exceeded 162 million ha in area, of which approximately 68.4 million ha were tallgrass prairie (Samson and Knopf 1994). Prairies are primarily defined by continuous cover of herbaceous vegetation, and their lack of woody vegetation (<10%) (Faber-Langendoen 2001). Tallgrass prairies are further defined by the presence of C_4 grasses that typically dominate the plant community, primarily big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Michx.), and Indian grass (*Sorghastrum nutans* (L.) Nash) (Faber-Langendoen 2001). In the 1800s, seven percent of Michigan consisted of prairie and savanna, primarily in the southwestern region (O'Connor et al. 2009).

As European settlers spread westward across North America in the 1800s, they cleared land for settlement and agricultural development. Prairies were the easiest land to clear because they lacked woody species, and they were particularly well-suited for agriculture because of their fertile soils (Iverson 1988, Samson et al. 2004). Since the 1800s, nearly 99.9% of North American prairies have been converted to other land covers, resulting in the greatest loss in extent of any ecosystem in North America (Samson and Knopf 1994). In Michigan, the majority of native prairie was converted to agriculture by European settlers, and remnants continue to be converted to other land use types or degraded by human activities (O'Connor et al. 2009). The remnant prairies in Michigan that persisted did so largely because they were situated in areas less suitable for agriculture (Iverson 1988). For this reason, many remnants are found on lower quality soils than was typical of historical prairies.

Diversity and invasion in tallgrass prairie

Prairies in the Great Lakes region once supported a large number of diverse plant and animal species (O'Connor et al. 2009). The few long-term studies of prairie restoration have shown that lost biodiversity can be difficult to replace. Even the oldest prairie restoration in existence, the Curtis Prairie at the University of Wisconsin, is threatened by abundance of invasive species and decreased native species (Wegener et al. 2008). Similarly, restored sites continued to have lower species richness than remnant sites thirty-five years after restoration began at a prairie in northeast Kansas, (Kindscher and Tieszen 1998), possibly because many native forbs failed to establish in restored areas, despite being seeded in. Restored prairies in Illinois ranging in age from 35 to 45 years old also had lower species richness than nearby remnant sites, though both site types had similar floristic quality index (FQI) values and percentage of alien species (Allison 2002). Restored sites likely had high FQI values in this study because sites were planted with species characteristic of high-quality prairies, though species distributions were much patchier in restored than in remnant sites. These three examples illustrate that prairie restoration is a long and challenging process, which often fails to produce communities with the same characteristics as high quality remnants. However, improvements to prairie restoration strategies can increase the effectiveness of this process.

Restoration activities may temporarily increase species or genetic diversity by deliberately introducing new species or genotypes into the system, but this diversity is often not maintained over time. Polley et al. (2005) found that plant species diversity was greater in remnant prairies than comparable restored prairies due to greater variability in species diversity among restored plots than among remnant plots. While some restored plots may have greater species diversity than remnant plots, species diversity in most restored plots is much lower, such that average species diversity is lower in restored sites. Gustafson et al. (2002) showed that remnant prairies were actually less genetically diverse than restored prairies. This was largely attributed to the use of multiple seed sources in restored prairies, which causes an increase in genetic diversity because multiple genotypes are mixed. Many remnant sites are isolated from other restored or remnant patches, and may contain less genetic diversity due to inbreeding and a lack of new genetic inputs.

Prairie diversity and ecosystem functioning in both remnant and restored sites are currently threatened by invasive species (Millenium Ecosystem Assessment 2005), which are a primary concern for land managers (Rowe 2010). These species rapidly colonize disturbed sites (Larson et al. 2001), often causing ecological and economic harm by displacing desirable native species (Bryson and DeFelice 2010, Randall 1996). Control of invasive species likely requires management strategies similar to historical disturbance regimes that formerly maintained prairie plant communities. Mowing is one possible management strategy that partially mimics effects of historical disturbances, and could improve invasive species control in prairies

Disturbance regimes and prairie management

HISTORIC DISTURBANCE REGIMES

One way to address problems with reduced plant species diversity and an influx of invasive species is to reestablish disturbance regimes to prairies. Prior to European settlement, disturbance in prairies came from four sources: fires set in spring by Native Americans (Packard and Mutel 1997), lightning-ignited fires in summer (Higgins 1984), grazing by bison (*Bison bison*) and other ungulates (Knapp et al. 1999), and burrowing by small mammals (Gibson 1989), all of which differentially promoted some plant species and suppressed others. In tallgrass prairie, fire and grazing were the most important forms of disturbance.

In the mid-1800s, the vast herds of bison that grazed prairie communities prior to European settlement were nearly eradicated (Knapp et al. 1999). The number of bison in the U.S. in the 1800s was at least in the millions, though their precise abundance is impossible to determine (Shaw 1995), and this species played an important role in maintaining prairie plant communities. Grazing activity by bison can increase plant species diversity in prairies, often by reducing abundance of dominant C_4 grasses (Hartnett et al. 1996, Veen et al. 2008) or increasing microsite variability (Hartnett et al. 1996). While bison grazing had great influence on prairies in the Great Plains region, bison are believed to have been much less abundant in the Great Lakes region, and consequently the effects of grazing in Michigan may have been less important than the effects of fire (O'Connor et al. 2009).

In the 20th century, the perceived need to protect human lives and property from uncontrolled wildfires prompted widespread fire suppression efforts in the United States. In turn, fire suppression substantially altered the composition of fire-adapted native plant communities. In Michigan, fire suppression substantially reduced the frequency of naturally occurring fires (Cleland et al. 2004) and has led to degradation of prairies and other fire-dependent ecosystems. In Wisconsin, much of the species loss in prairie remnants has been attributed to fire suppression in these ecosystems (Leach and Givnish 1996). Frequent fires are also important in preventing the encroachment of woody species into prairies, and fire suppression often results in significant increases in woody species abundance (Briggs et al. 2002). Without fire or bison to maintain prairie communities and suppress weed populations, many remnant prairies may be unable to persist without human intervention (Randall 1996). These remnants may experience reductions in diversity from invasive species colonization, or may become forests over time if invaded by woody species.

CURRENT MANAGEMENT OPTIONS

In the tallgrass prairie, prescribed burns are conducted primarily in early spring, and are among the most common prairie management practices in North America (Rowe 2010). However, spring prescribed burning does not reflect patterns of natural and human-initiated disturbances that historically shaped prairie ecosystems. These disturbances varied in type (e.g. fire and grazing), frequency within and between years, and timing. Mowing could be an effective tool to mimic some aspects of past disturbances, especially considering its flexibility in terms of application season and necessary conditions for safe and effective use. Prescribed fire use is more constrained by environmental conditions such as wind speed and direction than mowing (Rowe 2010). Grazing is also more constrained than mowing, but is not frequently used in prairie restorations (Rowe 2010).

Mowing and burning often have similar effects on tallgrass prairie vegetation, as demonstrated in spring (Diboll 1986, Hover and Bragg 1981) and summer (Hover and Bragg 1981). Biomass removal is one of the most important roles of disturbances such as fire and grazing (Hulbert 1969, MacDougall and Turkington 2007). Removing biomass near the time of invasive flowering negatively affects dominant invasives by reducing their size and preventing seed production (Benzel et al. 2009, MacDougall and Turkington 2007, Rinella et al. 2001), and favors sub-dominant species by increasing light levels and temperature at the soil surface. Removing inflorescences before invasive plants disperse seeds may be critical to prevent further spread of weedy species. This is particularly true for annual weeds, since the parent plant will not persist into the next growing season. However, both fire and grazing have additional impacts that are not replicated by mowing treatments. Prescribed fire alters nutrient cycling and blackens soil, which further increases soil temperatures (Hulbert 1988). In addition to biomass removal from grazing activity, bison increase nitrogen deposition through waste elimination, and alter soil characteristics by trampling and wallowing (Knapp et al. 1999).

Plant responses to mowing

Plant responses to mowing are largely mediated by plant traits. Mowing selects for and against species based on height; taller species are often more negatively affected by direct biomass removal, while short-statured species may benefit from increased light availability (MacDougall and Turkington 2007). Timing of mowing is also critical. In general, summer mowing (mid-June–August) favors cool-season species, and spring mowing (April–early-June) favors warm-season species (Hover and Bragg 1981, Howe 1999, Wilson and Clark 2001). Plants may also exhibit different responses depending on how frequently they are mowed within a growing season.

INFLUENCE OF TIMING OF MOWING

Effects on dominant species

Most mowing studies have focused exclusively on the dominant plant species in a community. This research has shown that summer mowing can be especially detrimental to the size of native C_4 grasses. For example, big bluestem and little bluestem biomass yields in Missouri were reduced by summer clipping, particularly in July (Vogel and Bjugstad 1968). Likewise, July mowing decreased cover of *A. gerardii* and *S. scoparium* in a Nebraska prairie (Hover and Bragg 1981). Two summer clipping treatments in a Kansas prairie reduced biomass production of *S. scoparium*, but a single summer clipping in this prairie did not affect biomass (N'Guessan and Hartnett 2011).

In contrast, mowing when C_4 grasses are dormant or just beginning to grow may promote their growth by suppressing other actively growing species and removing standing litter. May mowing in Wisconsin increased frequency of *S. scoparium* and side-oats grama (*Bouteloua curtipendula* (Michx.) Torr.) (Diboll 1986). Similarly, when big bluestem and little bluestem plants were clipped in the dormant stage (October–November), biomass yields increased the following season (Vogel and Bjugstad 1968).

Most native C_3 grasses exhibit the opposite response to mowing as C4 grasses; they are suppressed by early or late growing season (spring or fall) mowing, and promoted by summer mowing, which may reduce the amount of standing litter in the following growing season. For example, May mowing reduced cool season grass biomass production in Wisconsin prairies (Diboll 1986). Similarly, July (late season) mowing in a Texas switchgrass stand decreased shoot numbers (Haferkamp and Copeland 1984) and biomass production of big sacaton (*Sporobolus wrightii* Munro ex Scribn.), but biomass of mowed plants rebounded within three years after mowing ceased (Cox 1988). In contrast, summer mowing increased cover of porcupine grass (*Hesperostipa spartea* (Trin.) Barkworth) in Nebraska (Hover and Bragg 1981), and increased both cover and inflorescence production of California oatgrass (*Danthonia* *californica* Bol.) in Oregon (Wilson and Clark 2001). In a Wisconsin prairie, August mowing of the native forb, golden Alexanders (*Zizia aurea* (L.) W. D. J. Koch), doubled population size and number of flowering plants, but May mowing had no effect (Howe 1999).

Summer mowing can also help control non-native invasive species that flower near the time of treatment application. For example, July mowing in a Garry oak savanna reduced growth and flowering of the invasive grasses Kentucky bluegrass (*Poa pratensis* L.) and orchard grass (*Dactylis glomerata* L.), and increased native cover and flowering (MacDougall and Turkington 2007). In an Oregon prairie, mowing in either late spring or early summer decreased cover of the weedy species, tall oatgrass (*Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl and C. Presl) (Wilson and Clark 2001). Reductions were more apparent when plants were mowed around the time of *Arrhenatherum* flowering. Similarly, two studies in Montana on invasive spotted knapweed (*Centaurea stobe* L.) showed that mowing during the flowering stage is the most effective way to decrease density and reproductive output of this species (Benefield et al. 2001, Rinella et al. 2001). Benefield et al. (2001) suggest a similar strategy for control of yellow starthistle (*Centaurea solstitialis* L.) in California grasslands. Plants at the flowering stage have invested much of their energy and resources to inflorescence production, and may not have the time, energy, or resources to rebound from mowing treatments (Benzel et al. 2009). This control strategy is widely accepted, but has only been directly studied for a few individual species. Mowing may actually be counter-productive for control of some highly disturbance-adapted weeds, such as white sweetclover (*Melilotus alba* L.), however. For example, mowing Illinois prairies in late June increased white sweetclover biomass, but reduced total and grass biomass (Randa and Yunger 2001).

Community effects

Multiple studies have shown that summer mowing treatments have little influence on species richness and diversity in U.S. prairies. For example, neither species richness (Collins et al. 1998, Foster et al. 2009, Randa and Yunger 2001) nor species diversity (Randa and Yunger 2001) are altered by June mowing. While it is well established that nitrogen addition alone decreases plant species richness (Tilman 1987), mowing combined with fertilizer addition may increase species richness (Foster et al. 2009), or prevent richness from decreasing in burned plots (Collins et al. 1998). Removal of biomass is an important component of mowing, which may be especially important in fertilized plots where biomass production is greater and may cause losses of sub-dominant species (Collins et al. 1998).

Mowing has been found more often to influence species diversity and richness in grasslands outside of the U.S. Summer mowing increased species richness in South African grasslands (Fynn et al. 2004), in a Norwegian boreal hayfield (Antonsen and Olsson 2005), and in a Garry oak savanna in British Columbia (MacDougall and Turkington 2007). However, these increases may be largely attributable to germination of ruderal species from the seed bank, not to an increase in native species abundance (MacDougall and Turkington 2007). A combination of differently-timed mowing treatments may also effectively increase diversity by promoting plants with different flowering phenologies (Antonsen and Olsson 2005). However, increases in weedy (or ruderal) species are likely to contribute heavily to increased species richness following disturbance since they are, by definition, the first colonizers of newly disturbed sites. These results suggest that diversity metrics may be a poor indicator of mowing effects, particularly in highly disturbed or newly established sites.

INFLUENCE OF MOWING FREQUENCY

Increased frequency of mowing within a growing season can have greater impacts on plants than a single mowing. Repeated summer mowing can be especially damaging for native C_4 grasses, particularly for biomass production. For example, Aldous (1930) observed a decrease in end-of-season biomass yield of *A. gerardii* and *S. scoparium* that became more apparent as clipping frequency increased. Similarly, Wallace (1987) showed that *S. scoparium* clipped every 6 weeks produced less end-of-season aboveground biomass than un-clipped controls, though total biomass production was not calculated. In some cases, native grasses were unaffected by single mowing treatments, but were affected by repeated mowing. Two or more mows reduced biomass and tiller numbers of *S. scoparium* (N'Guessan and Hartnett 2011). In the same study, three or more mows reduced the ratio of flowering to vegetative tillers. In a Kansas big bluestem stand, additional clipping treatments reduced tiller numbers of *A. gerardii*, but did not further affect biomass production (Owensby et al. 1974).

In addition, frequent clipping may promote the establishment of forbs that are seeded into prairie restorations. For example, Williams (2007) found that seedling numbers were greater, and forbs were taller, in plots mowed every 1-2 weeks. This is likely because frequent mowing reduces competitive pressure from tall plants, such as grasses. However, seedlings in mowed plots also experienced greater over-winter mortality (Williams et al. 2007), possibly because less grass litter was present to insulate seedlings during the winter. Both Benzel et al. (2009) and Rinella et al. (2001) tested multiple mowing frequencies and found that repeated mowing has little additional impact on invasive spotted knapweed (*Centaurea stoebe* L.) compared to single mowing treatments. Both studies suggest that timing of treatments is most important for control of this species, and repeated mowing is unnecessary as long as inflorescences are removed before seeds are produced. Since plants have already invested the bulk of their energy and nutrient reserves into inflorescences, they are typically unable to regenerate lost biomass near the end of the growing season (Colin Phillippo, pers. obs.).

Need for research

Previous research on the effects of mowing in prairies has primarily focused on individual dominant species. However, mowing either directly or indirectly affects all plants in a community. Some studies have addressed the effects of mowing on the entire plant community, but did so using richness and diversity metrics, which treat all species equally. This approach neglects differences between species types, such as their desirability in restored prairies. There is need for more research that both assesses whole community responses to mowing and examines the consequences for each individual species.

Chapter 2

Effectiveness of Summer Mowing for Weed Control in Plantings of Native C_4 Prairie Grasses

Introduction

In the North American Midwest, native prairie communities add conservation and agronomic value to the landscape. For example, native prairie plants benefit adjacent agricultural fields by providing habitat for crop pollinators and arthropod natural enemies of crop pests (Fiedler and Landis 2007, Isaacs et al. 2009, Kremen et al. 2004, Olson and Wackers 2007). The restoration and re-creation of prairies is a top priority for conservation organizations throughout the U.S. because of their ecological and economic importance (The Nature Conservancy 2011). In addition, prairie restoration is of increasing importance as natural ecosystems are currently being considered to help meet demands for bioenergy. Prairie communities recently have shown considerable potential as biofuel crops (Palmer 2006, Tilman et al. 2006). However, there is much concern that biofuel crops will compete for land with traditional agricultural food crops. This concern could be lessened if prairies and other ecosystems could provide provisioning services such as plant biomass for biofuel production, while continuing to support wildlife populations and ecosystem services important to agricultural and urban areas. To achieve these economic and conservation goals simultaneously, diverse native plant communities are needed.

Establishment and persistence of such diverse native plant communities faces multiple challenges, particularly from invasive plant species. Invasive species, defined as non-native species that cause economic or environmental harm (NISIC 2011), are currently one of the primary threats to ecosystem structure and function (Millenium Ecosystem Assessment 2005, Rowe 2010). “Weeds,” defined more generally as plant species growing where they are unwanted and targeted for control (Blumenthal et al. 2003, Bryson and DeFelice 2010), refers to many different types of plants, including invasives. Weeds can be either native or introduced, and represent a wide range of life histories (Sutherland 2004) and taxonomic groups (Daehler 1998). Some native weeds may even provide food or habitat to animals, but generally spread aggressively and exclude other plants (Larson 2002). Weed species may cause economic losses in agricultural fields, decrease floristic diversity in native ecosystems, or threaten wildlife populations by displacing plant species that provide food or shelter (Bryson and DeFelice 2010, Randall 1996). Many weeds thrive in highly disturbed, low quality sites, and can rapidly invade newly disturbed sites (Larson et al. 2001). Often, the goal in weed management is to simply reduce the dominance and spread of weedy species (Rowe 2010), given that complete eradication is often nearly impossible to achieve, and may in fact be undesirable for some species that provide wildlife benefits at low densities.

Prairies are disturbance-adapted ecosystems in which community structure and plant diversity were historically maintained by a combination of grazing by large ungulates (Knapp et al. 1999), burrowing by small mammals (Gibson 1989), and landscape-scale wildfires (Higgins 1984, Packard and Mutel 1997). Fires included both i) fires deliberately set by Native Americans in spring (Packard and Mutel 1997) and ii) lightning-ignited fires that burned in summer (Higgins 1984, Howe 1994a). Since Europeans settled North America, large ungulate herds have been almost entirely extirpated (Knapp et al. 1999), and landscape fragmentation and fire suppression have significantly altered natural fire regimes (Cleland et al. 2004). Without historical patterns of burning and grazing, many prairie remnants have been infiltrated by woody species and aggressive non-native plant species (O'Connor et al. 2009).

Prairie managers sometimes attempt to re-establish historical patterns of natural disturbance, which can stimulate growth of native species while suppressing growth and proliferation of non-natives (Collins et al. 1998, Higgins 1984, Howe 1994b). One common tool is prescribed fire, which is most often applied once per year when plants are dormant or just beginning summer growth (Diboll 1986). In the absence of summer disturbance, plant community composition can shift toward dominance of summer-flowering weeds, which are unlikely to be suppressed by spring disturbances. Multiple studies have shown that effective control of undesirable plant species requires treatment timing that corresponds to flowering phenology of target plants (Benefield et al. 2001, Benzel et al. 2009, Wilson and Clark 2001). In many areas, burning is either not possible or not practical due to weather and seasonal constraints, and mowing is often used in its place.

Restoration practitioners generally view mowing as a more flexible technique that is not weather-dependent, and that can be utilized during the summer when burning is often not possible (Rowe 2010). Mowing can also be used to achieve alternative management goals such as hay production (Foster et al. 2009). For example, end-of-season biomass harvests have long been used to harvest hay in diverse Kansas prairies (Kindscher 2008) and could also be used to harvest biofuel crops. Mid-season mowing may be an effective strategy to control summer-flowering weeds, and could be congruent with biomass harvesting goals.

Despite its frequent use in prairie management, the effects of mowing on plant communities have not been well studied. Most previous research has focused on the influence of mowing on growth and reproduction of dominant species (e.g., Howe 1999, Vogel and Bjugstad 1968), and it has not addressed mowing effects on sub-dominants or on the plant community as a whole. However, mowing affects all plant species in a community, either directly by removing biomass or indirectly by increasing light availability (MacDougall and Turkington 2007). In the studies that have been done, some positive effects of mowing on desirable native species have been observed, such as increased population size of the May-flowering golden zizia (*Zizia aurea* (L.) W.D.J. Koch) (Howe 1999), and enhanced establishment of native forbs from seed (Williams et al. 2007). However, the size of individual native C_4 grasses, *Andropogon gerardii* Vitman (Owensby et al. 1974, Vogel and Bjugstad 1968) and *Schizachyrium scoparium* Michx. (Vogel and Bjugstad 1968, Wallace 1987), is reduced by mowing or clipping during the growing season. Additionally, increased mowing frequency within a growing season can have greater negative effects on plants, especially dominant C_4 grasses. (Owensby et al. 1974)

Mowing has had largely negative impacts on most weed species (e.g., Benzel et al. 2009, Diboll 1986, Rinella et al. 2001, Wilson and Clark 2001), but can increase biomass of the non-native weedy forb, white sweet-clover (*Melilotus albus* Medik.) (Randa and Yunger 2001). Effects also vary with mowing timing; in fact, multiple studies suggest that timing may be more important than treatment type (i.e., mowing, burning, or grazing) in determining influence on the plant community (Hover and Bragg 1981, Howe 1994b, MacDougall and Turkington 2007).

Some mowing experiments have addressed the entire plant community, but have focused mostly on richness and diversity metrics that treat both desirable natives and noxious weeds equally. In general, mowing increases species richness (Antonsen and Olsson 2005, Fynn et al. 2004, MacDougall and Turkington 2007) and diversity (Antonsen and Olsson 2005), or preserves diversity when added to a burning and fertilization regime, which reduces diversity when implemented without mowing (Collins et al. 1998). However, such observed increases in diversity may result from increased abundance of weedy species, not from recruitment of natives. In one study that grouped plants by growth form and native status, mowing stimulated growth of native species (Gonzales and Clements 2010). However, these groupings did not acknowledge that both desirable and weedy species may have the same growth form, and that many native plants are also weedy, so increased growth of native species could represent increased native weed growth. No previous study has investigated mowing effects on the entire plant community while addressing the value of individual species in tallgrass prairie. Additionally, only a small number of mowing studies have been conducted in the North American Midwest (most of those in Kansas). To address these deficiencies, I have grouped species occurring in this Michigan prairie restoration experiment based on their potential negative effects in natural and human-managed landscapes.

Species composition in prairies is also influenced by soil type, largely due to soil moisture and nutrient content differences (Weaver 1968), and plant communities on different soil types likely respond differently to mowing. This is particularly important since marginal lands are being considered for biofuels production (Hill et al. 2006), which would reduce pressure on food crops. However, plant responses to management treatments such as mowing on marginal lands will likely differ from responses on more productive land, though the nature of these responses is currently not well understood.

The following research investigated the effects of summer mowing on summer-flowering weeds, naturally colonizing native plants, and two dominant warm-season prairie grasses, big bluestem (*A. gerardii*) and little bluestem (*S. scoparium* Michx.), in experimental prairies established on both loamy and sandy soil. Two mowing regimes intended to control summer-flowering weeds in the Midwest (Kindscher 2008, Randa and Yunger 2001, Sargent and Carter 2001) were used: i) mowing in late June, when many summer-flowering weeds were producing inflorescences, and ii) mowing in both late June and late July, when both weeds and native grasses were flowering. The following questions were addressed in this research: 1) Does summer mowing control weeds? 2) How does summer mowing affect desirable native species? and 3) Is there any benefit from mowing twice within a growing season? I hypothesized that: 1) summer mowing a) suppresses growth and reproduction of summer-flowering weeds, and b) reduces size and seed production of mature native C_4 grasses; and that 2) repeated mowing within a growing season will cause greater size reductions of desirable plant species.

Methods

SITE DESCRIPTIONS AND LAND USE HISTORY

This study was conducted from May 2009 (Yr 1) to October 2010 (Yr 2) at two locations in Ingham County, Michigan: i) Michigan State University's Horticulture Teaching and Research Center in East Lansing, MI, and ii) Wildtype Native Plant Nursery in Mason, MI, approximately 11 km southeast of the East Lansing location (Fig. 1). Each site contained both sandy and loamy soil plots: one sandy plot at each site, two loamy plots at East Lansing, and one in Mason (Fig. 2a, b). The East Lansing sandy plot contained excavated fill (loamy sand), and the Mason sandy plot was established on Lamellic hapludalf (Alfisol) (Schrotenboer et al., in prep.). Soils in all loamy plots were Aquic glossudalf (Alfisol) (Schrotenboer et al., in prep.). Mason plots were planted in a corn-soybean-wheat rotation until prairie grass establishment in 2006, and were adjacent to corn in Yr 1 and soybeans in Yr 2. In East Lansing, past cultivation of the loamy plots varied annually due to research center use, and the sandy plot was never cultivated. East Lansing plots were adjacent to various agricultural research crops. Average growing season temperature in this region is 18.75°C and cumulative annual precipitation is 69.95 cm/yr. In Yr

1, average growing season temperature was 18.14°C and cumulative annual precipitation was 86.28 cm/yr. In Yr 2, average growing season temperature was 20.21°C and cumulative annual precipitation was 63.83 cm/yr (Enviro-weather 2011).

Plots were initially established in June 2006 as a common garden experiment to assess the influence of cultivation and local adaptation on native plant performance. Six varieties of *A. gerardii* and five varieties of *S. scoparium* were planted to represent the range of seed sources commonly used in Michigan prairie restorations (wild-Michigan, cultivated-Michigan and cultivated-non-local populations) (Schrotenboer et al., in prep.). In summer of Yr 1, 1,035 of the original 1,128 plants remained. All surviving *A. gerardii* and *S. scoparium* plants were in their fourth growing season when mowing treatments were first applied. In summer of Yr 2, I measured only *A. gerardii*; 607 of the original 616 plants remained.

All plots contained 19 blocks (2 m x 7 m each), except the East Lansing sandy plot, which contained 18 (Fig. 3). Within each block, 12 individual grass plants were planted: one each of the 11 varieties and a 12th randomly selected from among them. We harvested *A. gerardii* plants annually in October 2006 through 2010. *S. scoparium* plants were harvested in October of 2007 and 2009. Mowing treatments were applied in 2009 and 2010, so only data from these years is presented in this paper. In spring of Yr 1, I established one quadrat in the center of each block (0.5 m x 1 m) to monitor colonizing species. Flags marked the corner of each quadrat to ensure consistent sampling of the same quadrats between sampling periods and years.

Prior to this mowing experiment, all weeds within blocks were removed by hand and spot-treated with glyphosate as needed from spring 2006 until spring 2009. Weeding ceased at the end of May 2009 to allow time for summer-flowering weed establishment. No weeds were removed or treated with glyphosate in 2010.

CATEGORIZATION OF COLONIZING PLANTS

All plant species were categorized into one of three groups for analysis: desirable native species, Michigan-listed noxious species (all but one exotic; hereafter referred to as MI-noxious), and nuisance species (native and exotic). Scientific names follow the Michigan Flora Online (Reznicek et al. 2011). Desirable species included three native grasses (*A. gerardii, S. scoparium* and *Poa alsodes* A. Gray) and three native forbs (*Coreopsis lanceolata* L., *Epilobium coloratum* Biehler, and *Symphyotrichum lanceolatum* (Willd.) G.L. Nesom). Species were placed in the MI-noxious category if they appeared on the Michigan Department of Agriculture Prohibited and Restricted Weeds list (Pesticide and Plant Pest Management Division 2002). These plants are regulated under Michigan state law because they have the potential to cause significant economic losses or cause environmental problems.

Plants were categorized as nuisance species if they appeared in common weed keys for the Midwest (Bryson and DeFelice 2010, Uva et al. 1997), excluding those also listed as prohibited and restricted weeds. In addition, I included the one woody species encountered, *Acer rubrum* L. because it is not a prairie species. Plants in the nuisance species category are not regulated by state law, but are often problematic. Many of these species are common in disturbed areas, on waste ground, or in agricultural fields. Some native species encountered (e.g. *Solidago canadensis* L.) are regarded as weeds because they reproduce aggressively and have a tendency to become excessively abundant in a site. For these species, the goal of management is not to eradicate them completely, but to reduce their dominance.

MOWING TREATMENT DESCRIPTIONS

Treatments consisted of 1) a no-mowing control, 2) June mowing, and 3) June and July mowing (n = 6–7 blocks/treatment/site). Blocks were randomly assigned to each mowing treatment and mowed to 15–20 cm above ground level using a Stihl FS90 trimmer with a 'steel brush knife' blade (Stihl Inc., Waiblingen, Germany). In Yr 1, mowed material was left on the ground. In Yr 2, mowed *A. gerardii* material in the Mason plots was collected immediately following mowing and weighed to assess total seasonal biomass production; biomass of *S. scoparium* and weeds was left on the ground. Blocks were randomly assigned to each treatment and mowed on June 24 only, or June 24 and July 22 in Yr 1. Mowing was repeated in Yr 2 on June 28 only, or June 28 and July 26, depending on treatment.

GROWTH OF COLONIZERS

To monitor how mowing influenced the growth and phenology of colonizing plants, I placed a removable 1 m x 0.5 m sampling quadrat in each block between rows of mature grasses. Percent cover of each species present was measured in quadrats in August of both years. Seedlings of all plants in quadrats were counted in May of Yr 2, except seedlings of low-profile species (e.g. *Trifolium* spp.), which could not be counted. For these species, percent cover was measured instead. All colonizing plants were identified to species level when possible, and classified as described above. Plant biomass was harvested from quadrats at the Mason site in late August of Yr 2.

COMMUNITY SEED PRODUCTION

To assess the impact of mowing on seed deposition, seed traps were installed in each block at the Mason plots in July of Yr 2. Traps consisted of a PVC pipe placed in the ground (1-

2 cm above soil surface), with a 10.8 cm diameter funnel placed on top, and a mesh bag attached to the bottom of the funnel. Trap bags were exchanged every other week, July to October. All seeds were identified to species level when possible. Seeds of several species from the family Asteraceae could not be distinguished and were grouped.

GROWTH AND FLOWERING OF MATURE GRASSES

I measured the growth of *A. gerardii* in Yrs 1–2, and that of *S. scoparium* in Yr 1. Height of the tallest tiller and basal area of each plant were measured in September. For biomass measures, plants were cut at a 15 cm height in October, placed in a paper bag, dried at 70°C for 48-72 h, then weighed (In Yr 2, plants were harvested only from the Mason plots). Grass biomass removed by mowing treatments was also collected in Yr 2 and similarly processed.

Number of inflorescences was counted on two varieties of *A. gerardii* on sandy and loamy soils in Mason (40 individuals each) in late September of Yr 1. Number of flowering tillers (all varieties) was counted in September of Yr 2 at both Mason plots.

STATISTICAL ANALYSIS

Data were analyzed as a randomized complete block design using analysis of variance in PROC MIXED (SAS Institute, 2009). Statistical models for colonizer percent cover and seedling counts included the fixed effects of mowing treatment, soil, and site, and the random effect of block (nested in site*soil). Analysis of mature grass growth included fixed effects of mowing treatment, population type, soil, and site (East Lansing or Mason), and random effects of block (nested in site*soil) and population (nested in population type). *A. gerardii* and *S. scoparium* were analyzed using separate ANOVAs. *A. gerardii* basal area and colonizer percent cover were analyzed using repeated measures ANOVA to assess differences between years;

components of these models were as described above. Native grass flowering models included mowing treatment, population type, and soil as fixed effects, with block (nested in soil) and population (nested in population type) as random effects. Models of community seed production included mow and soil as fixed effects and block (nested in soil) as a random effect. Plots were analyzed separately when the mowing treatment*soil interaction was significant. Two pre-planned contrasts were used in each analysis: mowing vs. no mowing, and June vs. June and July mowing. When the main effect of mowing is significant, results of contrasts are presented. Significance was at the $\alpha = 0.05$ level for all tests. Results were considered marginally significant if $\alpha \leq 0.1$. Square-root and log transformations were used when necessary to meet the assumptions of normality.

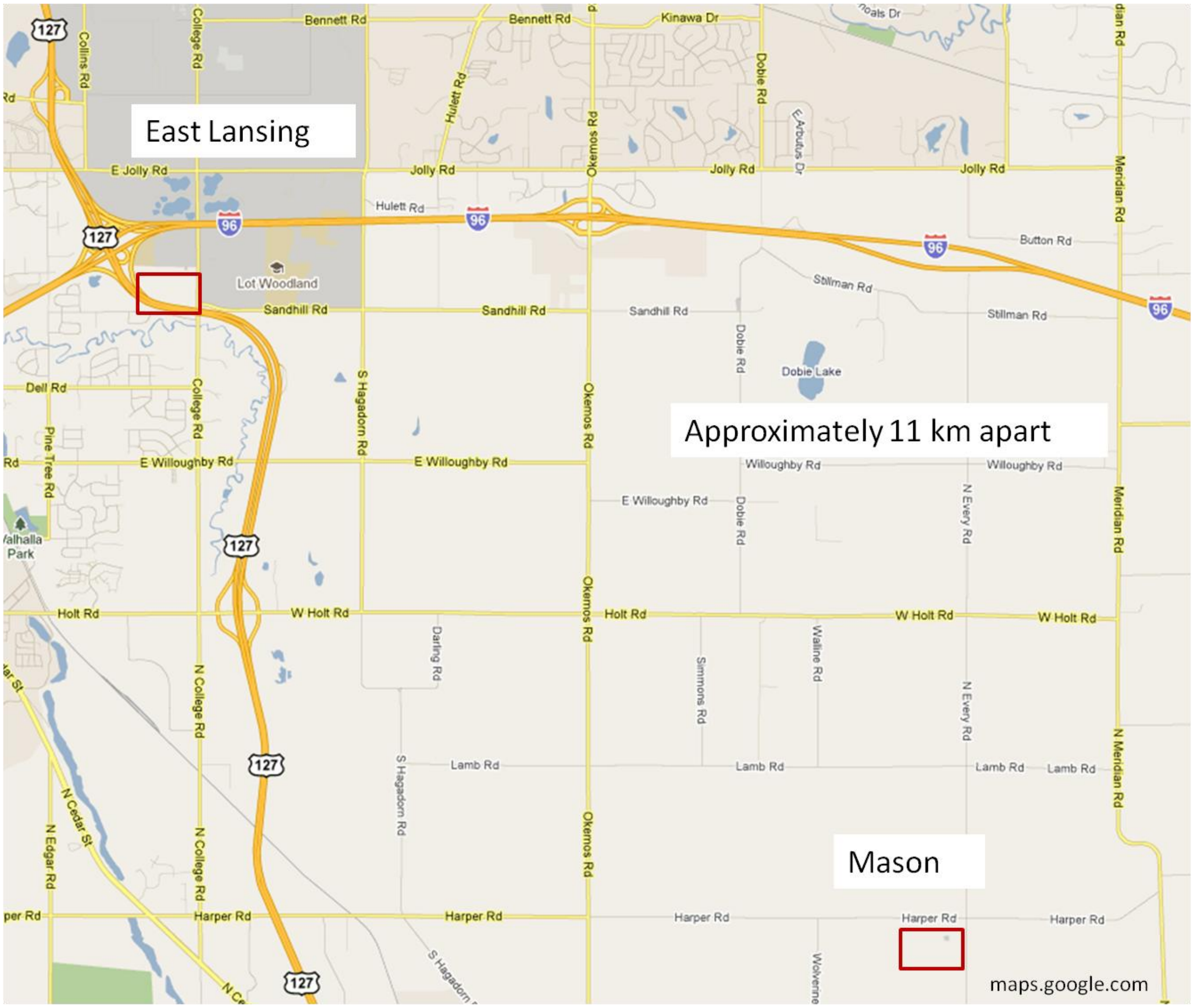


Figure 1. Sites in Ingham County, Michigan. East Lansing and Mason sites are approximately 11 km apart. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

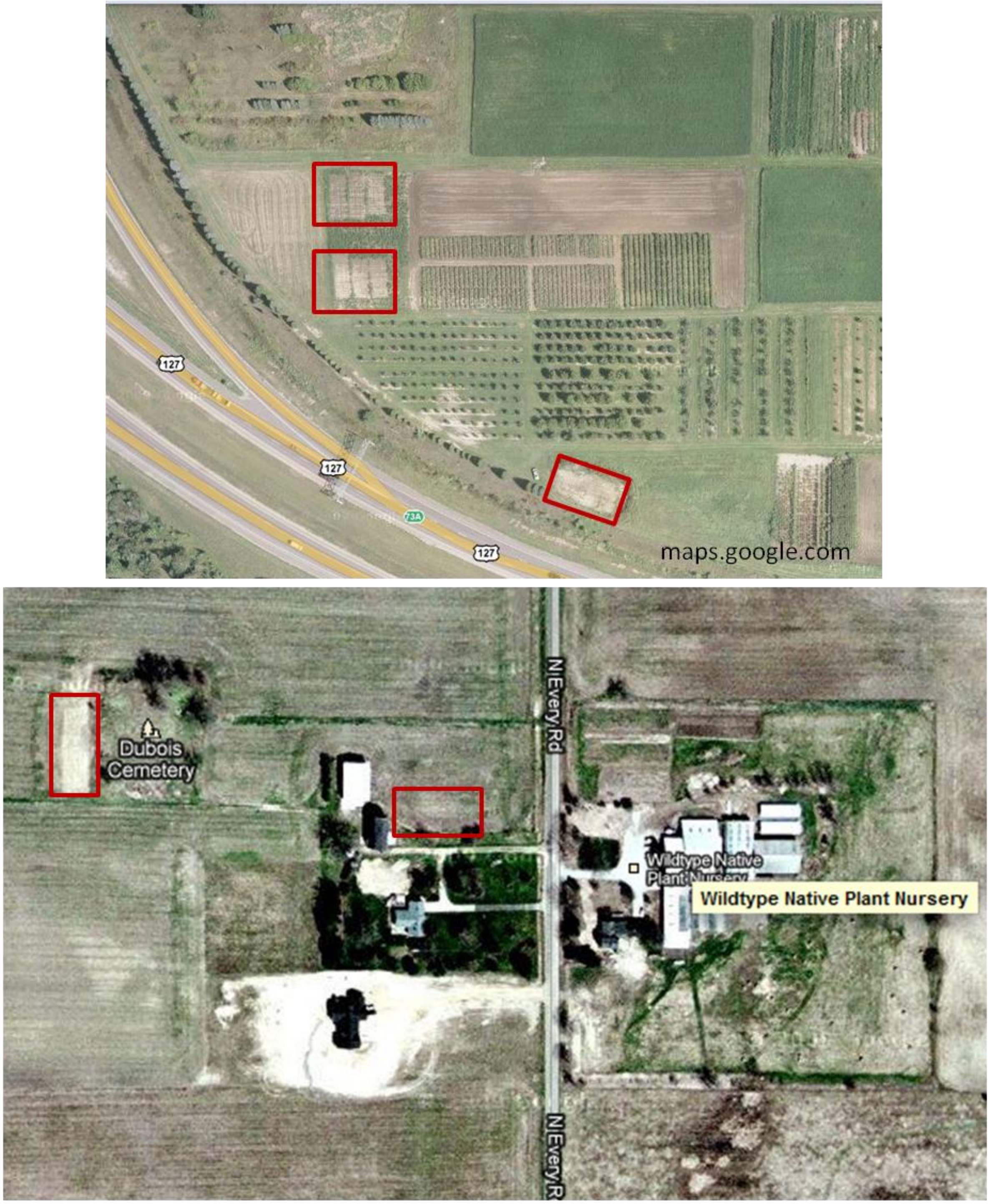


Figure 2. Plot placement at each site: a) East Lansing, and b) Mason.

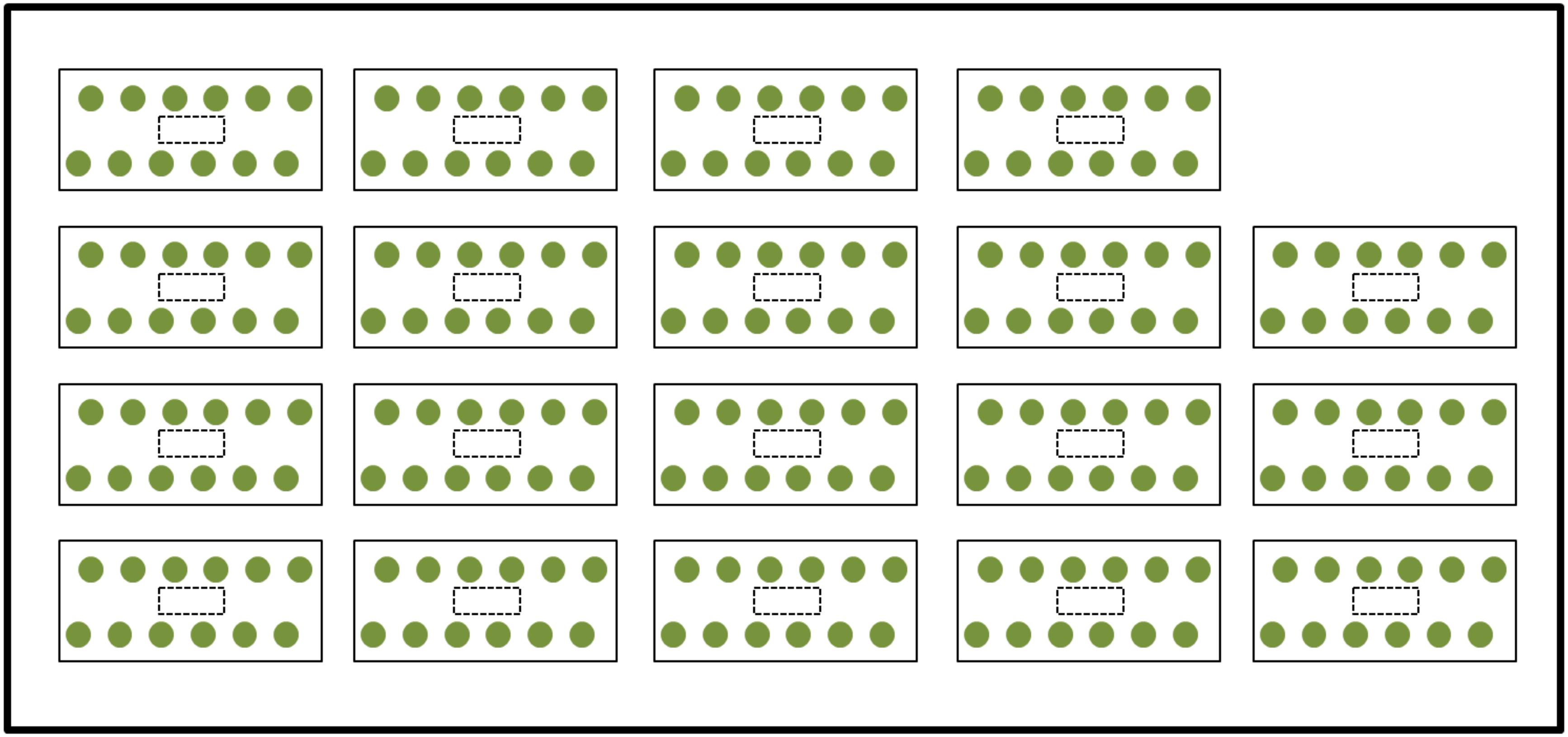


Figure 3. Representative plot layout containing 19 blocks. Outer border represents plot boundaries. Solid circles are mature native grass plant individuals, dashed rectangles are colonizer monitoring quadrats, and solid rectangles are block boundaries.

Results

COLONIZING SPECIES

After weed control efforts ceased (spring of Yr 1), colonizers invaded all mowed and unmowed blocks. Seventy-three colonizing plant species were present in the study plots (Table 1). Of these, 67 were categorized as weeds (13 MI-noxious species, 54 nuisance species), and six as desirable natives. Four species could not be identified and were excluded from subsequent analysis. Colonizer species richness was greater on loamy plots (36–40 species) than on sandy plots (23–30 species). Here, I present the effects of mowing on these key categories of colonizing plants; mowing effects on individual species are listed in Table 2.

MOWING EFFECTS ON WEEDS

Between Yr 1 and Yr 2, percent cover of MI-noxious species nearly tripled ($F_{1, 91} = 17.42$, $p < 0.0001$), though it remained the least abundant plant category. In Yr 1, MI-noxious species constituted only 10% of total plant community cover (Fig. 4a). In Yr 2, this group constituted 16% of total cover (Fig. 4b), 6% of total seedlings (Fig. 4c), and 4% of total seed production (Fig. 4d). Mowing did not alter percent cover of MI-noxious species in Yr 1 or Yr 2 ($F_{2, 82} = 0.32$, $p = 0.7257$), although there was some suggestion in Yr 2 that mowing might decrease cover with time (Fig. 5a). Mowing also did not influence May seedling counts of MI-noxious species ($F_{2, 82} = 0.47$, $p = 0.6253$) (Fig. 6a), though plants had been mowed only once at this point, or their seed production ($F_{2, 32} = 1.39$, $p = 0.2646$) (Fig. 7a).

Between Yr 1 and Yr 2, percent cover of nuisance species decreased by 10% ($F_{1, 91}$ = 33.03, $p < 0.0001$), and this category was consistently the largest portion of the plant community. In Yr 1, they constituted 88% of total plant community cover (Fig. 4a). In Yr 2 they constituted 53% of total cover (Fig. 4b), 59% of total seedlings (Fig. 4c), and 73% of total seed production (Fig. 4d). Mowing marginally increased cover of nuisance species by about 25% in Yr 1 ($F_{1, 167}$ = 3.74, $p = 0.0547$) and by 35% in Yr 2, relative to controls ($F_{1,167}$ = 5.61, $p = 0.019$), but once-mowed and twice-mowed plants did not respond differently (Yr 1 $F_{1, 167}$ = 0.23, $p = 0.6348$; Yr 2 $F_{1, 167}$ = 0.18, $p = 0.6714$) (Fig. 5b). Mowing did not influence seedling counts of nuisance species ($F_{2, 81.8}$ = 0.57, $p = 0.5697$) (Fig. 6a), or percent cover of low-profile nuisance species ($F_{2, 66}$ = 0.59, $p = 0.5591$) (Fig 6b).

There was a significant interaction between mowing treatment and soil (which was unreplicated) ($F_{2, 32}$ = 3.24, $p = 0.0521$), so I analyzed data from each soil type independently. In the loamy soil plot, mowing reduced nuisance species seed production by about 80% ($F_{1, 16}$ = 16.78, $p = 0.0008$), with both mowing treatments having similar effects ($F_{1, 16}$ = 0.02, $p = 0.8848$) (Fig. 7c). In contrast, mowing did not alter seed production in the sandy soil plot ($F_{2, 16}$ = 0.07, $p = 0.9305$) (Fig. 7c). In both plots, Asteraceae species accounted for nearly all seed production: 85% of nuisance seeds in the loamy plot and 89% of nuisance seeds in the sandy plot. These seeds could not be positively identified to species, but only one Asteraceae species was abundant in percent cover measurements from each plot. In the loamy plot, *Solidago* *canadensis* constituted 52% of August nuisance species cover, while *Erigeron annuus* (L.) Pers. constituted only 1%. In the sandy plot, *Conyza Canadensis* (L.) Cronq. constituted 5% of nuisance species cover.

Mowing decreased colonizer biomass (excluding native C_4 grasses) in the loamy plot by 53% ($F_{1, 16} = 23.72$, $p = 0.0002$), which was similar for both mowing treatments ($F_{1, 16} = 0.01$, $p = 0.9099$), but had no effect on biomass in the sandy plot ($F_{2, 16} = 1.64$, $p = 0.2256$) (Fig 8a). The colonizer biomass was primarily composed of weeds, since desirable natives (excluding native C_4 grasses) comprised only 6% of total percent cover in these plots.

MOWING EFFECTS ON DESIRABLE NATIVES

Desirable native colonizer cover increased 23-fold between Yr 1 and Yr 2 ($F_{1, 91} = 269.27$, $p = p < 0.0001$); the native cover increase was mostly *A. gerardii* in loamy plots, and mostly *S. scoparium* in sandy plots. Basal area of the mature *A. gerardii*, which were three and four years old, increased by 28% during the same period ($F_{1, 603} = 420.28$, $p < 0.0001$), but height and end-of-season biomass did not change. Desirable native colonizers were the smallest component of the plant community in Yr 1 (2% of total plant community cover) (Fig. 4a), but were more abundant than MI-noxious species in Yr 2 (31% of total cover, 35% of total seedlings, and 23% of total seed production) (Fig. 4b, c, d). Mowing increased percent cover of desirable native species ($F_{2, 82} = 3.13$, $p = 0.0490$) (Fig. 5c), but only the June vs. JuneJuly contrast in Yr 2 was marginally significant ($F_{1, 171} = 2.81$, $p = 0.0953$). May seedling counts tended to be greater in mowed blocks, but differences were not significant ($F_{2, 81.7} = 0.22$, $p = 0.8015$) (Fig.

6a). Mowing decreased desirable native seed production by 61–76% ($F_{1, 32} = 34.03$, $p < 0.0001$) (Fig. 7c). Twice-mowed blocks were not significantly different from once-mowed blocks ($F_{1, 32} = 1.19$, $p = 0.2828$). Biomass of colonizing native C_4 grasses increased by 55–247% in mowed blocks ($F_{1, 32} = 5.3$, $p = 0.0280$) and blocks mowed twice contained 55% less biomass than blocks mowed once ($F_{1, 32} = 5.61$, $p = 0.0241$) (Fig. 8b).

In mature *A. gerardii*, mowing reduced height by 12–25% in Yr 1 ($F_{1, 81.1} = 125.51$, $p < 0.0001$) and by 17–34% in Yr 2 ($F_{1, 107} = 547.22$, $p < 0.0001$) (Fig. 9a). In *S. scoparium* (only measured in Yr 1), mowing reduced end-of-season height by 7–17% ($F_{1, 75.1} = 35.23$, $p < 0.0001$) (Fig. 9a). Grasses mowed twice in a season were shorter at the end of the season than those mowed only once. Twice-mowed *A. gerardii* was 15% shorter than once-mowed plants in Yr 1 ($F_{1, 87.4} = 47.03$, $p < 0.0001$), and 21% shorter in Yr 2 ($F_{1, 134} = 189.45$, $p < 0.0001$). Twice-mowed *S scoparium* was 11% shorter in Yr 1 than once-mowed plants ($F_{1, 78.4} = 20.63$, $p < 0.0001$).

Mowing reduced the basal area of mature *A. gerardii* by 14–15% in Yr 1 ($F_{1, 103} = 15.69$, $p = 0.0001$) and 9–21% in Yr 2 ($F_{1, 103} = 26.45$, $p < 0.0001$) (Fig. 9b). The second mowing treatment had no effect on basal area in Yr 1 ($F_{1, 112} =0.01$, $p =0.9153$), but reduced it by an additional 13% in Yr 2 ($F_{1, 112} = 8.7$, $p = 0.0039$). *S. scoparium* basal area was not altered by mowing ($F_{2, 86.3} = 1.63$, $p = 0.2023$) (Fig. 9b).

In Yr 1, mowing substantially reduced end-of-season biomass of mature *A. gerardii* by 56–83% ($F_{1,\ 80.7} = 500.21$, $p < 0.0001$), and that of *S. scoparium* by 47–67% in Yr 1 ($F_{1,\ 78.5} = 97.81$, $p < 0.0001$) (Fig. 9c). The second mowing decreased *A. gerardii* biomass by an additional 62% ($F_{1,\ 88.5} = 104.63$, $p < 0.0001$) and *S. scoparium* biomass by 37% ($F_{1,\ 79.7} = 15.81$, $p < 0.0001$). In Yr 2, total harvested biomass of *A. gerardii* in mowed blocks, which included both biomass removed by mowing and residual biomass remaining in October, was 15–50% lower than in control blocks ($F_{1,\ 31.7} = 30.97$, $p < 0.0001$), and was 40% lower in twice-mowed blocks than in once-mowed blocks ($F_{1,\ 32.3} = 15.77$, $p = 0.0004$) (Fig. 9c).

Mowing reduced inflorescences and flowering tillers in mature *A. gerardii*, and these mowing effects were greater for twice-mowed plants than for once-mowed plants. Plants in mowed blocks had 51–87% fewer inflorescences at the end of Yr 1 ($F_{1,\ 33.4} = 73.64$, $p < 0.0001$) (Fig. 10a) and 38–77% fewer flowering tillers in Yr 2 ($F_{1,\ 32.4} = 106.93$, $p <0.0001$) (Fig. 10b). The second mowing event decreased inflorescence counts in Yr 1 by an additional 74% ($F_{1,\ 33.6} = 21.33$, $p < 0.0001$), and reduced flowering tillers in Yr 2 by an additional 64% ($F_{1,\ 32.3} = 56.7$, $p < 0.0001$). Reductions in flowering tillers appeared to be correlated to reductions in vegetative tillers (Colin Phillippo, pers. obs.).

MOWING RESPONSE DIFFERENCES BETWEEN SOIL TYPES

Plant responses to mowing treatments differed between soil types for some measurements. End-of-season biomass of both *A. gerardii* ($F_{2,\ 84.4} = 8.39$, $p = 0.0005$) and *S.*

scoparium ($F_{2, 78}$ = 5.01, p = 0.0090) in Yr 1 was more reduced by mowing in sandy plots than in loamy plots. In contrast, Yr 2 *A. gerardii* height ($F_{2, 101}$ = 7.12, p = 0.0013), total *A. gerardii* biomass ($F_{2, 32}$ = 9.35, p = 0.0006), and colonizer biomass (excluding native C_4 grasses) ($F_{2, 32}$ = 4.87, p = 0.0143) were reduced more by mowing in loamy soil plots than in sandy soil plots.

Table 1. Plant species found in study plots. Each species was categorized as either a Michigan-listed noxious species (MI-noxious), a nuisance species, or a desirable native. All species names follow Reznicek et al. (2011).

Category	Scientific name	Common name	Native Status	Duration
MI-noxious species	*Abutilon theophrasti* Medik.	Velvet-leaf	Introduced	Annual
	Berteroa incana (L.) DC.	Hoary alyssum	Introduced	Ann./bienn./per.
	Centaurea stoebe subsp. micranthos (Gugler) Hayek	Spotted knapweed	Introduced	Biennial/per.
	Cirsium arvense (L.) Scop.	Canada thistle	Introduced	Perennial
	Cirsium vulgare (Savi) Ten.	Bull thistle	Introduced	Biennial
	Convolvulus arvensis L.	Field bindweed	Introduced	Perennial
	Daucus carota L.	Queen Anne's lace	Introduced	Biennial
	Elymus repens (L.) Gould	Quack grass	Introduced	Perennial
	Plantago lanceolata L.	Narrow-leaved plantain	Introduced	Ann./bienn./per.
	Rumex crispus L.	Curly dock	Introduced	Perennial
	Sinapis arvensis L.	Wild mustard	Introduced	Annual
	Solanum ptychanthum Dunal	Black nightshade	Native	Annual
	Sonchus arvensis L.	Field sow-thistle	Introduced	Perennial
Nuisance species	*Acer rubrum* L.	Red maple	Native	Perennial
	Achillea millefolium L.	Yarrow	Native/introduced	Perennial
	Amaranthus retroflexus L.	Rough amaranth	Native	Annual
	Ambrosia artemisiifolia L.	Common ragweed	Native	Annual
	Anagallis arvensis L.	Scarlet pimpernel	Introduced	Annual/biennial
	Arenaria serpyllifolia L.	Thyme-leaf sandwort	Introduced	Annual
	Asclepias syriaca L.	Common milkweed	Native	Perennial
	Bidens frondosa L.	Common beggar-ticks	Native	Annual
	Bromus secalinus L.	Cheat	Introduced	Annual
	Bromus tectorum L.	Cheat grass	Introduced	Annual
	Carex vulpinoidea Michx.	Sedge	Native	Perennial

(**Table 1.** continued)

Nuisance species	*Cerastium fontanum* Baumg.	Mouse-ear chickweed	Introduced	Biennial/perennial
	Chenopodium album L.	Lambs-quarters	Native/introduced	Annual
	Cichorium intybus L.	Chicory	Introduced	Biennial/perennial
	Conyza canadensis (L.) Cronq.	Horseweed	Native	Annual/biennial
	Crepis tectorum L.	Hawk's beard	Introduced	Annual
	Dactylis glomerata L.	Orchard grass	Introduced	Perennial
	Echinochloa crusgalli (L.) P. Beauv.	Barnyard grass	Introduced	Annual
	Equisetum arvense L.	Common horsetail	Native	Perennial
	Erigeron annuus (L.) Pers.	Daisy fleabane	Native	Annual
	Euphorbia maculata L.	Nodding spurge	Native	Annual
	Fallopia convolvulus (L.) Á. Löve	Black-bindweed	Introduced	Annual
	Geranium maculatum L.	Carolina crane's-bill	Native	Annual/biennial
	Hieracium caespitosum Dumort.	Yellow hawkweed	Introduced	Perennial
	Juncus tenuis Willd.	Path rush	Native	Perennial
	Lactuca serriola L.	Prickly lettuce	Introduced	Annual/biennial
	Lepidium virginicum L.	Common peppergrass	Native	Ann./bienn./per.
	Lolium perenne L.	Ryegrass	Introduced	Perennial/annual
	Medicago lupulina L.	Black medic	Introduced	Annual/perennial
	Mollugo verticillata L.	Carpetweed	Native	Annual
	Oxalis stricta L.	Yellow wood-sorrel	Native	Perennial
	Panicum capillare L.	Witch grass	Native	Annual
	Persicaria maculosa A. Gray	Lady's thumb	Introduced	Annual/perennial
	Phleum pratense L.	Timothy	Introduced	Perennial
	Plantago major L.	Common plantain	Introduced	Perennial
	Poa annua L.	Annual bluegrass	Introduced	Annual
	Polygonum aviculare L.	Knotweed	Introduced	Annual/perennial
	Portulaca oleracea L.	Purslane	Introduced	Annual

(**Table 1.** continued)

Nuisance species	*Potentilla argentea* L.	Silvery cinquefoil	Introduced	Perennial
	Potentilla norvegica L.	Rough cinquefoil	Native	Ann./bienn./per.
	Ranunculus sceleratus L.	Cursed crowfoot	Native	Annual/perennial
	Schedonorus arundinaceus (Schreb.) Dumort.	Tall fescue	Introduced	Perennial
	Setaria viridis (L.) P. Beauv	Green foxtail	Introduced	Annual
	Silene antirrhina L.	Sleepy catchfly	Native	Annual
	Silene latifolia Poir.	White campion	Introduced	Biennial/perennial
	Solidago canadensis L.	Canada goldenrod	Native	Perennial
	Sonchus asper (L.) Hill	Prickly sow-thistle	Introduced	Annual
	Taraxacum officinale F. H. Wigg.	Common dandelion	Introduced	Perennial
	Tragopogon dubius Scop.	Goat's beard	Introduced	Annual/biennial
	Trifolium pratense L.	Red clover	Introduced	Biennial/perennial
	Trifolium repens L.	White clover	Introduced	Perennial
	Urtica dioica L.	Stinging nettle	Native/introduced	Perennial
	Verbascum thapsus L.	Common mullein	Introduced	Biennial
	Veronica arvensis L.	Corn speedwell	Introduced	Annual
Desirable native species	*Andropogon gerardii* Vitman	Big bluestem	Native	Perennial
	Coreopsis lanceolata L.	Sand coreopsis	Native	Perennial
	Epilobium coloratum Biehler	Cinnamon willow-herb	Native	Perennial
	Poa alsodes A. Gray	Bluegrass	Native	Perennial
	Schizachyrium scoparium Michx.	Little bluestem	Native	Perennial
	Symphyotrichum lanceolatum (Willd.) G. L. Nesom	Panicled aster	Native	Perennial

Table 2. Yr 2 responses of seedlings of individual plant species to mowing. The one-mow effect was calculated as the % difference between the response of control plants and that of June-mowed plants. The two-mow effect was calculated as the % difference between the response of control plants and that of plants mowed in June and July. “0” indicates no change in seedling counts. One symbol in either direction (“-“ or “+”) represents a 10–25% change. Two symbols (“--“ or “++”) represents a 25–50% change. Three symbols (“---“ or “+++”) represents a change > 50%.

			Yr 2 seedlings	
Category	Scientific name	Common name	One mow effect	Two mow effect
MI-noxious species	*Berteroa incana* (L.) DC.	Hoary alyssum	---	---
	Cirsium arvense (L.) Scop.	Canada thistle	0	--
	Daucus carota L.	Queen Anne's lace	-	0
	Plantago lanceolata L.	Narrow-leaved plantain	--	+++
	Rumex crispus L.	Curly dock	---	--
	Sonchus arvensis L.	Field sow-thistle	+++	++
Nuisance species	*Ambrosia artemisiifolia* L.	Common ragweed	+++	+++
	Arenaria serpyllifolia L.	Thyme-leaf sandwort	+++	---
	Bromus tectorum L.	Cheat grass	---	--
	Chenopodium album L.	Lambs-quarters	+++	+++
	Conyza canadensis (L.) Cronq.	Horseweed	---	---
	Erigeron annuus (L.) Pers.	Daisy fleabane	--	0
	Geranium carolinianum L.	Carolina crane's-bill	---	--
	Hieracium caespitosum Dumort.	Yellow hawkweed	+++	---
	Juncus tenuis Willd.	Path rush	---	---
	Lactuca serriola L.	Prickly lettuce	+++	-
	Lepidium virginicum L.	Common peppergrass	+++	+++
	Lolium perenne L.	Ryegrass	++	+
	Medicago lupulina L.	Black medic	+++	+++
	Oxalis stricta L.	Yellow wood-sorrel	-	++
	Panicum capillare L.	Witch grass	---	+++
	Schedonorus arundinaceus (Schreb.) Dumort.	Tall fescue	++	-

(**Table 2.** continued)

Nuisance species	*Solidago canadensis* L.	Canada goldenrod	-	++
	Sonchus asper (L.) Hill	Prickly sow-thistle	+++	+++
	Taraxacum officinale F. H. Wigg.	Common dandelion	-	-
	Tragopogon dubius Scop.	Goat's beard	--	++
	Trifolium pratense L.	Red clover	---	++
	Trifolium repens L.	White clover	+++	+++
Desirable species	*Andropogon gerardii* Vitman	Big bluestem	+++	--
	Coreopsis lanceolata L.	Sand coreopsis	0	+++
	Epilobium coloratum Biehler	Cinnamon willow-herb	---	---
	Schizachyrium scoparium Michx.	Little bluestem	+++	+++
	Symphyotrichum lanceolatum (Willd.) G. L. Nesom	Panicled aster	+++	+++

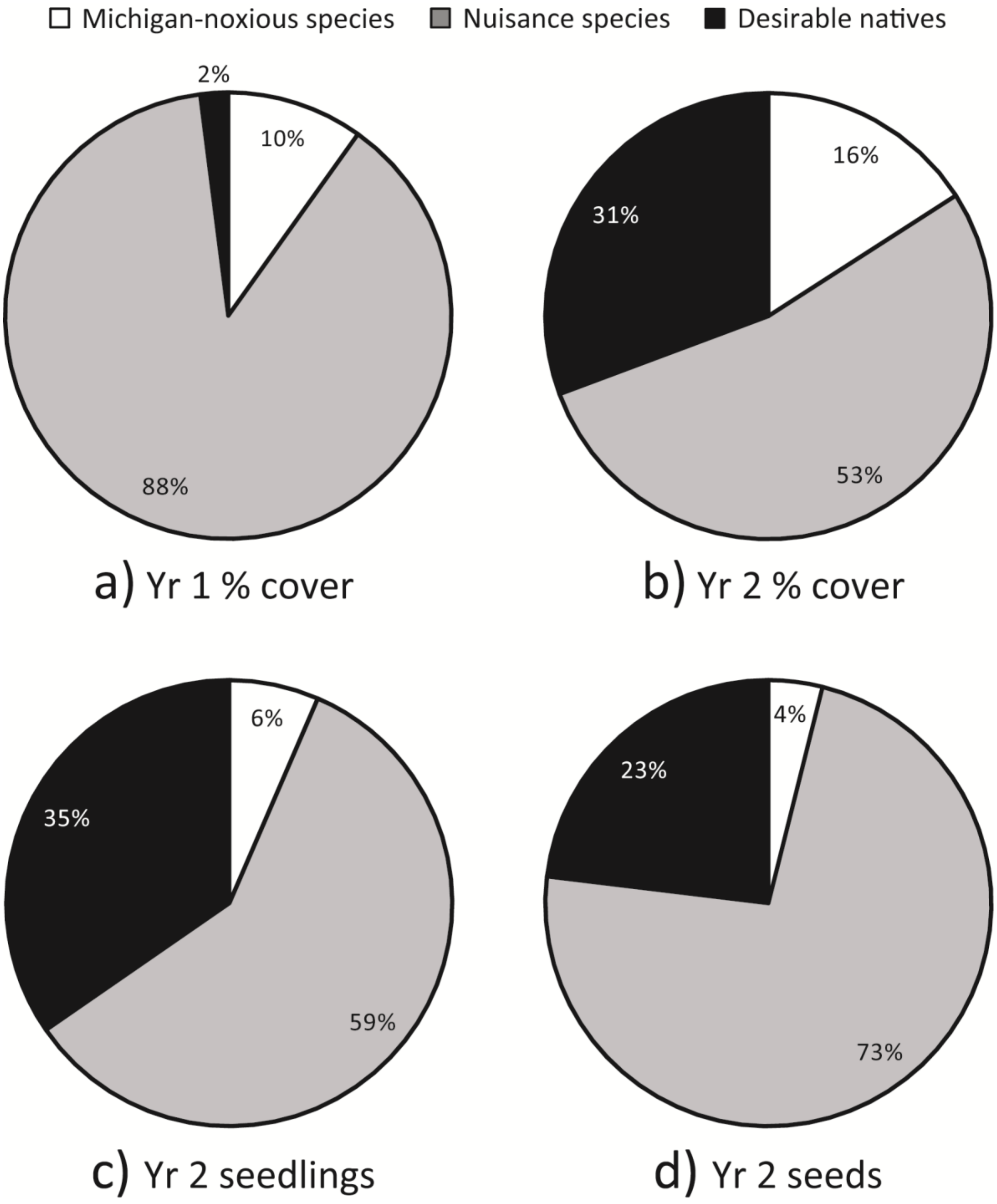


Figure 4. Composition of colonizing plant community summed across mowing treatments, as measured by a) Yr 1 % cover in August, b) Yr 2 % cover in August, c) number of seedlings per m^2 in May of Yr 2, and d) number of seeds trapped in 10.8 cm diameter seed traps from July to October of Yr 2.

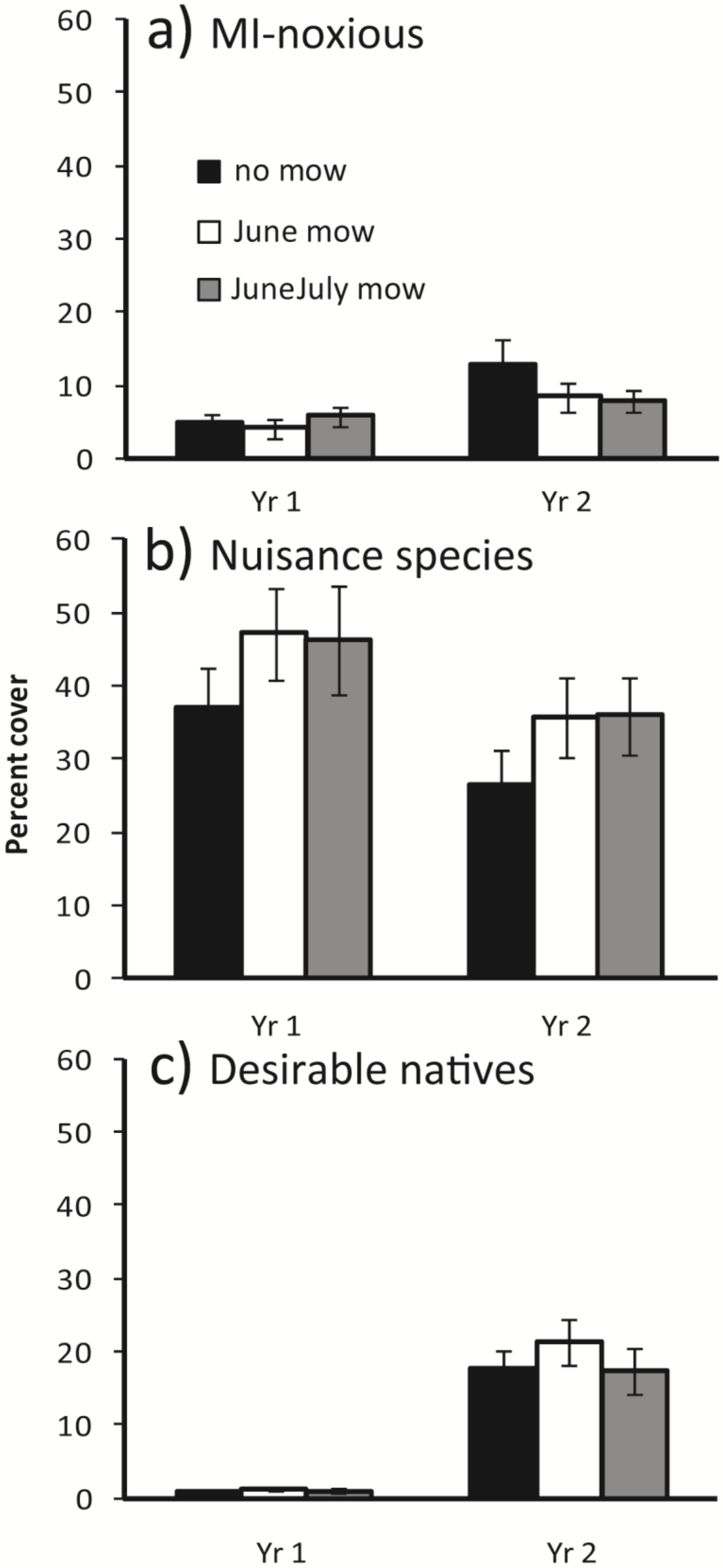


Figure 5. Percent cover of colonizing species in August of Yr 1 and Yr 2: a) MI-noxious species, b) nuisance species, and c) desirable natives. Means ± one standard error are presented.

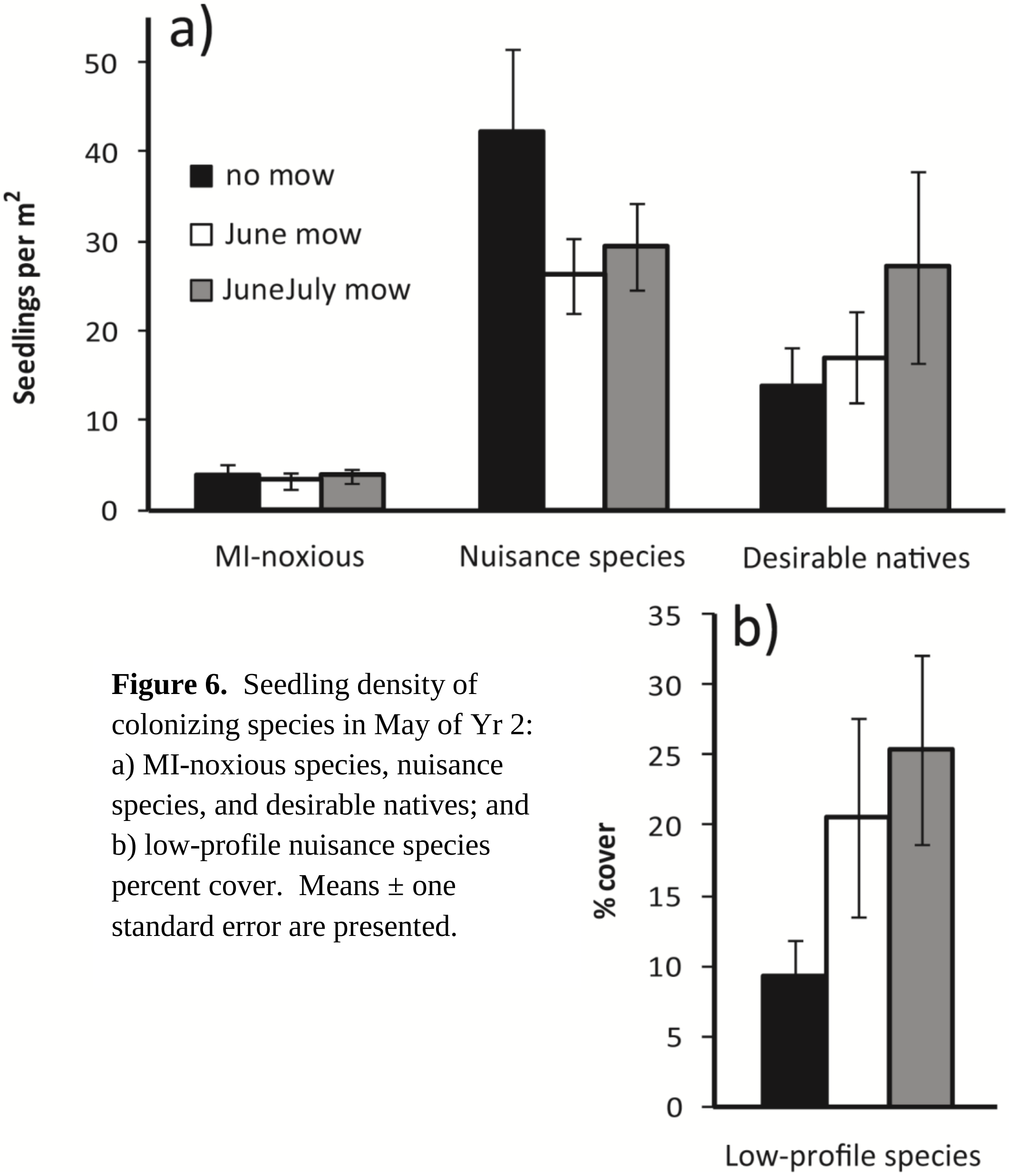


Figure 6. Seedling density of colonizing species in May of Yr 2: a) MI-noxious species, nuisance species, and desirable natives; and b) low-profile nuisance species percent cover. Means ± one standard error are presented.

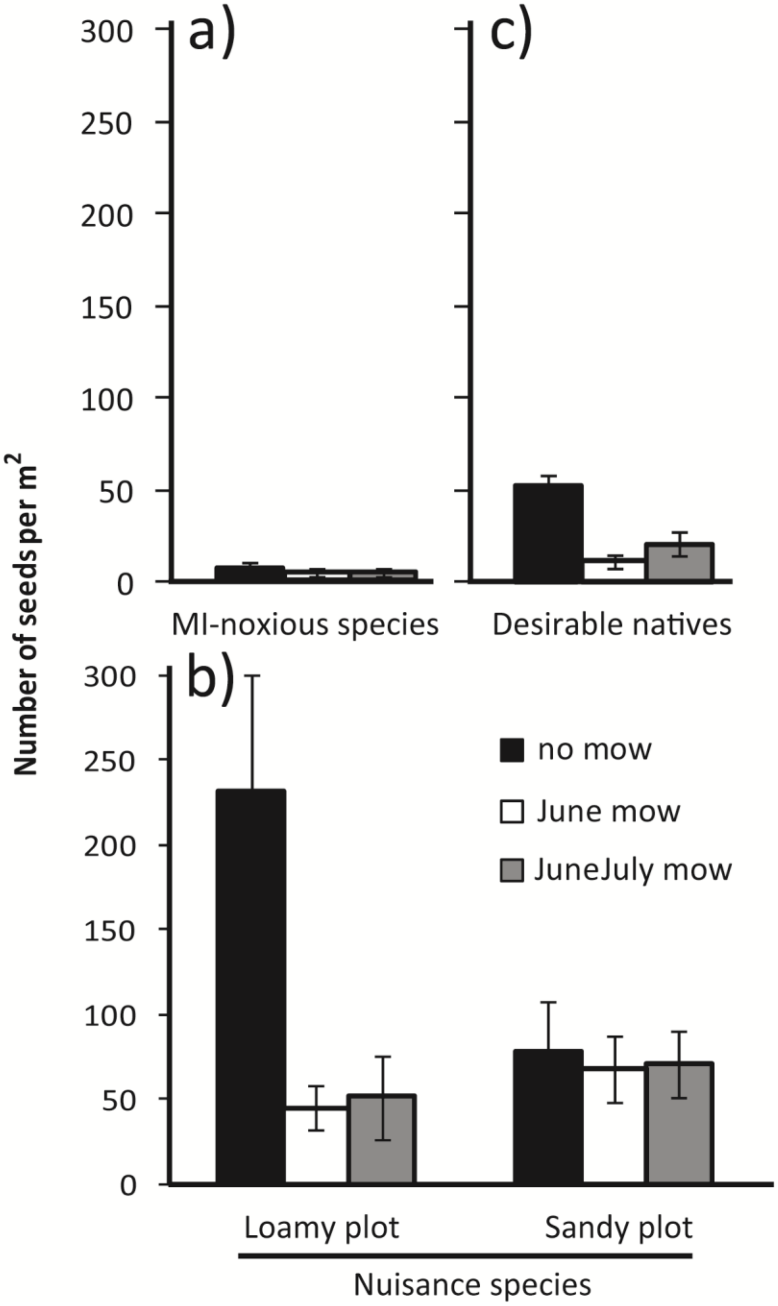


Figure 7. Mowing effects on seed production of colonizers measured from July to October of Yr 2 using 10.8 cm diameter seed traps: a) MI-noxious; b) nuisance species on the loamy plot and on the sandy plot; and c) desirable natives. Means ± one standard error are presented.

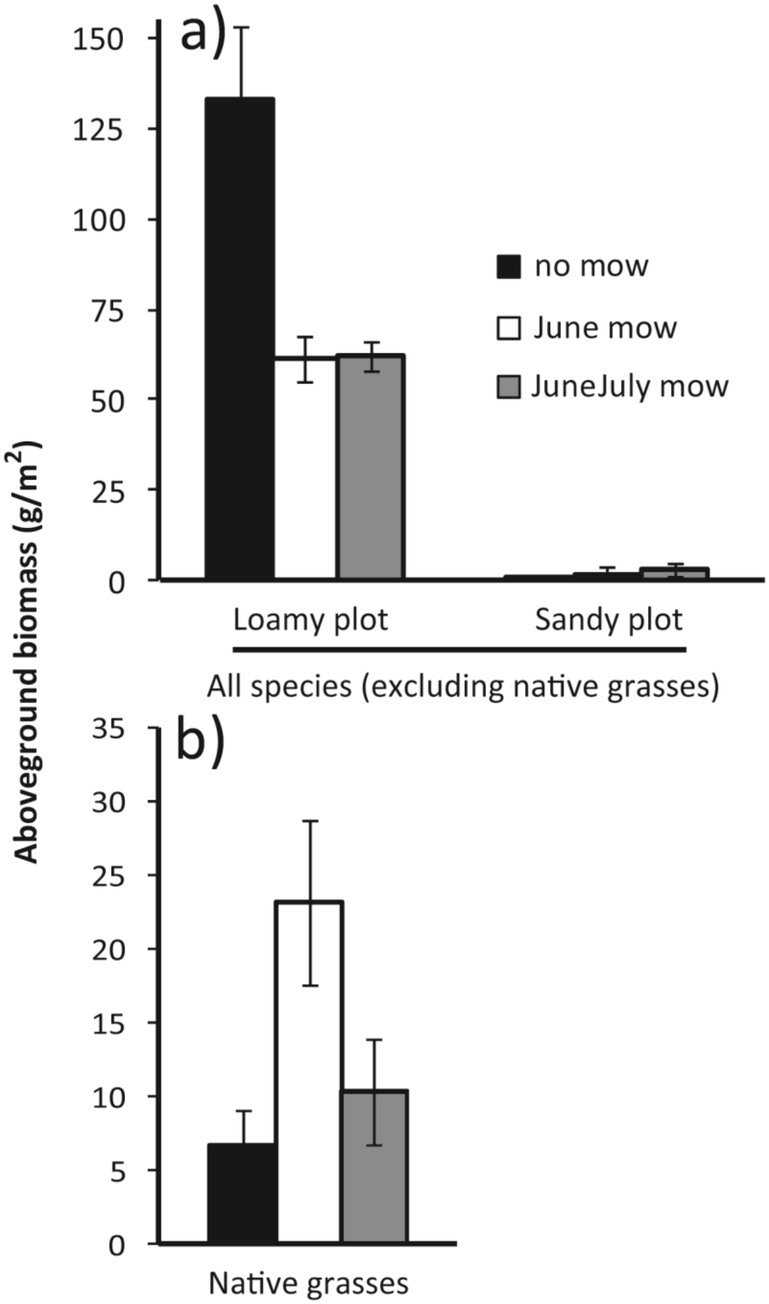


Figure 8. Mowing effects on colonizer biomass harvested in late August of Yr 2 (dry weight): a) all species (excluding native C_4 grasses) in the loamy plot, and in the sandy plot; and b) native C_4 grass biomass (*A. gerardii* and *S. scoparium*). Means ± one standard error are presented.

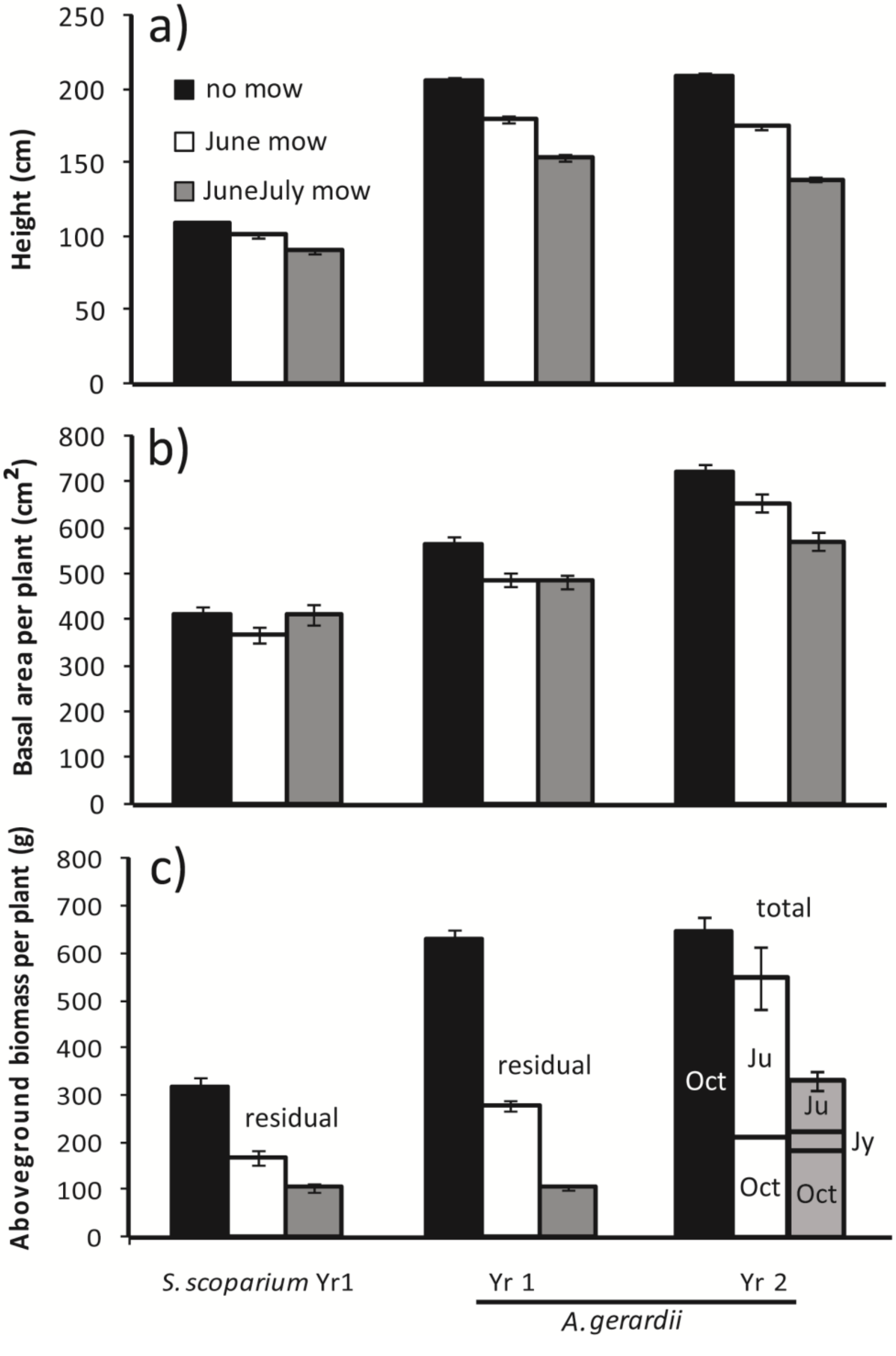


Figure 9. Mean responses of individual mature plants to mowing. In Yr 1, plants were three years old. The panels show Yr 1 measures for *S. scoparium* and Yr 1 and Yr 2 measures for *A. gerardii*: a) end-of-season height, b) end-of-season basal area, and c) aboveground biomass. Panel c shows a further breakdown of values. In Yr 1, residual biomass was harvested in October. In Yr 2, *A. gerardii* mowed biomass was also collected after the June ('Ju') and July ('Jy') mowing. Means ± one standard error are presented.

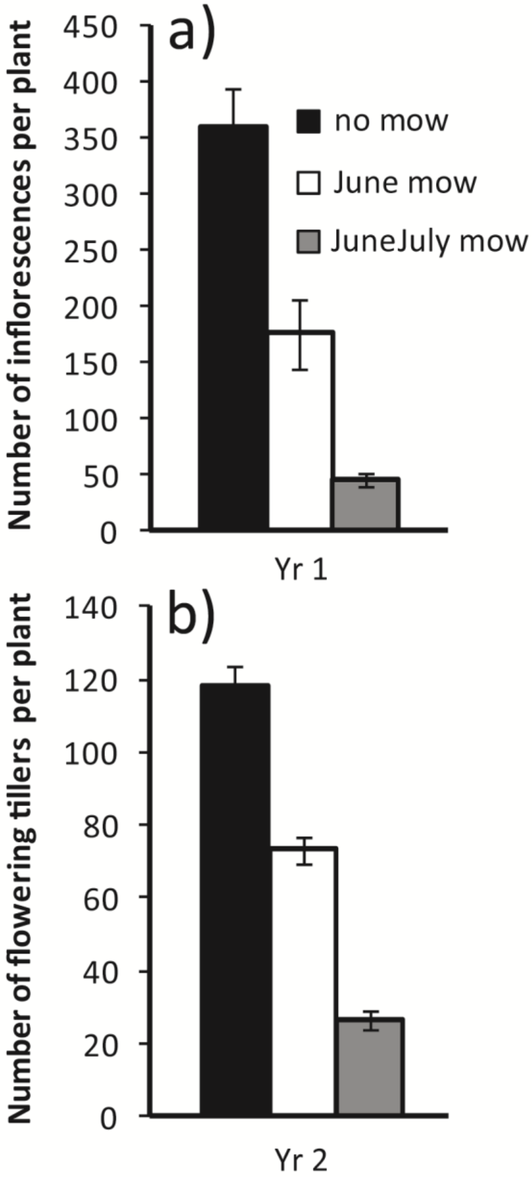


Figure 10. Flowering response of individual mature *A. gerardii* to mowing. a) Yr 1 inflorescence counts, and b) Yr 2 flowering tiller counts. Means ± one standard error are presented.

Discussion

Grassland restoration and management is a growing industry worldwide because of the capacity for grasslands to provide multiple ecosystem services and conservation value (Weigelt et al. 2009; Tilman et al. 2006). Because grasslands are generally disturbance-adapted, a notable focus of grassland management lies in application of disturbance regimes that optimize development and maintenance of desired grassland characteristics, such as species composition and productivity. In regions such as the United States, many guidelines for prairie management emphasize the need for prescribed burns (e.g., NRCS 2006, Packard and Mutel 1997), but implementing prescribed burns can be logistically difficult, and thus many practitioners have employed mowing as an alternative management tool. For North American tallgrass prairies, quantitative information about the effects of different mowing regimes has been limited, and guidelines about the use of mowing reflect conflicts between different management goals (e.g., NRCS 2006 vs. NRCS 2011).

This study advances understanding of mowing strategies during key summer periods and their effects on dominant warm-season grasses, other desirable native species, and noxious and nuisance weeds. I found that two years of summer mowing treatments increased cover and biomass per unit area of colonizing native species, primarily C_4 grasses, while reducing weed biomass per unit area and decreasing nuisance seed production. Mowing reduced the size of mature native grasses within the community as well, but the effects of one mow were notably less deleterious than that of two mows. Mowing twice within a growing season did not increase weed control.

SUCCESSIONAL PROCESSES

Many of the nuisance species in this study are considered to be early successional and often are found in disturbed, nutrient-poor sites (Bryson and DeFelice 2010, Reznicek et al. 2011, Uva et al. 1997). These annual and short-lived perennial plants are frequently displaced over time by longer-lived perennial species. In this study, successional processes were evident in the un-mowed control blocks, in which percent cover of nuisance species declined while basal area of mature *A. gerardii* and percent cover of native species increased between years. These changes indicate that the plant community at these sites would likely become increasingly dominated by longer-lived perennials in the future if no further management were applied (Kosola and Gross 1999).

INFLUENCE OF SUMMER MOWING ON WEEDY COLONIZERS

Mowing can both stimulate and inhibit plant growth, depending on the traits of the species to which it is applied and the timing of its application (Hover and Bragg 1981, Vogel and Bjugstad 1968, Wilson and Clark 2001). Mowing has been used to reduce the growth and reproduction of non-native weedy species in numerous grassland ecosystems, and seems to be most effective when weeds are mowed at or near the flowering stage. Much of this research has focused on control of invasive grass species. For example, mowing was shown to reduce the size of several non-native, cool-season grasses, including quack grass (Elymus repens (L.) Gould) in Wisconsin prairies (Diboll 1986), tall oatgrass (*Arrhenatherum elatius* (L.) J. Presl & C. Presl) in Oregon (Wilson and Clark 2001), and both Kentucky bluegrass (*Poa pratensis* L.) and orchard grass (*Dactylis glomerata* L.) in British Columbia, Canada (MacDougall and Turkington 2007).

However, mowing had no effect on cover of the invasive warm-season King Ranch bluestem (*Bothriochloa ischaemum* (L.) Keng) in Texas (Simmons et al. 2007).

Studies of mowing on weedy forbs in grasslands, such as those examined here, appear to be fewer but also have found notable effects. For example, mowing reduced the density (Rinella et al. 2001) and seed production (Benzel et al. 2009) of spotted knapweed (*Centaurea stoebe* L.) in Montana, and reduced biomass and seedhead production of yellow starthistle in California (Benefield et al. 1999). Likewise, I found that summer mowing reduced the biomass per unit area of the weedy forb species (which were much more abundant than weedy grasses) invading my experimental prairie grass plantings, with the most marked effect seen on loamy soils.

More critically, summer mowing also reduced seed production of nuisance weed species, which were the dominant weed group at my sites. This effect was not evident for MI-noxious weed species, in part due to their relative lack of abundance at the study sites; nearly 30% of blocks contained no MI-noxious seedlings at the beginning of Yr 2, while only one block (out of 94) lacked nuisance species.

The response of nuisance species to mowing in tallgrass prairie communities has received somewhat less attention than that of noxious weeds. In other grasslands, mowing typically increases abundance of short-statured species such as white clover, which are not directly affected by mowing, but benefit from increased light availability (Fulkerson and Michell 1987). In this study, the observed reduction in weedy biomass and the reduction in nuisance species seed abundance suggest that the effects of mowing might become more notable over time. If seed rain or seed banks are limited, reduction in seed production could result in reduced seedling recruitment in subsequent years (Rinella et al. 2001). At this site, as is likely at sites of other agricultural field conversions, the seed bank was relatively species-poor (see Chapter 3) and thus perhaps easier to manage than seed banks that have developed in weed-rich regions.

Evaluation of the weed metrics employed in this study suggests that biomass and seed production are more useful measures than percent cover, which is strongly dependent on mowing influence on plant structure. These mowing responses are influenced by the location of plant meristems. In forbs, apical meristems are often located at stem tips and inhibit growth of other branches. Removal of these meristems by mowing can cause rapid lateral branching, often resulting in a prostrate growth form (Radosevich et al. 1997). In contrast, meristems on grasses are located nearer to the base of plants, so this response to defoliation is less often observed. Thus, mowing can often drive release of apical dominance in forbs when their apical meristems are removed. For example, Randa and Yunger (2001) observed an increase in cover following June mowing for the invasive white sweet-clover (Melilotus albus Medik.) in an Illinois prairie, but they also observed a biomass reduction from mowing. In forb-dominated blocks in my study, vertical plant growth removed by mowing was replaced by lateral branches from surviving plants, which increased percent cover of nuisance species. However, the biomass of nuisance species did not in fact increase in response to mowing; in the loamy plot it decreased, and in the sandy plot it was not affected. Instead, the growth form of dominant forb species, most notably Canada goldenrod (*Solidago canadensis* L.), became more lateral than vertical in response to mowing (Colin Phillippo, pers. obs.). These results illustrate that mowing of some forb species may appear to increase their abundance (i.e., more ground area covered), but biomass of these plants is reduced.

INFLUENCE OF SUMMER MOWING ON NATIVE SPECIES

Consistent with management recommendations to mow newly-established prairies (NRCS 2006, Packard and Mutel 1997), I found that June mowing promoted notable increases in the cover and biomass per unit area of young plants of native C_4 grass species, with *A. gerardii* showing the greatest responses on loamy soil and *S. scoparium* on sandy soil. However, in contrast to recommendations that young plants should be mowed as frequently as every 30 days (NRCS 2006) the June mow treatment was more beneficial than the two-mow June and July treatment, in which the biomass response wasn't significant.

Mowing has long been found to reduce size of more mature native C_4 prairie grasses, particularly during peak plant growth in the summer (Aldous 1930, Randa and Yunger 2001, Vogel and Bjugstad 1968). However, Owensby (1974) saw no effect of a single clipping on *A. gerardii* tiller density, but found that tiller density rose with two or more clippings. Consistent with the former set of observations, the mature native grasses examined in this study (*A. gerardii* and *S. scoparium)* were negatively affected by mowing treatments, with effects influenced by soil type.

Flowering of native plant species can be notably altered by summer mowing treatments. For example, June mowing decreased flowering stem density and height of *A. gerardii* and *S. scoparium* in June-mowed plots in a Nebraska prairie (Hover and Bragg 1981). However, MacDougal & Turkington (2007) observed an increase in the flowering of native plants from July mowing. In Texas, July-mowed switchgrass (*Panicum virgatum*) (Haferkamp and Copeland 1984), and May-mowed *S. scoparium* and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.) produced more tillers than un-mowed plants did, but these plants were mowed prior to their flowering stages, which likely stimulated inflorescence production. Mature native grasses in my study were mowed at peak flowering time, and mowed plants consequently had fewer inflorescences, since little time remained for re-growth.

Frequent mowing during the growing season typically has greater influence on native grasses than a single mowing. Previous studies of both *A. gerardii* (Aldous 1930) and *S. scoparium* (Aldous 1930, N'Guessan and Hartnett 2011) have shown that twice-mowed mature grasses were more negatively affected than once-mowed plants. Frequent clipping has had mixed results in other studies. Wallace (1987) showed that clipping treatments removing 10-20% of leaf area every six weeks stimulate tillering of *S. scoparium*, but Owensby (1974) reported that clipping more than once during the growing season can actually reduce tillering of *A. gerardii*. In my June and July mowed plots, plants grew little after the second mowing treatment, and few tillers of mature plants were apparent at the end of the growing season. Even though a single mowing treatment increased colonizing native grass biomass, this increase was no longer evident when blocks were mowed twice (June and July). Here, I have show that there are increased costs of repeated mowing on native grasses, and no apparent benefits.

DURATION, FREQUENCY, AND TIMING OF MOWING

Mowing for several years may be necessary before differences in plant community composition become apparent (MacDougall and Turkington 2007, Packard and Mutel 1997). Short-term mowing can stimulate production of belowground structures such as rhizomes (Dickinson and Polwart 1982), so a long-term commitment to mowing (i.e. more than two years) is particularly important for controlling rhizomatous species, such as Canada thistle (*Cirsium arvense* (L.) Scop. (Sheley et al. 2003).

In addition to the duration of mowing, the frequency of mowing needed for weed control is an important consideration (Sheley et al. 2003). Two studies on spotted knapweed in Montana prairies found that repeated mowing conferred few or no additional weed control benefits beyond those obtained by mowing just once (Benzel et al. 2009, Rinella et al. 2001). Similarly, mowing yellow starthistle in California at the early flowering stage is as effective as repeated mowing at other growth stages (Benefield et al. 1999). Likewise, I found that mowing both in June and July did not produce results that differed from those of a single June mowing for any measurement or weed category. In contrast, de Kroon et al. (1987) observed increased abundance of hairy cat's ear (*Hypochaeris radicataI* L.) as mowing frequency increased in a grassland in the Netherlands, because removal of inflorescences induced another flowering period.

The June and July mowing treatment may have had a greater negative effect on mature native grasses than the single June mowing not only because of the increased mowing frequency, but also because of the difference in mowing timing. However, mowing timing was not directly addressed in this study, as all mowed plants were first mowed in June. In general, summer mowing favors C_3 species by suppressing late-germinating C_4 species, and spring mowing has the opposite effect (Hover and Bragg 1981, Howe 1999, Wilson and Clark 2001). July mowing can be particularly detrimental to biomass production of native C_4 grasses (Haferkamp and Copeland 1984, Vogel and Bjugstad 1968) because plants have little time to re-grow biomass removed by mowing. For weed control, management strategies targeting flowering stages of weeds are most effective for long-term population reductions (Benefield et al. 2001, Benzel et al. 2009). Rinella (2001) also demonstrated that a single mowing treatment, if timed appropriately, can be as effective for weed control as repeated mowing treatment applications. Similarly, I showed that June-mowed nuisance species produced significantly fewer seeds than controls, but a second mowing did not further reduce seed production. Determining demographic characteristics of weed populations can improve weed control techniques by targeting key stages (e.g. floral development) of undesirable plants (Jordan 1992, Magda et al. 2004).

Current prairie mowing recommendations suggest using spring (e.g. Prairie Nursery 2011) or fall (e.g. Sargent and Carter 1999) treatments in the first few years after planting. This strategy is suggested to reduce weed abundance, particularly annuals, and to avoid harm to summer-nesting birds, such as the Henslow's sparrow (*Ammodramus henslowii*) and Grasshopper sparrow (*Ammodramus savannarum*). However, spring or fall mowing treatments would be unlikely to reduce seed production by summer-flowering weeds, which are frequently problematic. In addition, prairies were historically maintained by multiple disturbance regimes varying in timing, frequency, and extent (Knapp et al 1999, Packard and Mutel 1997), and a management approach using multiple treatment options may most effectively aid prairie restoration. Mowing is a valuable tool in prairie restoration that is particularly influential for summer-flowering plant species, and could be used to partially simulate historical summer disturbances, provided precautions are taken to avoid harm to bird communities.

MOWING IN ADAPTIVE MANAGEMENT

Response of grasslands to implementation of disturbance regimes is community specific because it depends in large part on the phenological and structural differences of the plant species present, and their relative susceptibility to the particular disturbance applied at a particular time point (Vogel and Bjugstad 1968). From this perspective, disturbance can be thought of as a filter that selects for particular species on the basis of their specific traits. The challenge in management is how to select and implement strategies that can increase the abundance of desired species and reduce those that are less desired. To achieve this, managers can benefit from flexibility in choosing tools appropriate for their particular systems and desired outcomes. However, in an attempt to balance requirements of conflicting management goals, guidelines for tallgrass prairie management have become relatively prescriptive. For example, summer mowing is generally recommended only in the first few years of prairie establishment (e.g., NRCS 2006; Packard and Mutel 1997). To protect wildlife in established prairies, it is recommended that mowing occur only in late summer (August 1-20 in Michigan), and only every three years (NRCS 2011), and these restrictions are compulsory on Conservation Reserve Program lands, which provide economic incentives to landowners for converting cropland into perennial plant cover.

This study, in conjunction with studies of weed control in other grasses (Benefield et al. (1999), Benzel et al. 2009, and Rinella et al. (2001)), suggests that mowing applied immediately before or during the flowering periods of summer-flowering weeds can help control their populations in tallgrass prairie plantings. Moreover, June mowing may facilitate native grass colonization of newly planted sites, where rapid colonization by dominant grasses is desirable. In addition, June mowing reduces seed inputs from nuisance species, which can improve long-term weed control by minimizing inputs to the seed bank. Preventing seed production in the first few years of a restoration could reduce weed populations in future growing seasons, and would be especially beneficial if the majority of weedy species at a site were annuals. In sites with perennial weeds, mowing for multiple years may be necessary to effectively reduce weed populations, but this may also reduce populations of natives with similar phenologies.

Mowing has potential to play important roles in the management of multiple-use ecosystems, such as biofuel crops or hay meadows, by increasing both total productivity (Weigelt 2009) and plant species diversity (Antonsen and Olsson 2005), and by providing control of summer-flowering weeds, as demonstrated here. While residual, end-of-season *A. gerardii* biomass was reduced 50% by June mowing, reductions in total biomass (residual and that removed by mowing) were only 15%. Cox (1988) observed that July mowing reduced forage production of big sacaton (*Sporobolus wrightii* Munro ex Scribn.*)*, but by the third growing season after mowing treatments had ceased, mowed plants were similar to controls. I observed no lasting effects of either mowing treatment in Yr 1 on mature *A. gerardii* growth in Yr 2, suggesting that this species may be tolerant to biomass removal without experiencing long-term negative effects.

My work here indicates that summer mowing could be a valuable addition to the adaptive management tool kit, and thus merits more consideration in management guidelines. This study suggests that June mowing would likely be particularly valuable for cases in which grasslands contained i) weedy summer-flowering forbs, ii) well established native C_4 grasses, iii) little or no C_3 grasses, which were not abundant at my sites but could be stimulated by June mowing in other situations (Hover and Bragg 1981, Wilson and Clark 2001), and iv) few well established, vegetatively propagating perennial weeds. In addition, it is likely that mowing treatments would need to be sustained over multiple years to effect control in systems where weed seed banks were highly developed, and could contribute to weed abundance for many years (Jordan 1992).

The biggest conflict that managers of tallgrass prairies face in implementing summer mowing to control summer flowering weeds is the need to prevent harm to birds that ground-nest in grasslands during this same period. While mowing likely has less negative influence on invertebrate and aquatic communities than alternative methods such as herbicide application might, preservation of limited grassland bird populations is a key priority (Van Dyke et al. 2004).

Given this study's quantitative demonstration that June mowing offers weed control benefits while maintaining productivity of native grasses, it would be helpful to evaluate multiple means for implementing June mowing strategies that would also protect summer ground-nesting birds. Such strategies could include conducting breeding bird surveys prior to mowing, or mowing only a portion of a prairie each growing season. In addition, it would be valuable to develop precision agricultural methods for locating and avoiding nesting birds during harvest periods.

Chapter 3
Assessing Seed Abundance in Prairies

To assess the potential for mowing to influence weed populations, it is important to evaluate the composition of the seed bank and seed rain at a site, since both are important determinants of plant community composition. Here, I describe methods for assessing seed bank composition, and methods for assessing seed deposition in prairie ecosystems. Seed bank species composition data and photographs taken during my own seed trap study are presented.

Methods for Conducting a Seed Bank Study

I used the greenhouse germination methods of Gross (1990) to assess seed bank composition in my research sites. Seven soil cores (1.9 cm diameter x 5 cm depth) were taken from each block in May and homogenized into a single sample per block (19 blocks per site). Soil cores were spread in pots on Fafard superfine seedling mix (Conrad Fafard Inc., Agawam, MA). Pots were incubated in a greenhouse and seedlings were counted periodically until December.

An alternative method could also be used to assess seed bank composition. Gross and Renner (1989) proposed a soil elutriation method, in which soil cores are collected and sieved to separate seeds from soil. Seeds are then identified under a microscope. This method yields comparable numbers of large seeds, but may miss smaller seeds (Gross 1990). Additional testing is also needed to determine if seeds are viable. I chose the greenhouse germination method because many of the weeds present in my research sites have very small seeds, and may be missed by the soil elutriation method. Additionally, the soil elutriation method includes seeds that are not viable, while the greenhouse germination method necessarily only counts viable seeds.

Seed Trap Design and Use

One seed trap was installed in each block of the Mason plots in July. My traps were modeled after those developed by Chabrerie and Alard (2005). Each trap consisted of a 7.6 cm diameter, 22.9 cm long PVC pipe placed in the ground (1-2 cm above soil surface), with a 10.8 cm diameter funnel placed on top, and a mesh bag attached to the bottom of the funnel (Fig. 8). Trap bags were exchanged every other week until October. Seeds from known species were collected directly from plants and were photographed using a Dino-lite digital microscope (Model # 413T, AnMo Electronics corp., New Taipei City, Taiwan) to aid in identification of seeds in seed traps (Fig. 9). Additional species found in seed traps were also photographed (Fig. 9). All seeds were identified to species when possible. Seeds from several species in the family Asteraceae could not be easily distinguished and were grouped.

Figure 11. Seed trap used to assess plant community seed deposition.

Table 3. Abundance of species found in seed banks of sandy and loamy plots in Mason, Michigan (600 cm^3 of soil sampled per plot). Seven species did not grow beyond the seedling stage and could not be identified. Here they are listed separately as unknowns.

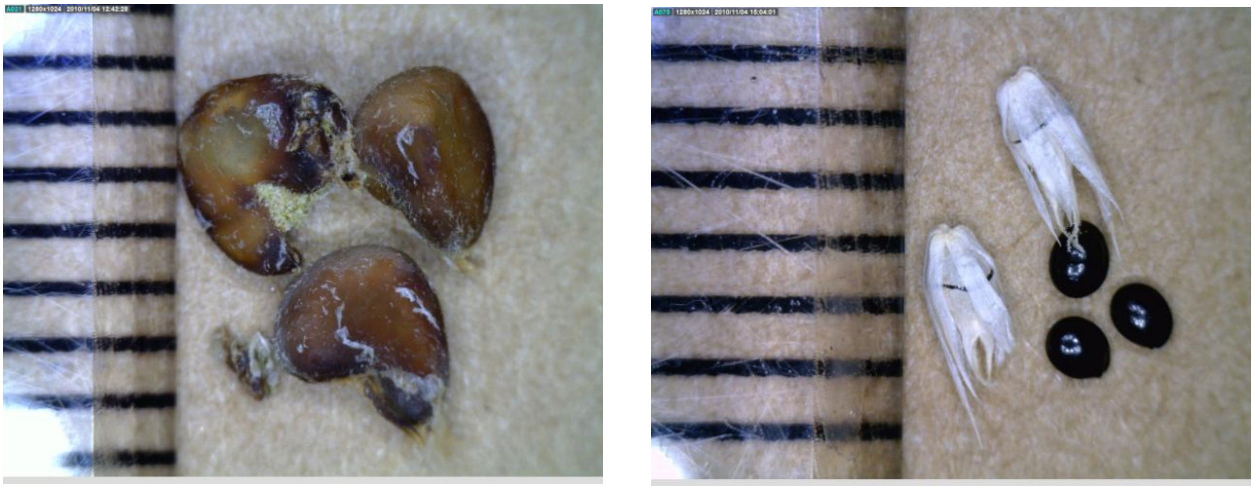
Site	Species	Total seedling count
Sandy plot	*Amaranthus retroflexus* L.	2
	Ambrosia artemisiifolia L.	1
	Andropogon gerardii Vitman	2
	Chenopodium album L.	16
	Conyza canadensis (L.) Cronq.	44
	Mollugo verticillata L.	40
	Oxalis stricta L.	22
	Portulaca oleracea L.	2
	Schizachyrium scoparium Michx.	3
	Taraxacum officinale F. H. Wigg.	1
	Unknown 1	1
	Unknown 2	1
	Unknown 3	1
	Unknown 4	1
	Unknown 5	1
	Veronica arvensis L.	26
Loamy plot	*Amaranthus retroflexus* L.	20
	Ambrosia artemisiifolia L.	1
	Andropogon gerardii Vitman	51
	Chenopodium album L.	23
	Conyza canadensis (L.) Cronq.	194
	Cyperus esculentus L.	1
	Echinochloa crusgalli (L.) P. Beauv.	10
	Elymus repens (L.) Gould	4
	Epilobium coloratum Biehler	5
	Geranium maculatum L.	7
	Medicago lupulina L.	1
	Oxalis stricta L.	26
	Panicum capillare L.	1

(**Table 3.** continued)

Loamy plot	*Plantago major* L.	196
	Platanus spp.	1
	Persicaria maculosa A. Gray	9
	Portulaca oleracea L.	1075
	Potentilla spp.	40
	Solanum ptychanthum Dunal	3
	Sonchus asper (L.) Hill	27
	Taraxacum officinale F. H. Wigg.	63
	Unknown 2	69
	Unknown 5	2
	Unknown 6	2
	Veronica arvensis L.	3

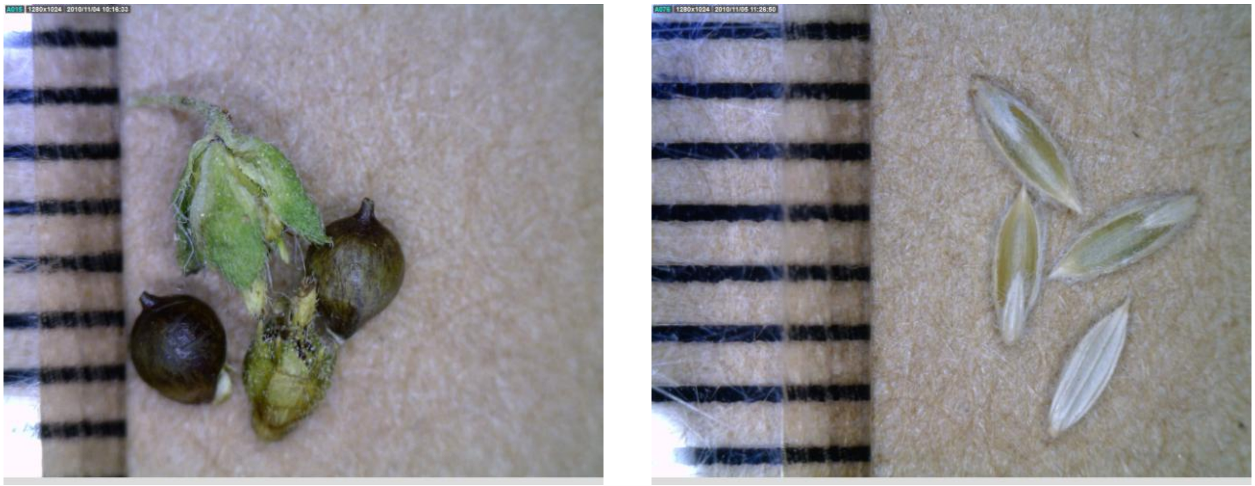
Seed Photographs

Figure 12. Seeds collected directly from plants and from seed traps in Ingham county, MI. Photographs were taken using 10x–200x magnification. The scale shown is divided into 1 mm increments.



a) *Abutilon theophrasti* Medik

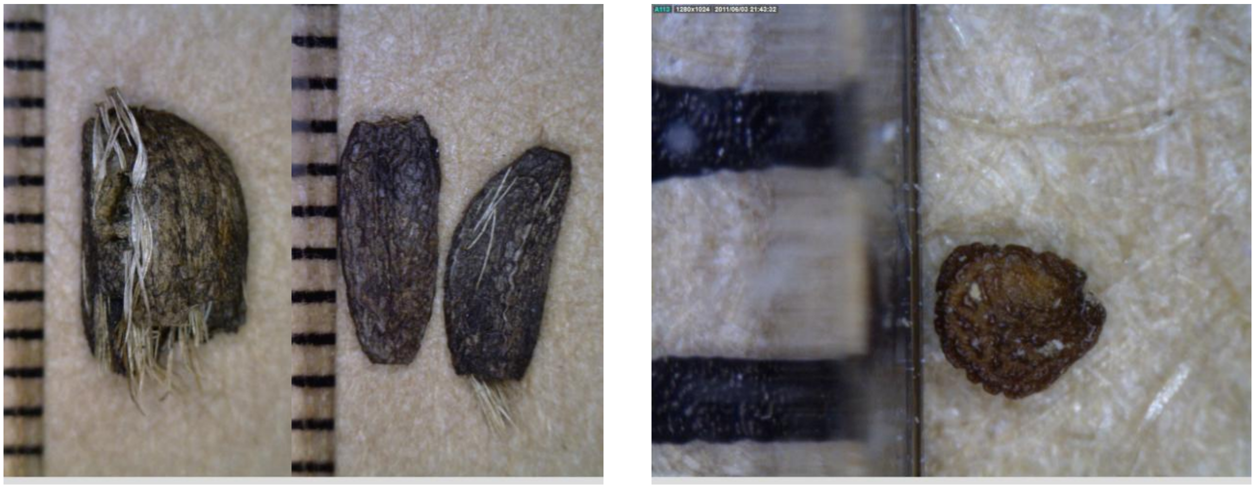
b) *Amaranthus retroflexus* L.



c) *Ambrosia artemisiifolia* L.

d) *Andropogon gerardii* Vitman

(**Figure 12.** continued)

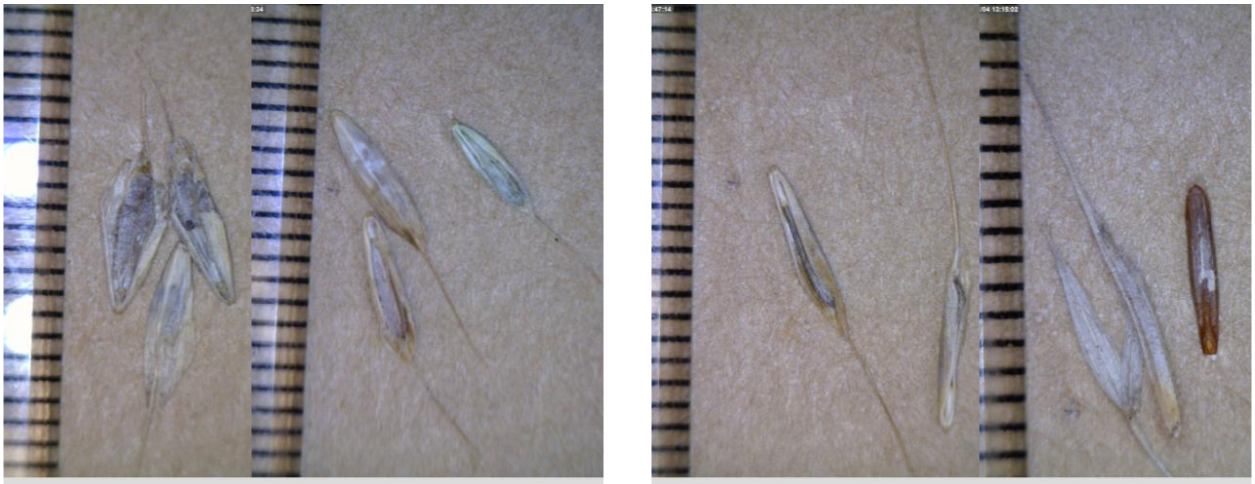


e) *Arctium minus* Bernh.

f) *Arenaria serpyllifolia* L.

g) *Berteroa incana* (L.) DC.

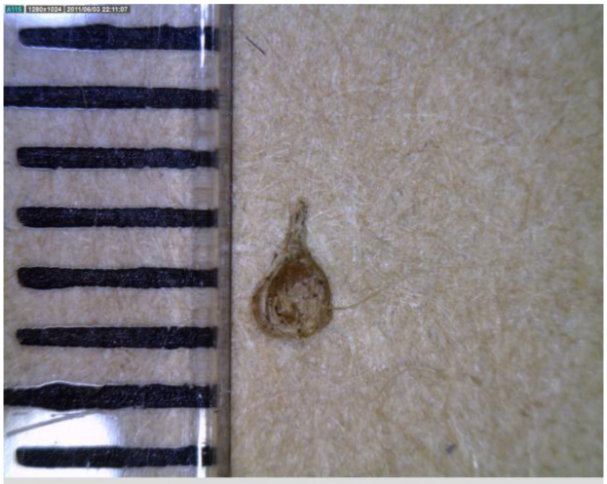
h) *Bidens frondosa* L.



i) *Bromus secalinus* L.

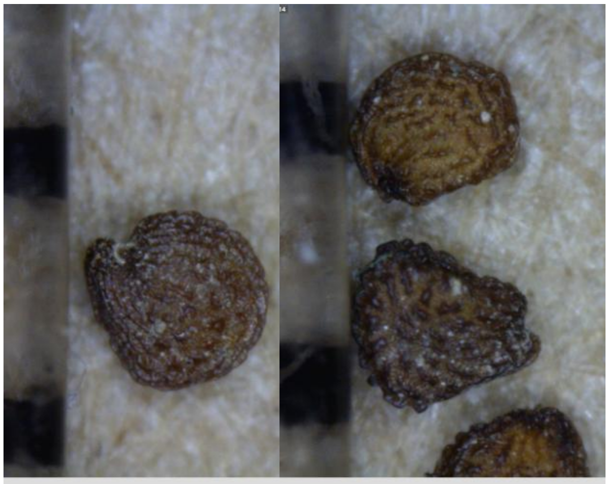
j) *Bromus tectorum* L.

(**Figure 12.** continued)

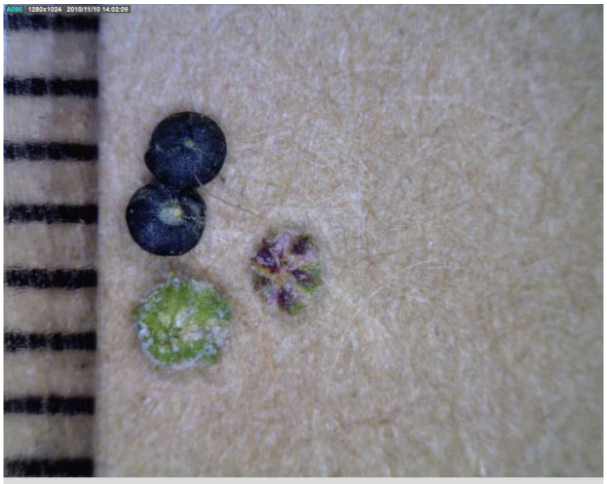


k) *Carex vulpinoidea* Michx.

l) *Centaurea stoebe* L.



m) *Cerastium fontanum* Baumg.



n) *Chenopodium album* L.

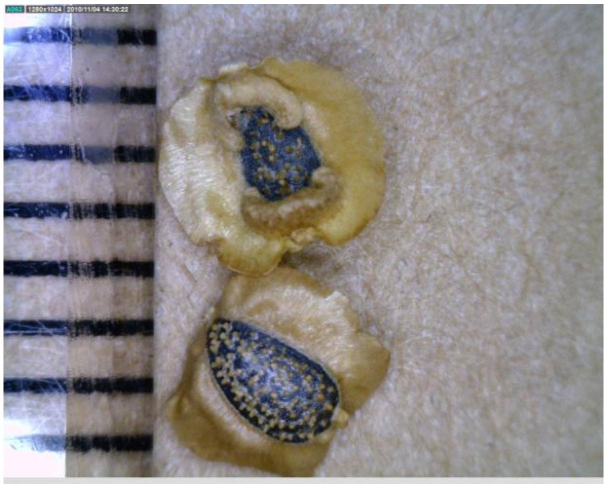
o) *Cichorium intybus* L.

p) *Cirsium arvense* (L.) Scop.

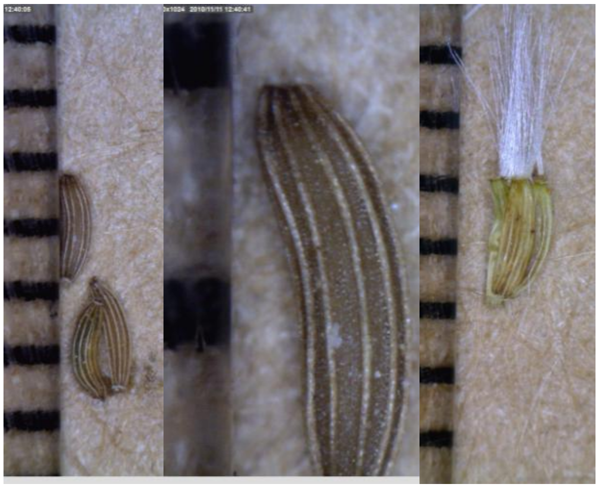
(**Figure 12.** continued)

q) *Cirsium vulgare* (Savi) Ten.

r) *Conyza canadensis* (L.) Cronq.



s) *Coreopsis lanceolata* L.

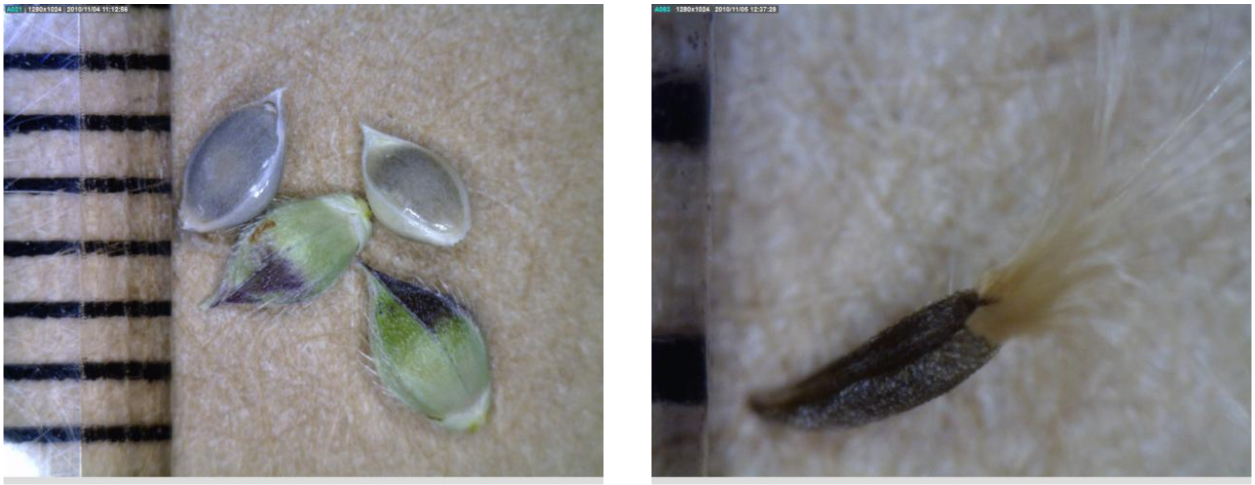


t) *Crepis capillaris* (L.) Wallr.

u) *Cyperus esculentus* L.

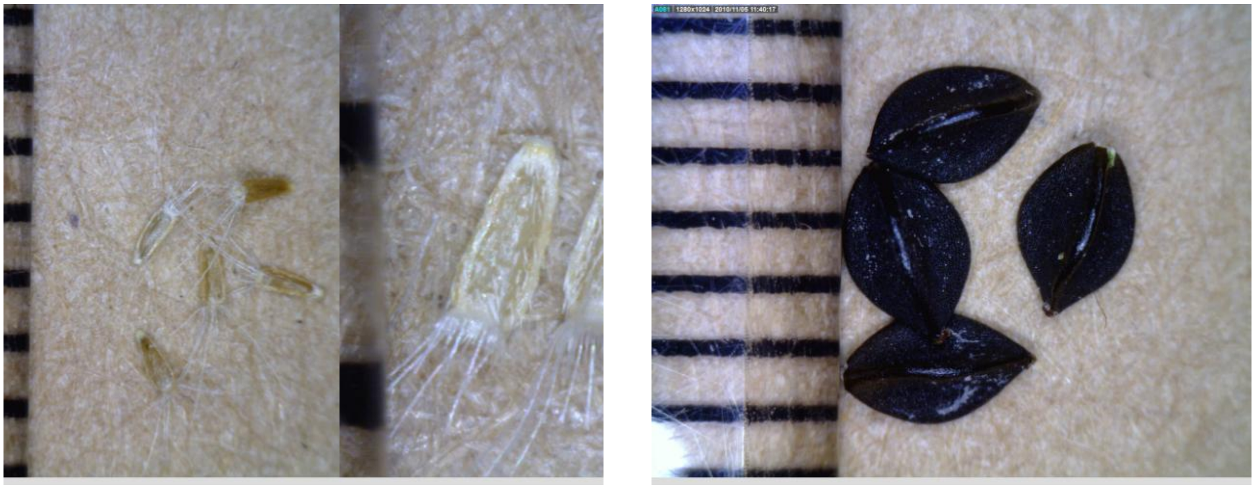
v) *Daucus carota* L.

(**Figure 12.** continued)



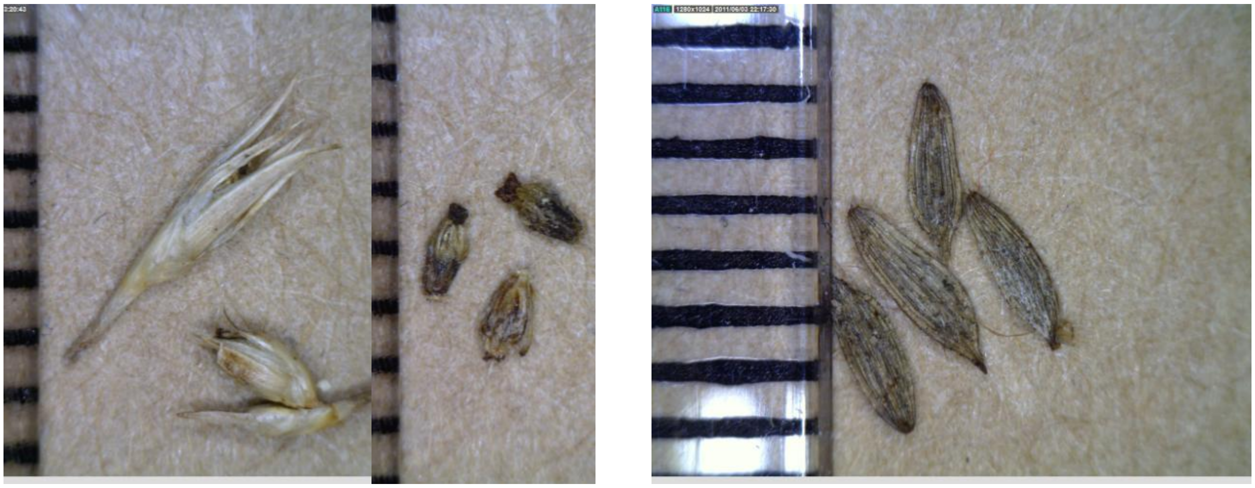
w) *Echinochloa crus-galli* (L.) P. Beauv.

x) *Epilobium coloratum* Biehler



y) *Erigeron annuus* (L.) Pers.

z) *Fallopia convolvulus* (L.) À. Löve

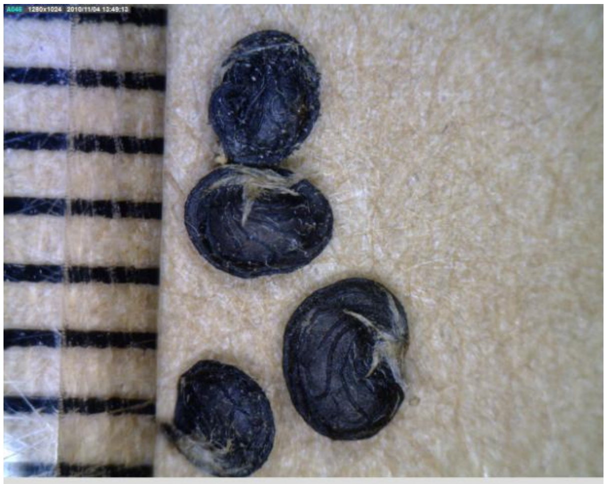


aa) *Juncus tenuis* Willd.

ab) *Lactuca serriola* L.

(**Figure 12.** continued)

ac) *Lolium perenne* L.



ad) *Medicago lupulina* L.

ae) *Melilotus albus* Medik.

af) *Melilotus officinalis* (L.) Pall.

ag) *Mollugo verticillata* L.

ah) *Oxalis stricta* L.

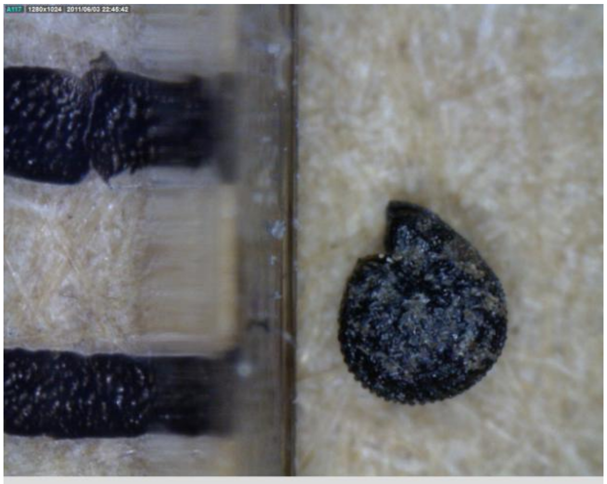
(**Figure 12.** continued)

ai) *Panicum capillare* L.

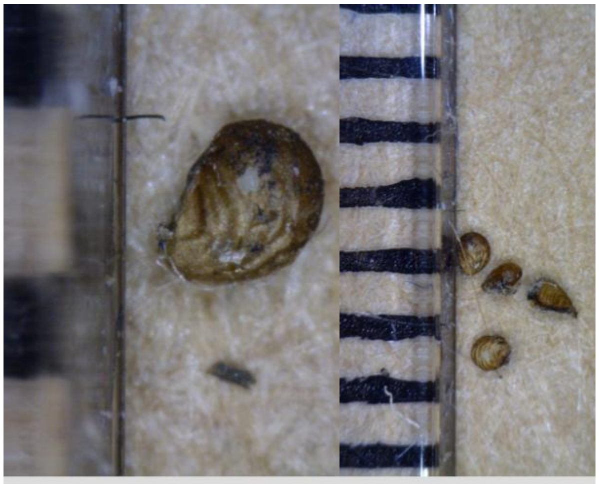
aj) *Persicaria maculosa* A. Gray

ak) *Phalaris arundinacea* L.

al) *Poa alsodes* A. Gray



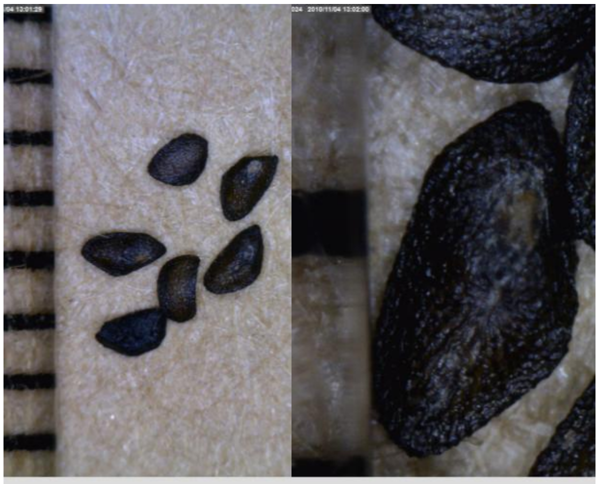
am) *Portulaca oleracea* L.



an) *Potentilla norvegica* L.

(**Figure 12.** continued)

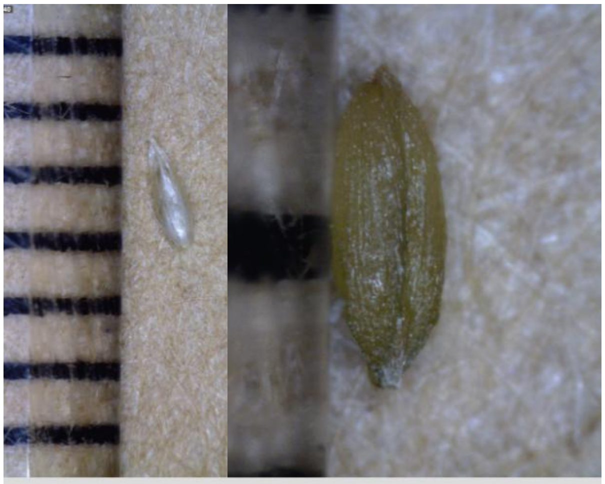
ao) *Plantago lanceolata* L.



ap) *Plantago major* L.

aq) *Ranunculus scleratus* L.

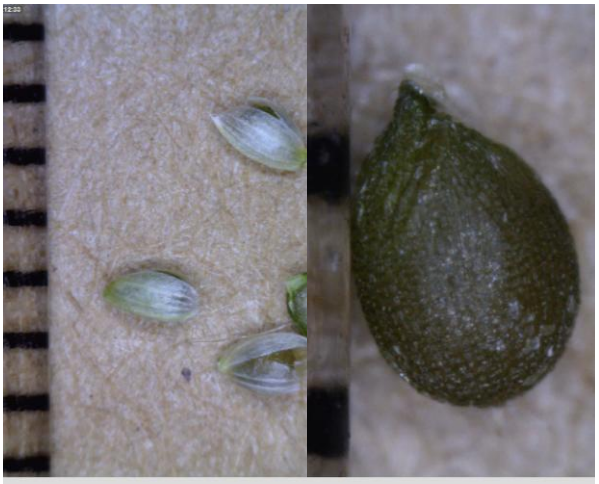
ar) *Rumex crispus* L.



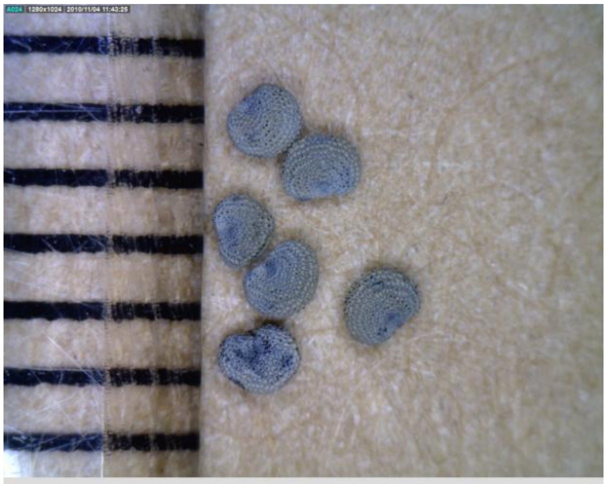
as) *Schedonorus arundinaceus* (Schreb.) Dumort.

at) *Schizachyrium scoparium* Michx.

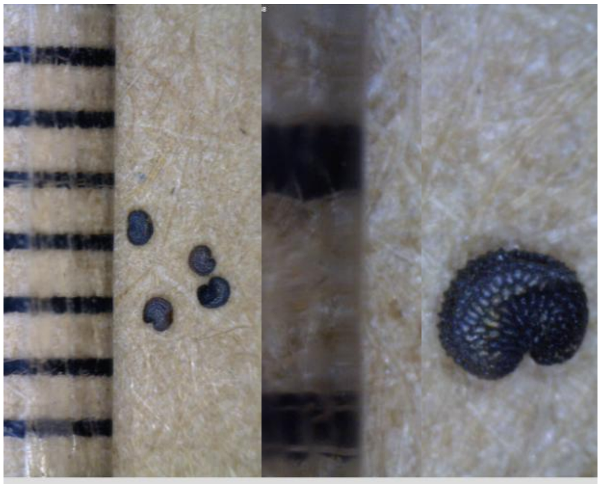
(**Figure 12.** continued)



au) *Setaria viridis* (L.) P. Beauv.



av) *Silene alba* Poir.



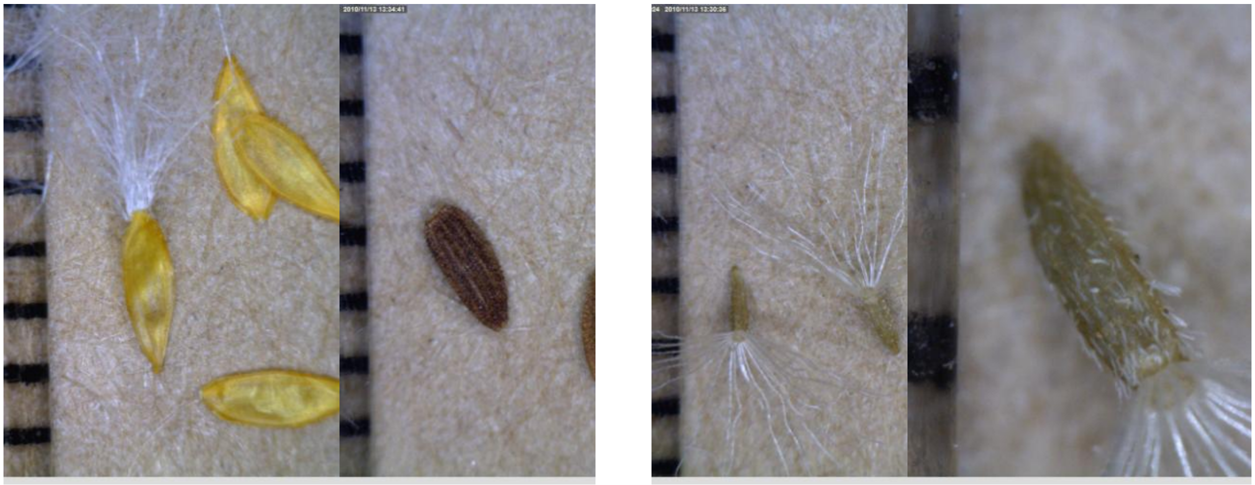
aw) *Silene antirrhina* L.

ax) *Solanum ptychanthum* Dunal

ay) *Solidago canadensis* L.

az) *Sonchus arvensis* L.

(**Figure 12.** continued)

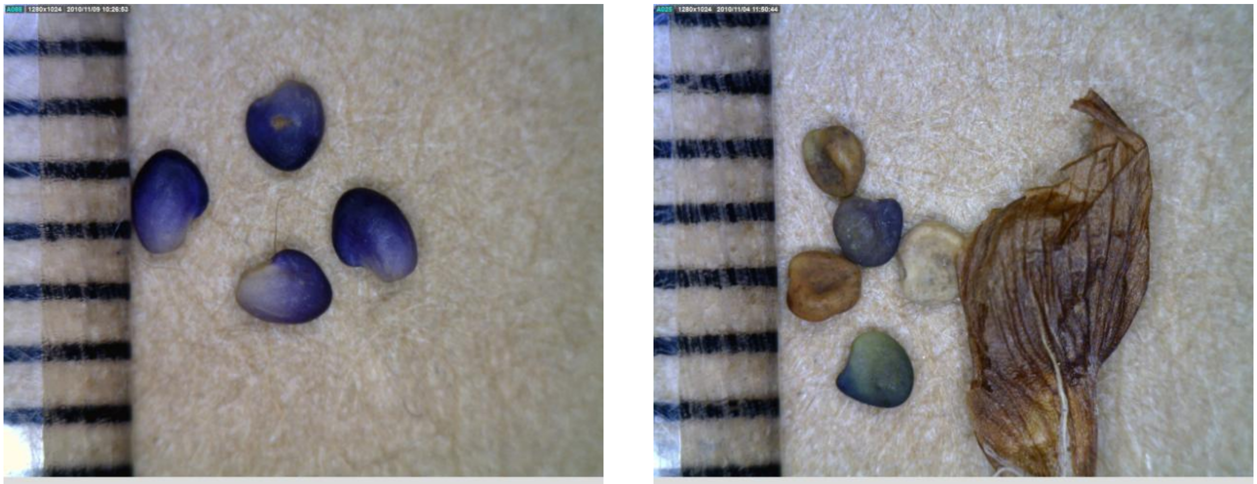


ba) *Sonchus asper* (L.) Hill

bb) *Symphyotrichum lanceolatum* (Willd.) G. L. Nesom

bc) *Taraxacum officinale* F. H. Wigg.

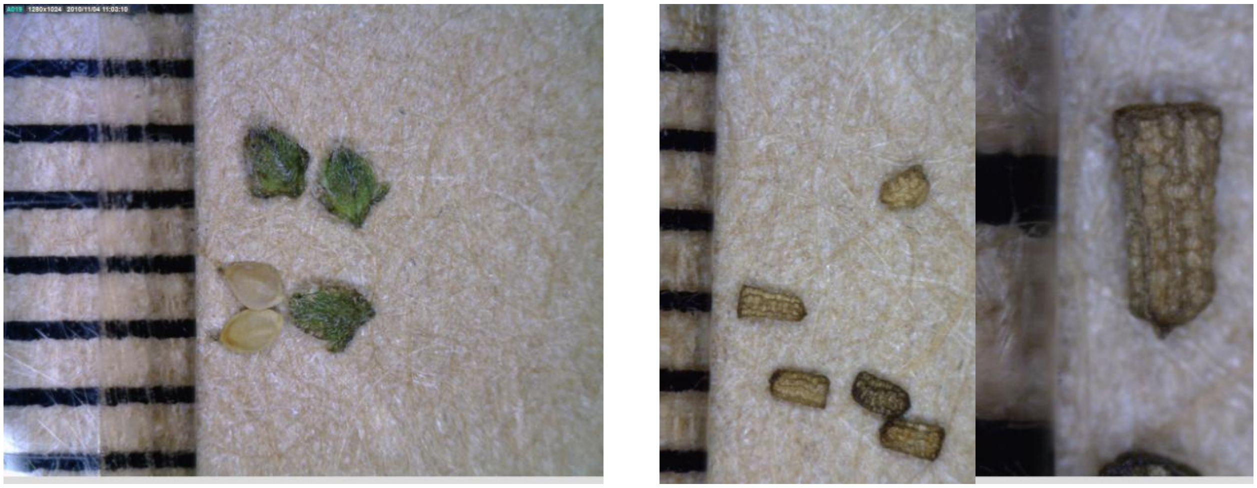
bd) *Tragopogon dubius* Scop.



be) *Trifolium pratense* L.

bf) *Trifolium repens* L.

(**Figure 12.** continued)



bg) *Urtica dioica* L.

bh) *Verbascum thapsus* L.

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