Slug grazing effects on seedling and adult life stages of North American Prairie plants used in designed urban landscapes

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Abstract

This study investigated the effect of slug grazing on the establishment and longer-term development of 26 species of North American prairie forbs and grasses used in sown or planted naturalistic communities in urban greenspace. The experiment was designed to provide slugs with the opportunity to choose between the plant species used, to mirror the situation that prevails in landscape practice. Baiting with metaldehyde at different frequencies was used to manipulate mollusc numbers. Seedlings of prairie species were more palatable to slugs than adults. Establishment of seedlings was significantly reduced in most species by slug grazing, with only 7 species showing no significant increase in establishment in response to baiting with metaldehyde. In many species successful establishment was based on the combination of moderate or greater unpalatability and very large or fast growing seedlings. Adult prairie plants were typically more able to withstand slug damage as their shoots emerged in spring, and once they reached a certain size, grazing greatly reduced. This was not however true of the most highly palatable species, which even as adults were eventually eliminated by grazing in the absence of baiting. Phenology seems to play an important role in the survival of adults, with early emerging species potentially subject to severe damage due to the limited availability of alternate food plants. As a group, prairie forbs are typically highly palatable to slugs, and their establishment and long-term development is likely to be significantly impaired in slug-rich landscapes.

Key words

Defoliation; growth phenology; metaldehyde baiting; mollusc grazing; prairie plants; seedling establishment

Introduction

There is increasing evidence that in temperate regions with seasonally moist climates, mollusc herbivory is a significant factor affecting the development and composition of semi-natural vegetation (Bruelheide and Scheidel 1999; Wilby and Brown 2001; Holland et al. 2007). At the landscape scale, it can profoundly affect the distribution of plant species and the composition of semi-natural plant communities. For example, *Arnica montana*, a rare perennial forb occurring in heathland and acidic grassland, is restricted to a montane altitudinal band by the increasing density of molluscs at lower altitudes (Bruelheide and Scheidel 1999). However, whilst mollusc grazing may be catastrophic for individual species, it can potentially benefit community diversity by restricting the productivity of more palatable community dominants that would otherwise out-compete less competitive species (Buschmann et al. 2005).

Seedlings are typically more palatable than adult plants, as they tend to i) contain lower concentrations of secondary metabolites (Hanley et al. 1995; Fenner et. al 1999), and ii) possess fewer hairs and other morphological structures that reduce palatability (Scheidel and Bruelheide 1999). Irrespective of palatability, seedlings, because of their smaller size, also tend to be more seriously damaged by slug grazing than adult plants. However, in spring, adult herbaceous perennials, while regenerating shoots and leaves from buds located at the soil surface, are also potentially vulnerable. By contrast, woody species regenerating from buds above the soil surface are generally much less vulnerable as adults than as seedlings (Nystrand and Granström 1997).

Grasses tend to be unpalatable (Briner and Frank 1998; Fenner et al. 1999), possibly due to the common occurrence of fungal endophytes and / or the generally high silica content of grass leaves, both of which are known to reduce palatability to other herbivores (e.g., Gali-Muhtasib et al. 1992; Clay et al. 1993; Massey et al. 2006). On the other hand, because of their morphology, and high silica content, grass seedlings often lose whole leaves to slug grazing due to decapitation at the base of the flag leaf (Hulme 1994). They do however retain high potential for recovery from the basal meristem even when grazed down to the soil surface (Dirzo and Harper 1980).

The palatability of forbs varies substantially between species (Fenner et al. 1999). Work by Hulme (1994) suggests that species-specific differences in seedling size and / or in seedling chemistry may affect a species' vulnerability to slugs grazing its seedlings. Species with larger seedlings were more likely to be encountered by slugs in Hulme's (1994) study. This may have been because larger seedlings might be more apparent to slugs, however, whilst less frequently encountered by slugs, small seedlings are likely to be less able to recover after grazing. Given the strong correlation between seed size and initial seedling size (Hanf 1973; Baskin and Baskin 1998), seed size may therefore indicate both the likelihood of individual species being grazed by slugs and the likely outcome of this interaction.

Established plant strategy may also affect how vulnerable a species is to slug grazing. According to CSR strategy theory, slow-growing, stress-tolerant forb species from unproductive habitats invest a relatively larger part of their resources into morphological structures and chemical compounds that reduce palatability than do more competitive species, and are thus likely to be less palatable to generalist herbivores, such as slugs (Grime 2001). The impact of mollusc grazing on forb seedlings can be severe; entire seedling cohorts of a species can be eliminated (Bruelheide and Scheidel 1999; Hitchmough 2003). This may contribute to rarity or the patchy distribution of species, for example, *Pulsatilla vulgaris* (Wells and Barling 1971) and *Trollius europaeus* (Hitchmough 2003). Less palatable species may survive grazing, but be disadvantaged by the defoliation experienced amplifying the shading and root competition posed by other, less palatable, species in a community (Sessions and Kelly 2002; Hitchmough and de la Fleur 2006).

Although mollusc occurrence is often positively correlated with the degree of urbanization in a landscape (Holland et al. 2007), the disciplines that design and manage urban vegetation have historically been little concerned with mollusc herbivory. Over the past 50 years, the lower strata of designed planting have often consisted of monocultures of highly unpalatable shrub species (Thoday 2004). More intensively maintained areas of greenspace may contain garden-like plantings of perennial forbs that are potentially vulnerable when their shoots emerge in spring. In these plantings, forbs are planted at wide spacings that reduce competition for resources (Schwinning and Weiner 1998), and are regularly weeded or mulched to restrict weed cover. This maintains a relatively open ground-level stratum that is less favourable to molluscs (Dowling and Linscott 1985), reducing the damage experienced even by highly palatable species. This, in combination with the nocturnal and largely invisible damage to very young shoots, is reflected in the ambiguity shown in the horticultural literature to the importance of mollusc grazing as an ecological factor (Jelitto et al. 1990; Rice 2006).

In the past two decades interest has grown in using designed, species-rich herbaceous vegetation that mimics semi-natural stereotypes such as meadow and prairie, as an alternative to monocultural woody and herbaceous plantings (Kingsbury 2004). This has often been driven by the belief that this vegetation requires lower resource inputs for establishment and management than traditional plantings (Oudolf and Kingsbury 2005) whilst providing superior habitat for native fauna (Baines 2000) and colourful seasonal displays of flowers that are attractive to urban people (Dunnett and Hitchmough 2004). Such planting is seen as more sustainable, and adaptive to environmental change.

What has not been appreciated, is that the appearance of this vegetation and the persistence and recruitment of individual species, is potentially heavily influenced by selective mollusc grazing. In naturalistic herbaceous planting, higher plant densities result in shadier and moister conditions at ground level, resulting in more intense grazing for longer, and consequently higher levels of damage (Friedli and Frank 1998; Hitchmough 2003). Nystrand and Granström (1997) found a three-fold increase in seedling predation when the soil surface was moistened. Hitchmough (2009) found that the robust forb *Cephalaria alpina,* a species regarded as unpalatable in garden cultivation (Rice 2006), was eliminated by spring slug grazing when planted in managed urban meadow grassland.

An additional factor that necessitates a re-appraisal of the effects of molluscs on designed herbaceous vegetation is the increasing use of seed sowing *in situ* (e.g. Luscombe and Scott 2004) to establish naturalistic herbaceous vegetation. This practice greatly increases the risk that the most palatable species will be eliminated soon after emergence (Frank 2003), resulting in an initial loss of diversity as described for urban meadow vegetation by Hitchmough et al. (2008). For designed naturalistic plantings to be sustainable in the longer term there is a need for component species that are not extremely long-lived to be capable of recruitment from self-sown seed (Hitchmough and de la Fleur 2006).

The impacts of molluscs on these processes are in many cases more profound in designed urban vegetation than in rural habitat restoration/agri-environmental schemes (Wilby and Brown 2001; Buschmann et al. 2005), as with common native species there is the possibility that these will eventually re-colonize from populations outside the sown area during periods of reduced mollusc activity. This is highly unlikely for non-native species used in urban contexts to provide seasonal colour effects or physical structures that are not possible with native species alone (Hitchmough and Dunnett 2004). The former is extremely important in maintaining public support for vegetation in these contexts (Hands and Brown 2002; Todorova et al. 2004). Hitchmough and de la Fleur (2006) have found that it is possible to prevent the elimination of attractive but palatable species through the application of a 50mm mulch of coarse sand. Where resource shortfalls do not permit such approaches, knowledge of the relative palatability of different species at various stages of development to molluscs is required to inform the design of sustainable, naturalistic plant communities. There are only a few published studies commenting on mollusc predation of seedling and adult plants in designed vegetation (Hitchmough, et al. 2004; Hitchmough and de la Fleur 2006). Inclusion of information on palatability in horticultural texts, for example Rice (2006), is inconsistent at best.

This study looked at 26 species of North American prairie forbs and grasses commonly used as components of summer and autumn flowering, prairie-like herbaceous plantings in North Western Europe (Schmidt 2004a,b,c; Kühn 2005a,b; Hitchmough and de la Fleur 2006), and in North America (Ahern and Boughton 1994). These species are also an important food and habitat resource for many invertebrates and contribute to the high native invertebrate richness that has been recorded in designed urban landscapes in western Europe (Owen 1991; Smith et al. 2006). The overall aim of the study was to rank these species in terms of seedling and adult palatability to slugs under conditions that mimic those prevailing when such plant communities are i) established in practice by sowing seed *in situ*, and ii) during the emergence of adults shoots in spring.

Specific objectives were to study how: i) palatability varied between seedlings and adult plants, ii) manipulation of slug abundance related to observed levels of plant damage, iii) patterns of slug grazing varied between seedlings and adult plants, and iv) seed and adult plant characteristics influenced the outcome of slug grazing.

Materials and methods

Study species

Twenty four species of prairie forb and two prairie grasses (Table 1) were selected for use in this study. All of the species have attractive flowers and/or growth habit. The species were also chosen to include a wide range of seed sizes, to test the hypothesis that larger-seeded species are less prone to fatal damage from slug grazing at the seedling stage. They also represent strongly contrasting levels of potential productivity, to allow testing of the hypothesis that stress-tolerant species from unproductive habitats are typically less susceptible to generalist herbivores than more competitive species from productive habitats (Grime 2001).

#Table 1 approximately here#

Field methods

Rather than offering captive slugs leaf disks of adult plants under laboratory conditions to generate a palatability index (Fenner et al. 1999; Hendriks, et al. 1999), we carried out a two-year field study. Wild-living slugs were offered a free choice of co-occurring seedlings in a "cafeteria" style experiment of the tested prairie species in the spring of year one. In spring of year two they were offered the emerging young shoots and foliage of the plants that had survived seedling herbivory in the first year. This design more realistically incorporates factors that affect herbivore choice under field conditions, such as density (Weiner 1993, Fagan and Bishop 2000) and spatial arrangement of individual plant species, phenology (Breadmore and Kirk 1998), morphology (Scheidel and Bruelheide 1999), plant growth rate (Scheidel, and Bruelheide 2005), size (Hanley et al. 1995) and the total range of plant species present in a particular habitat (Hendriks et al. 1999).

The chosen study site was located within an area of derelict vegetable growing allotments in Walkley, Sheffield (53 ^{o}24'N, 1^{o}30'W, altitude 54m a.s.l.) that supported high densities of slugs. The experiment was surrounded on all sides by unmown grassland (dominated by *Holcus lanatus, Arrhenatherum elatius* and *Lolium perenne*) that represented an excellent habitat for slugs. The soil type was a clay loam, pH 6.2, and soil fertility was high (plant available N = 110 mg/L, P = 65 mg/L, K = 500 mg/L). In both years of the study, May rainfall in the Sheffield area was close to the long-term average, whereas April rainfall was substantially higher, particularly in 2000 (Table 2). Mean air temperatures exceeded the long-term average in spring 1999, but were meteorologically average in spring 2000 (Table 2).

#Table 2 approximately here#

Between autumn 1998 and early spring 1999, four 1.5m wide x 7m long sowing strips (henceforth referred to as strips A,B,C, and D) were sprayed with the herbicide glyphosate to create a plant-free surface into which replicate blocks of the experimental species were sown. Slug density was manipulated in these strips by applying slug pellets at different time intervals. Sown strips ran in parallel in a north-south direction and were separated from neighbouring strips by 5m wide bands of the previously described unmown grassland. In each strip, six replicate blocks of 1.9m x 0.75m were set up within which the twenty six species were sown in parallel monocultural rows of 600mm length, with neighbouring rows being separated by 70mm guard strips. The assignment of species to rows was randomized. A more conventional randomized block design was not possible given the need to achieve independence between treatments within a finite experimental area whilst also applying metaldehyde pellets to manipulate the slug density across the four sowing strips.

Given the experimental design employed, nocturnal (11.00pm) slug density was assessed before and during the experiment to provide an indication of how this varied across the site and of how efficient different regimes of slug pellet application were in creating a gradient in slug grazing pressure. Within each sowing strip, four 100mm Petri dishes containing 50g of a 1:1:4 mixture of “Somerfield Supermeat with beef”catfood:bran:water as a bait were placed on a grid at approximately 1.5m spacings. At each density assessment, slugs within a 300mm radius of the dish were counted and identified.

Slug density was manipulated in 1999 by applying Bayer Slug and Snail pellets (active ingredient: metaldehyde at 3.5% w/w) to the sown strips at 100 pellets/m^2 at differing frequencies, including no baiting (control, strip A), baiting once (May 2nd, strip B), baiting twice (May 2nd and May 16th strip C), and baiting continuously (at approximately 2 week intervals during May-September, Strip D). The role of strip D was primarily to preserve a predation-free population of seedlings that could be used in the following year, 2000, to assess slug damage to the emerging shoots of adult prairie plants.

As the seeds of many of the species used have a chilling requirement for germination, seed were pre-chilled in packets of moist sand in a fridge at 4^{o}C for varying durations to ensure that their chilling requirements were sufficiently satisfied to achieve temporally uniform germination of all species across the experiment. Commencing 14th April, within each replicate one hundred cold-stratified seed of each species was sown into separate 600 mm rows. The first emergents were recorded on the 30th April.

Within each sown row, emerged seedlings were counted on May 2nd, May 7th and then at 7-day intervals until May 28th. From May 7th, seedlings were apportioned to one of three categories: no visible damage; some damage; complete defoliation. May 1999 was unusually warm with average rainfall and seedlings grew very rapidly. By the end of May, surviving seedlings were large enough to escape intense predation, and assessment of slug damage ceased at that point.

Surviving seedlings were thinned out to a maximum of 10 seedlings per sowing row between June 14th and 20th 1999 to minimize self-thinning and thus increase plant size uniformity for year two of the study. On March 15th 2000, all rows of species in the sowing strips that had been pelleted once (strip B), twice (strip C) and continuously during 1999 (strip D), were assessed and scored in terms of their bud phenology-development. Strip A was excluded from consideration as many species had been eliminated from the replicates by intense slug grazing in 1999. Strip B was reassigned for 2000 as the control (no metaldehyde pellets applied), Strip C as pelleted once (March 20th 2000) and Strip D as pelleted twice (March 20th and April 14th 2000). Nocturnal slug numbers were monitored as previously described for 1999, from March 19th to May 5th 2000.

The degree of defoliation of all emerging shoots in all rows was assessed from March 15th at approximately 7-day intervals. Individual plants were assigned to one of 4 defoliation categories: <10%; 10-40%; 40-70%; >70%. At the same time, the stage of development of the emerging shoots was also assessed, using a four-point nominal scale (bud/leaf rosettes absent; bud/leaf rosettes present but no active growth; some initial stem-leaf growth; active stem and leaf growth).

Data analysis

Slug fauna and seedling establishment in the first year

Seedling establishment in relation to baiting regime was analyzed using the data on establishment collected on 28 May 1999. By then, the spring peak in slug density had already passed, and the plants established from the sown seed had grown enough to be considered past the critical stage. Also, at that point in time, sowing strips C and D still had a similar history of slug-pellet application. Data collected from these two strips in 1999 was therefore analyzed as being from the same baiting regime, and in the context of these analyses, strips C and D were treated as one individual sowing strip (CD) containing twice the number of sown rows and twice the number of Petri dish stations to assess slug numbers, compared to the other two sowing strips that were baited only once or not at all.

Using repeated-measures ANOVAs, we tested for differences in slug numbers between sowing strips subjected to different metaldehyde baiting regimes both prior to the first baiting on 2 May 1999, using slug count data from four sampling dates between 16 April 1999 and 1 May 1999, and after baiting had commenced, using data from three sampling dates between 7 May 1999 and 20 May 1999, i.e. prior to the final assessment of seedling establishment on 28 May 1999. Again, data from sowing strips C and D were pooled, as up to then, their baiting regimes were identical. All slug count data were square-root transformed prior to analysis to improve data distributional properties. Time was treated as the within-subjects factor, and baiting regime as a between-subjects factor. In case of significant between-subjects effects we used a Games-Howell post-hoc test, which is known to handle unequal group sizes of data well, to establish pairwise differences in slug density between baiting treatments. The sphericity assumption specific to repeated measures analysis was reasonably well fulfilled for both analyses, and therefore statistical testing of within-subjects effects was based on uncorrected F-ratios.

Analyses of seedling establishment were based on the summed proportion of seedlings established from the sown seed showing either no damage or only some damage on 28 May 1999, excluding those seedlings that were completely defoliated. To test for differences in seedling establishment between treatments, we analyzed each species separately with one-factor analyses of variance. Prior to analysis, the data was arcsine-transformed. ANOVAs were based on type III sums of squares, and baiting regime was treated as the fixed factor. In case of significant treatment effects, we carried out post-hoc comparisons using the Tukey-Kramer method devised to deal with unequal group sizes. To characterize the relative susceptibility of the different species to fatal damage by slug grazing, we calculated the percent difference in mean numbers of undamaged plus slightly damaged seedlings in the twice pelleted treatment, compared to the numbers achieved in the control treatment. To test the hypothesis that the seedlings of small-seeded species were more susceptible to fatal damage by slugs, we then carried out a Spearman rank correlation of these percent difference values vs. mean seed weights, extracted from the Kew Gardens Seed Information Database (Liu et al. 2008), of the 21 species that successfully established. As we had a specific hypothesis regarding the sign of the relationship, we tested its significance using a one-sided test. Using relative adult growth productivity, as specified in Table 1, as a surrogate for competitiveness *sensu* Grime (2001), we also tested the hypothesis that the seedlings of more competitive species are more susceptible to slug herbivory, again using Spearman rank correlation and significance testing using the one-sided test. Finally, to gain some indication of the probability for each species of getting attacked by slugs, we calculated the relative proportions of undamaged seedlings vs. moderately damaged seedlings.

Slug fauna, plant emergence phenology, and slug-related damage in the second year

As with the slug data collected in 1999, repeated-measures ANOVA was used to test for differences in slug numbers between baiting regimes in the second year of the study, 2000. However, as fewer slug censuses were carried out in 2000, with only one prior to the first application of slug pellets, the data was not split into pre-baiting data and post-baiting data, but jointly analyzed. The analysis was carried out in the same way as the analyses of the data collected in 1999. Again, the sphericity assumption was fulfilled and the testing of within-subjects effects was based on uncorrected F-ratios.

Emergence phenology for the second-year plants was assessed visually by drawing a phenology diagram based on qualitative data, to indicate which of the phenological stages of a species, as defined in the Field Methods section, were present at a particular point in time. Only data from strip D, which was most regularly pelleted, were used for the drawing of this diagram, as in the less frequently pelleted strips, grazing by slugs may have delayed the emergence of some species (personal observation by J. Hitchmough). As this assessment was based on qualitative data, we could also include those species that on the basis of their low emergence were excluded from the analysis of seedling establishment.

In many instances, several of the ten plants left per sowing row for the second year trial died between the last census in the first year of the study and the resumption of censuses in the following spring. Thus, the number of one-year old plants available for the second year of the study varied strongly among sowing rows. This variation in numbers of plants among replicate sowing rows precluded us from performing standard statistical analyses of proportions of plants defoliated, as this would invariably have lent more weight to plants in sowing rows with only few plants, compared to sowing rows with many surviving plants. We thus decided to explore proportions of slug-damaged plants visually, based on pooled data from all sowing rows per species and baiting treatment. Throughout the recording period in the second year of the study, 2000, only a few of the individual plants damaged by slug grazing experienced more than 40% defoliation during any given census. Therefore, we did not look at individual damage categories separately, but instead at summed proportions of plants exhibiting >10% defoliation. Slug-related plant damage in the second year was thus explored using bar charts showing for each census date the proportion of emerging shoots exhibiting >10% defoliation in the various slug baiting treatments. In addition to the five species that, due to poor seedling emergence, could not be included in the first-year analyses, three additional species – *Asclepias tuberosa*, *Coreopsis* *lanceolata*, and *Monarda fistulosa*, were also excluded from this graphic exploration of second-year slug damage. In the case of *A. tuberosa*, slugs feeding on the fleshy white rhizomes of this species caused considerable mortality over winter, and of the few individuals that emerged at the very end of the census period, those in sowing strips B and C experienced high levels of defoliation (J. Hitchmough, personal observation). In the other two species, *C. lanceolata* and *M. fistulosa*, only a few individuals were left at the end of the winter, thus rendering an accurate characterization of second-year slug damage in the various baiting treatments impossible.

Results

First-year results

Slug fauna

The four most abundant slug species, in descending order, were *Arion subfuscus* > *Arion hortensis* > *Arion ater* > *Deroceras reticulatum*, with the first two species being approximately four times more abundant than the latter two. *Limax flavus* and *Milax budapestensis* were encountered only occasionally. Overall slug numbers per Petri dish station for individual counts are indicated in Fig. 1.

Slug numbers prior to baiting on May 2nd (Table 3) did not differ significantly between the sown strips A, B, and CD (Baiting regime: $P = 0.098$), nor did they change differently among strips (Time × Baiting regime: $P = 0.795$), although there were large and highly significant treatment-independent differences in slug numbers between individual count dates (Time: $P < 0.001$; Fig. 1). These differences between count dates seemed to depend on soil moisture and air temperature at the time of the count, with the highest counts on warmer, wet nights. There were similarly significant differences in slug numbers between count dates after the initiation of slug baiting (Fig. 1, grey bars), as indicated by the results of a second analysis covering this latter period (Time: P < 0.001; see Table 3). At the same time, in this latter period there were highly significant differences in the number of slugs counted on sowing strips characterized by different baiting frequencies (Baiting regime: P < 0.001), with the size of these differences differing between counts (Time × Baiting regime: P = 0.020). Games-Howell post hoc testing indicated that slug numbers in this latter period were significantly lower in the baited sowing strips B and CD, compared to the unbaited sowing strip A (B vs. A: P = 0.004; CD vs. A: P < 0.001), but failed to discern any significant differences between strip B and strip CD (P = 0.932).

#Table 3 approximately here#

#Figure 1 approximately here#

Seedling establishment

Levels of seedling emergence were very low in five of the sown plant species (*A. laevis, C. tripteris, E. purpurea, L. pycnostachya, S. heterolepis*), not exceeding 5% of the sown seeds in any of the baiting treatments. Results for these species do not allow the drawing of any conclusions regarding the susceptibility of their seedlings to slug grazing, and are thus not presented in more detail. First-year results for the other species are shown in Fig. 2.

#Figure 2 approximately here#

We found significant differences in seedling establishment between different baiting regimes in 14 out of 21 analyzed species. In 13 species, baiting with slug pellets resulted in an increased proportion of sown seeds that successfully established as seedlings. In eight of these 13 species – *Asclepias tuberosa*, *Cacalia atriplicifolia*, *Coreopsis lanceolata*, *Echinacea pallida*, *Helianthus mollis*, *Liatris aspera*, *Monarda fistulosa* and *Ratibida pinnata* – both baiting once and baiting twice resulted in a significant increase in establishment compared to no baiting, but baiting twice did not result in a significant further increase compared to baiting only once. In a further five species – *Aster oolentangiensis*, *Eupatorium maculatum*, *Solidago rigida*, *Solidago speciosa* and *Veronicastrum virginicum* – baiting twice did result in a significant increase in the number of seedlings established, whereas baiting once did not. Finally, in one species, *Schizachyrium scoparium*, significantly higher proportions of sown seed successfully established as seedlings in the strips baited twice than in the strip baited once, although neither of these treatments significantly differed from the unbaited control treatment. In seven species, seedling establishment was not significantly influenced by the baiting regime. This group of species included all four *Silphium* species (*S. integrifolium, S. laciniatum*, *S. perfoliatum*, and *S. terebinthinaceum*), *Solidago ohioensis*, and also two species with a small but non-significant increase in seedling establishment in response to baiting, *Rudbeckia subtomentosa* and *Baptisia australis*, the latter being the only legume species included in the study.

#Figure 3 approximately here#

While Figure 2 illustrates the effect of baiting on seedling establishment within each species, Figure 3, by showing for each species the percent change in numbers of seedlings established when baited twice, compared to the treatment without baiting, illustrates relative effects between the species as a whole. The most pronounced positive effect was found for *Liatris aspera*, with an increase in seedling establishment of 660 % when baiting twice, compared to no slug baiting.

Other species that benefited from baiting with an increase in seedling establishment of between 250 % and 500 %, included *Cacalia atriplicifolia*, *Monarda fistulosa*, *Asclepias tuberosa*, and *Veronicastrum virginicum*. By contrast, seedling establishment in all four tested *Silphium* species was much the same on the strips baited twice as it was on the unbaited strip. While no statistically significant effects of baiting were found in the cases of *Baptisia australis* and *Rudbeckia subtomentosa*, seedling establishment in these two species nevertheless was 46 % and 78 %, respectively, higher in these species when baited twice, compared to no baiting.

A negative Spearman rank correlation ($r_S = -0.43$) that was significant according to the one-sided test ($P = 0.026$; see Figure 4a) indicated that, in line with our hypothesis, there may be a negative relationship between seed weight and the susceptibility of a species' seedlings to slug grazing. A hypothesized positive relationship between a species response to baiting and relative adult growth productivity could not be confirmed; the negative correlation coefficient suggested that if any relationship existed this would more likely to be negative (Spearman $r_S = -0.32$, one-sided test: $P = 0.076$; see Figure 4b).

#Figure 4 approximately here#

Without any slug control measures, all species, with the possible exception of *Schizachyrium scoparium*, are attacked by slugs (Figure 5). Without any slug control the large-seeded test species, such as *Baptisia australis* and *Silphium* species, have a larger proportion of damaged seedlings, than many small-seeded test species, such as *Eupatorium maculatum, Monarda fistulosa, Solidago ohioensis* and *Veronicastrum virginicum.*

#Figure 5 approximately here#

Second-year results

Slug fauna

In 2000, the slug fauna at the experimental site was dominated by the same four species as in 1999. However, in 2000, *Deroceras reticulatum* made up about 50% of all individuals recorded in 2000, and was thus far more prominent than the three *Arion* species, which were, in descending order, *A. subfuscus* > *A. hortensis* > *A. ater*. In addition, a few individuals of *Milax budapestensis* were also recorded.

As in 1999, slug numbers differed strongly between counts, depending on weather conditions at the time of the counts (Time: $P < 0.001$; see also Fig. 6). There also were highly significant differences in slug numbers between different baiting frequencies (Baiting regime: $P = 0.008$), with post hoc Games Howell tests indicating that slug numbers were significantly lower in the twice-baited sowing strip D, compared to the unbaited sowing strip B ($P = 0.033$). There were however no significant differences between either of these two strips and strip C that was only baited once (B vs. C: $P = 0.102$; D vs. C: $P = 0.343$). There was a slight, but non-significant tendency for these differences among sowing strips to vary between counts (Time × Baiting regime: $P = 0.089$).

#Figure 6 approximately here#

#Table 4 approximately here#

Plant emergence phenology and levels of slug-related defoliation

At the time of the first second-year field census on 17 March 2000, five species – *Aster laevis, A. oolentangiensis, Coreopsis lanceolata, Monarda fistulosa*, and *Solidago rigida* – were already actively growing, and active growth in several other species had just started (Figure 7). Nevertheless, in a group of seven species – *Liatris aspera, L. pycnostachya, Helianthus mollis, Schizachyrium scoparium, Baptisia australis, Eupatorium maculatum,* and *Asclepias tuberosa* – no active growth was observed until several weeks later. Within this latter group, *S. scoparium* began active growth relatively early, but then growth stopped during a cold spell and only resumed a few weeks later.

#Figure 7 approximately here#

Figure 8 indicates for individual test species the proportion of plants exhibiting >10% slug-related defoliation in the various baiting regimes at the six plant census dates in year 2. Defoliation levels generally were much lower on the plots that were baited twice than on the plots that remained unbaited or were only baited once. High levels of defoliation were observed in *Ratibida pinnata*, in particular at the first two census dates. Levels of defoliation were slightly lower in *Cacalia atriplicifolia*, but in this species marked levels of defoliation were observed throughout the census period. In *Aster oolentangiensis,* one of the test species with a very early emergence phenology, marked defoliation was only observed during the early censuses, whereas in the late emerger *Liatris aspera*, levels of defoliation peaked during the later censuses (Figure 8). By contrast, the majority of species, including all tested *Solidago* and *Silphium* species, but also *B. australis, E. pallida, E. maculatum, H. mollis, R. subtomentosum, S. scoparium* and *V. virginicum,* were generally not heavily defoliated (Figure 8).

#Figure 8 approximately here#

Discussion

The slug fauna

Prior to baiting, slug numbers were relatively uniform across the experimental site, and dominated by *Arion* species. Snails were extremely rare. Nocturnal slug abundance varied considerably across census dates, and, as with previous studies (Barnes and Weil 1945; Crawford-Sidebotham 1972), was highest, and damage greatest (Nystrand and Granström 1997), when the soil surface was moist. Slug numbers at the stations declined on cold nights, due to a reduction in slug activity commonly associated with temperatures below 5.0^{o}C (White 1959). In 1999, baiting once with metaldehyde was sufficient to significantly reduce live slug numbers, no significant further reduction was achieved by a second application. By contrast, in 2000, two applications of metaldehyde were required for a significant reduction of slug numbers, baiting only once did not significantly reduce slug numbers compared to no baiting.

These differences between the two years regarding the efficacy of a single application may be due to the spring of 2000 having been markedly wetter than the spring of 1999 (Table 2), and this may have reduced the duration of action of a single metaldehyde application in 2000 and necessitated a second application. Also, due to these differences in rainfall, whilst slug numbers in 2000 overall were similar to those recorded in 1999, slugs were probably able to forage for longer and hence cause more damage in 2000. Duration of foraging may have been further facilitated by the dense cover of prairie plants in 2000; in 1999 these plants were still seedlings and less of the soil surface was shaded. A preference of shaded microhabitats is known for a number of slug species (Sturm

2007), and may provide one explanation for slug damage being greater in more shaded conditions (Liang and Stehlik 2009), and is also in agreement with our own observation that under shaded conditions, slugs seemed to feed for longer periods, often throughout the day, rather than being restricted largely to after dark (J.Hitchmough, personal observation).

Seedling establishment in the first year

Seedling size, adult growth productivity, and palatability

The results of our study demonstrate that seedlings of large-seeded species, whilst being more likely to be grazed by slugs, were less likely to be killed as a result than seedlings of small-seeded species. Seed size tends to correlate closely with initial seedling size (Baskin and Baskin 1998), suggesting that this is not because seedlings from large-seeded species are less palatable *per se*, but because their above-ground parts are less likely to be removed in a single feeding event, enabling them to maintain a supply of carbohydrates to fuel recovery. Accordingly, the seedlings of the small-seeded *V. virginicum*, a species that appears unpalatable as an adult, strongly benefited at the seedling stage from slug baiting (Figure 3). Similarly, the five largest-seeded species in our study – *Silphium laciniatum, S.integrifolium*, *S.terebinthinaceum*, *B. australis,* and *S. perfoliatum* (see Table 1 for seed weights) – were all in the group of seven species whose establishment from seed was not significantly enhanced by baiting (Figure 2). The seedlings of all of these species were obviously palatable to slugs, as evidenced by the large proportions grazed in the absence of slug baiting (Figure 5). For species with small to medium-sized seeds, unpalatability *per se* seems to be a prerequisite for ensuring survival in the presence of slugs. The remaining two species whose establishment was not improved by baiting (*Rudbeckia subtomentosa*, 0.94mg and *Solidago ohioensis*, 0.21mg) are clearly unpalatable. Conversely, three of the species whose establishment was most improved by baiting, *Liatris aspera* (2.1mg), *Cacalia atriplicifolia* (2.42mg), and *Asclepias tuberosa* (6.8mg) have much larger seed and seedlings but are nevertheless susceptible to slug grazing. A few prairie species, irrespective of size and growth rate, are highly unpalatable as young seedlings, presumably because of high silica (Blackman 1971), as in the case of *Schizachyrium scoparium*, or secondary metabolite content (Albrectsen 2004) for example, *Solidago ohioensis*.

Contrary to our hypothesis, there was no evidence for species characterized by lower adult growth productivity, that might invest more resources in defence instead of growth, being less palatable at the seedling stage than more productive species. Defence against herbivores as postulated by CSR strategy may be more applicable to adult plants than to seedlings. Levels of secondary metabolites acting as herbivore defense seem to be particularly low in young seedlings, and increase steadily with plant age through to adulthood (Albrectsen et al. 2004; Elger et al 2009). Structural defence mechanisms such as spines, trichomes, or sclerophylly, also tend to be poorly developed in seedlings (Hanley et al. 1995). It may therefore not be so surprising that a known link between adult growth rate and adult palatability (Grime, 2001) does not extend to adult growth rate and early palatability. Instead, seedling/juvenile growth rate tends to be a much better predictor of seedling palatability to slugs (Kelly and Hanley 2005). In our study, dense coverings of epidermal hairs were evident on the first true leaves/petioles/stems of seedlings of species whose establishment was significantly reduced (*Asclepias tuberosa, Echinacea pallida, Helianthus mollis*) and not significantly reduced by slugs (*Silphium laciniatum* and *S. terebinthinaceum*). Contrary to our initial hypothesis, the more productive species in this study were typically better able to survive slug herbivory, presumably through being able to escape the most vulnerable stages more quickly. Across the study it was evident that individuals that were not attacked by slugs grew faster than those that were. This is not surprising given the known role of nutrient reserves in cotyledons in boosting seedling growth (Milberg and Lamont 1997; Hanley et al. 2004). Theoretical classifications on the basis of plant productivity may be less meaningful for plants growing in cultivation under more productive conditions, which may restrict the degree to which means of defence develop. Accordingly, it has been hypothesized that many invertebrate herbivores may preferentially feed on more vigorous plants, compared to plants growing in stressful conditions (Price 1991). There is evidence that this also applies to the seedling stage of plants, as Albrectsen et al. (2004) found that faster-growing fertilized seedlings were more palatable, although they also reached the size threshold to deter slug herbivory, and the physiological threshold for producing defensive secondary metabolites, sooner than slower growing seedlings. In support of this line of argument, the more stress-tolerating species in our study, for example *Asclepias tuberosa*, and *Echinacea pallida*, show marked morphological differences in their wild habitat (J. Hitchmough, personal observation), compared to in cultivation in the UK, with much tougher stems and leaves, and possibly higher levels of defense compounds. Nutrient levels in the topsoil of the experimental site indicate high levels of site productivity (N = 110mg/L, P = 65mg/L, K = 500mg/L). This is considerably higher than comparable values for a productive North American prairie silt loam (N= 15mg/L, P= 50mg/L, K=250mg/L), and much higher than values measured for the infertile sandy soils that support more stress tolerating prairie species (N=10mg/L, P=3mg/L, K=60; see Bradshaw & Chadwick 1980).

Effects of baiting on individual species

Based on the percent change in seedling establishment caused by two applications of slug pellets compared to the unbaited control treatment, species can be grouped into three categories: (1) species whose establishment from seed is only slightly influenced by slug baiting; (2) species whose establishment can be significantly, but still relatively moderately improved by the application of slug pellets; and (3) species for which successful establishment from seed is highly dependent on control of slug populations (Fig. 2). On the basis of long experience in practice (Hitchmough 2004), North American prairie species as a group are considerably more palatable to molluscs than are for example, European meadow plants. Although the literature is rather fragmentary, slugs appear to be minor herbivores in prairie ecosystems in North America and hence natural selection pressure to evolve specific defences is presumed to be limited.

Slugs and adult plants in the second year

Adult prairie plants were typically less severely damaged by slugs than were seedlings of the same species. Similar results have been described by Fenner et al. (1999) and Hitchmough (2003). However, three species in the present study – *C. atriplicifolia, L. aspera,* and *R. pinnata* sustained pronounced slug-related damage as adults, indicating high levels of adult palatability. Although not included in the analysis due to its very late emergence, where not baited, *Asclepias tuberosa* was also seriously damaged (J.Hitchmough, personal observation). Observation of many of the species discussed in this paper over a five year period in sown prairie plant communities in Northern England (Hitchmough and de la Fleur 2006) suggests that in the absence of slug control measures, *A. laevis, E. pallida, E. purpurea,* and *M. fistulosa* are likely to be eliminated or greatly reduced in number by slug herbivory. *Baptisia australis, C. lanceolata, H. mollis, R. subtomentosa, S. integrifolium, S. integrifolium, Solidago ohioensis* and *V. virginicum* generally exhibit little damage as adults (Hitchmough and de la Fleur 2006).

In common with other studies (Bruelheide and Scheidel 1999; Albrectsen et al. 2004), plant phenology and morphology markedly influenced the degree of slug damage experienced by adult prairie plants. Nocturnal slug densities, whilst heavily affected by soil moisture, are typically lower in March than later in spring. Early emerging herbaceous plants may therefore encounter fewer molluscs, but in the case of palatable species this advantage may be negated by being the only “food on the table”. *Monarda fistulosa* overwinters as miniature leaf-rosettes and these were continually grazed between autumn and spring, leading ultimately to elimination of this species. The early-leafing *Ratibida pinnata* was almost completely defoliated by slug grazing at the first two census dates but even when not baited, was eventually able to recover. This may have been due to a decline in grazing pressure as more food options became available. Another factor that may potentially have played a role may be a decline in palatability of this species as it passed peak spring growth and started to allocate more resources to defence mechanisms (Elger and Barrat-Segretain 2004), but this has to remain speculation as an investigation of this aspect was beyond the scope of this study. Later-emerging species face the scenario of higher densities of slugs that are able to feed for longer as emergent shoots increase shading at the soil surface. The larger range of food plants present does not seem to result in a reduction of the grazing pressure experienced by the most palatable species. *Cacalia atriplicifolia* appeared to actively attract slugs to feed on it even in the baited treatments.

Many of the species eventually grew tall enough for their growth points and leaves to escape intense herbivory (Rathcke 1985). Slugs are capable of climbing into the canopy (Albrechtson, et al. 2004) but generally choose not to. Species that are palatable and maintain most of their leafage in a basal rosette or on the lower portions of their stem close to the ground, for example, *A. tuberosa, E. pallida, E. purpurea, L. aspera, R. pinnata,* and *S. rigida,* continue to be subject to heavy grazing. In potentially palatable species with tall leafy stems, such as *E. maculatum, R. subtomentosa,* and *S. speciosa* slug grazing is typically restricted to early spring as shoots emerge from the soil. Young shoots of *B. australis* are often heavily browsed as they emerge from the soil but then adopt a thrusting shoot behaviour (Grime 2001) and elongate rapidly out of the reach of most slugs. This mechanism is found in a number of highly successful clonal colonizing herbaceous species and whilst often thought of primarily as a means of pushing through litter and foliage canopies to intercept light (Williamson and Fitter 1996), it also provides a successful means of escaping spring slug predation.

Conclusions

This study provided an evaluation of the effect of slug predation on North American prairie plants under conditions that closely approximated to their use in naturalistic plantings in landscape practice, where slugs are simultaneous offered a range of different species to feed upon, initially as seedlings but then as adults. As seedlings, prairie species varied considerably in palatability. Palatability interacted with physical size and growth rate of seedlings to determine capacity to establish in the presence of slug grazing. Palatable species that did not have very large, or fast growing seedlings were generally eliminated from unbaited plots. Some of the species whose establishment from seed was significantly reduced by slug grazing were able to withstand grazing as adults in the second year of the study, although the most highly palatable species, for example *Cacalia atriplicifolia,* were largely eliminated by the end of the second year in the absence of baiting. This study suggests that, in line with recent findings on the negative effect of native generalist herbivores on the success of invasion by non-native plants (Levine et al. 2004; Parker et al. 2006), the risk of North American prairie species escaping beyond the planting site may be low in slug-rich temperate European climates, and may likely be restricted to relatively few species that have either atypically large seed, rapid growth or unusually low palatability. On the other hand, the findings of our study also suggest that, as hypothesized by Maze (2009), high densities of introduced European slugs may have the potential to affect population and community dynamics of prairie plants in their native range, although findings from Australia where European slugs have also been introduced suggest that this may most likely be the case near urban settlements (Holland et. al 2007).

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Table 1. Prairie forbs and grasses used in the study (nomenclature follows; www.efloras.org/flora)

Species	Family	Seed weight (mg)	Relative adult growth productivity	Typical soil moisture regime in habitat
Asclepias tuberosa	Asclepiadaceae	6.8	low	dry-mesic
Aster laevis [A]	Asteraceae	0.31	medium	mesic
Aster oolentangiensis[B]	Asteraceae	0.17	medium	mesic
Baptisia australis	Fabaceae	18	medium	mesic
Cacalia atriplicifolia [C]	Asteraceae	2.42	high	mesic-wet
Coreopsis lanceolata	Asteraceae	1.3	medium	dry-mesic
Coreopsis tripteris	Asteraceae	2.56	high	mesic-wet
Echinacea pallida	Asteraceae	5.66	low	dry-mesic
Echinacea purpurea	Asteraceae	2.42	medium	mesic-wet
Eupatorium maculatum	Asteraceae	0.28	high	wet
Helianthus mollis	Asteraceae	4.7	medium-high	dry-mesic
Liatris aspera	Asteraceae	2.1	low	dry
Liatris pycnostachya	Asteraceae	1.9	low-medium	mesic-wet
Monarda fistulosa	Lamiaceae	0.4	medium	dry-mesic
Ratibida pinnata	Asteraceae	0.87	medium	mesic
Rudbeckia subtomentosum	Asteraceae	0.94	medium-high	mesic-wet
Schizachyrium scoparium	Poaceae	1.5	low	dry
Silphium integrifolium	Asteraceae	30.65	medium-high	dry-mesic
Silphium laciniatum	Asteraceae	78.05	medium-high	dry-mesic
Silphium perfoliatum	Asteraceae	6.85	very high	wet
Silphium terebinthinaceum	Asteraceae	25.8	medium-high	mesic-wet
Solidago ohioensis	Asteraceae	0.21	medium	wet
Solidago rigida	Asteraceae	0.9	medium	dry-mesic

Solidago speciosa	Asteraceae	0.3	low-medium	dry-mesic
Sporobolus heterolepis	Poaceae	1.9	low	dry-mesic
Veronicastrum virginicum	Scrophulariaceae	0.07	medium	wet

[A] = *Symphyotrichum laeve* is the revised name for *Aster laevis. The latter is retained here as Symphyotrichum is not widely used outside the USA.*

[B] = *Symphyotrichum oolentangiense* is the revised name for *Aster oolentangiensis.*

[C] = *Arnoglossum atriplicifolium*, is the revised name for *Cacalia atriplicifolia*.

Table 2. Weather during the main period of slug grazing in the spring of the study years 1999 and 2000, as compared with the long-term average 1971-2000 (Met Office 2008a,b).

Weather parameter	Month	1999	2000	1971-2000
Total rainfall [mm]	April	91.6	153.3	62.5
	May	51	63.9	55.5
Mean temperature [°C]	April	9.6	8.0	8.0
	May	13.2	12.0	11.4

Table 3. Results of repeated measures analyses of slug numbers in 1999.

	Within-subjects effects				Between-subjects effects			
Period	Source	df	*F*	*P*	Source	df	*F*	*P*
Prior to first baiting	Time	3	29.07	< **0.001**	Intercept	1	181.58	< **0.001**
	Time × Baiting regime	6	0.51	0.795	Baiting regime	2	2.79	0.098
	Error	39			Error	13		
Between first baiting and final seedling census	Time	2	18.03	< **0.001**	Intercept	1	398.56	< **0.001**
	Time × Baiting regime	4	3.50	**0.020**	Baiting regime	2	21.32	< **0.001**
	Error	26			Error	13		

Table 4. Results of a repeated measures analysis of slug numbers in 2000.

Within-subjects effects				Between-subjects effects			
Source	df	*F*	*P*	Source	df	*F*	*P*
Time	4	7.98	**< 0.001**	Intercept	1	1336.74	**< 0.001**
Time × Baiting regime	8	1.91	0.089	Baiting regime	2	8.65	**0.008**
Error	36			Error	9		

Figure 1. Number of slugs per Petri dish station in the different slug baiting regimes in 1999. Back-transformed mean values ± standard errors are shown for the seven counts carried out prior to the final seedling assessment. The dates of slug pellet applications are indicated by black arrows.

Figure 2. Effects of slug baiting on seedling establishment in 21 prairie plant species one month after the onset of seedling emergence. Values represent number of seedlings in the “no damage” to “some damage” categories on May 28th 1999 expressed as a percentage of the total number of sown seeds. Back-transformed mean values ± standard errors are shown.

Figure 3. Percent difference in the number of undamaged or only slightly damaged seedlings that were established on strips C and D that were pelleted twice at the time of the seedling census on 28 May 1999, compared to the numbers of seedlings established on the untreated control strip A.

Figure 4. Relationship between the relative response in seedling emergence of a species to slug baiting, expressed as percent difference in the number of undamaged or only slightly damaged seedlings established on 28 May 19999, and (a) seed weight, (b) relative adult growth productivity. As the seed weight distribution in our data setw as strongly skewed, with a large number species having relatively small seeds, and only a small number of species characterized by large seeds, graph (a) shows log-transformed seed weights for a better illustration of the relationship.

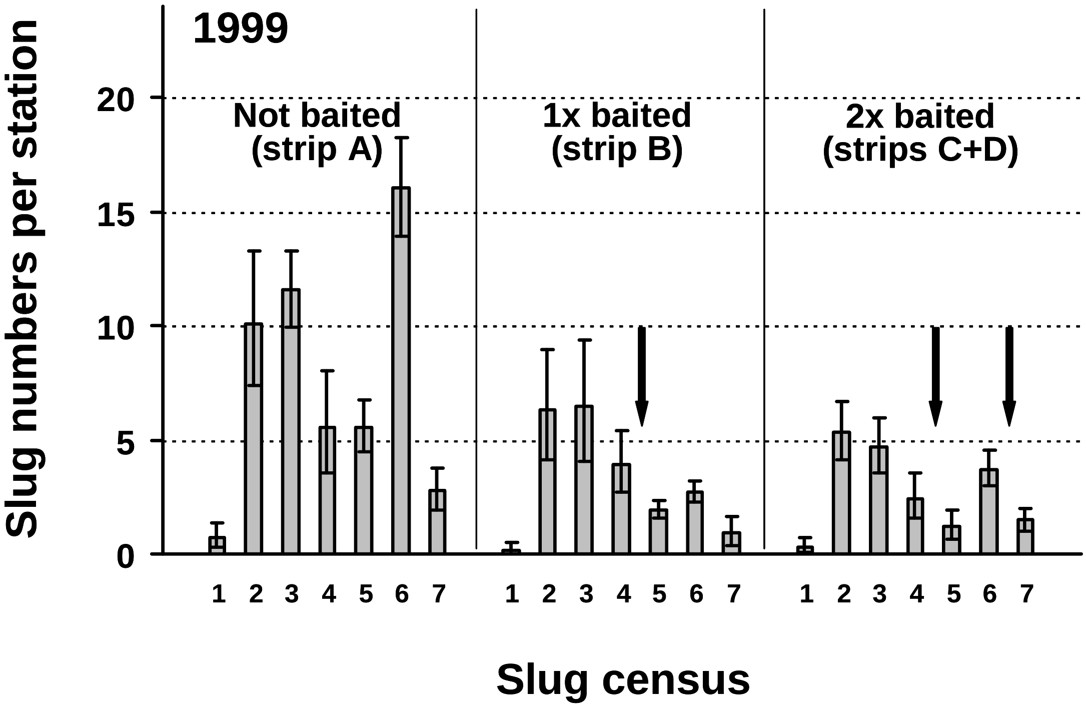
Figure 5. Relative proportions of undamaged and moderately damaged seedlings in 21 prairie plant species.Values are based on numbers of seedlings in two catregories on the May 28th 1999 census.

Figure 6. Number of slugs per Petri dish station in the different slug baiting regimes in 2000. Back-transformed mean values ± standard errors are shown for the five counts carried out prior to the final plant defoliation assessment. The dates of slug pellet applications are indicated by black arrows.

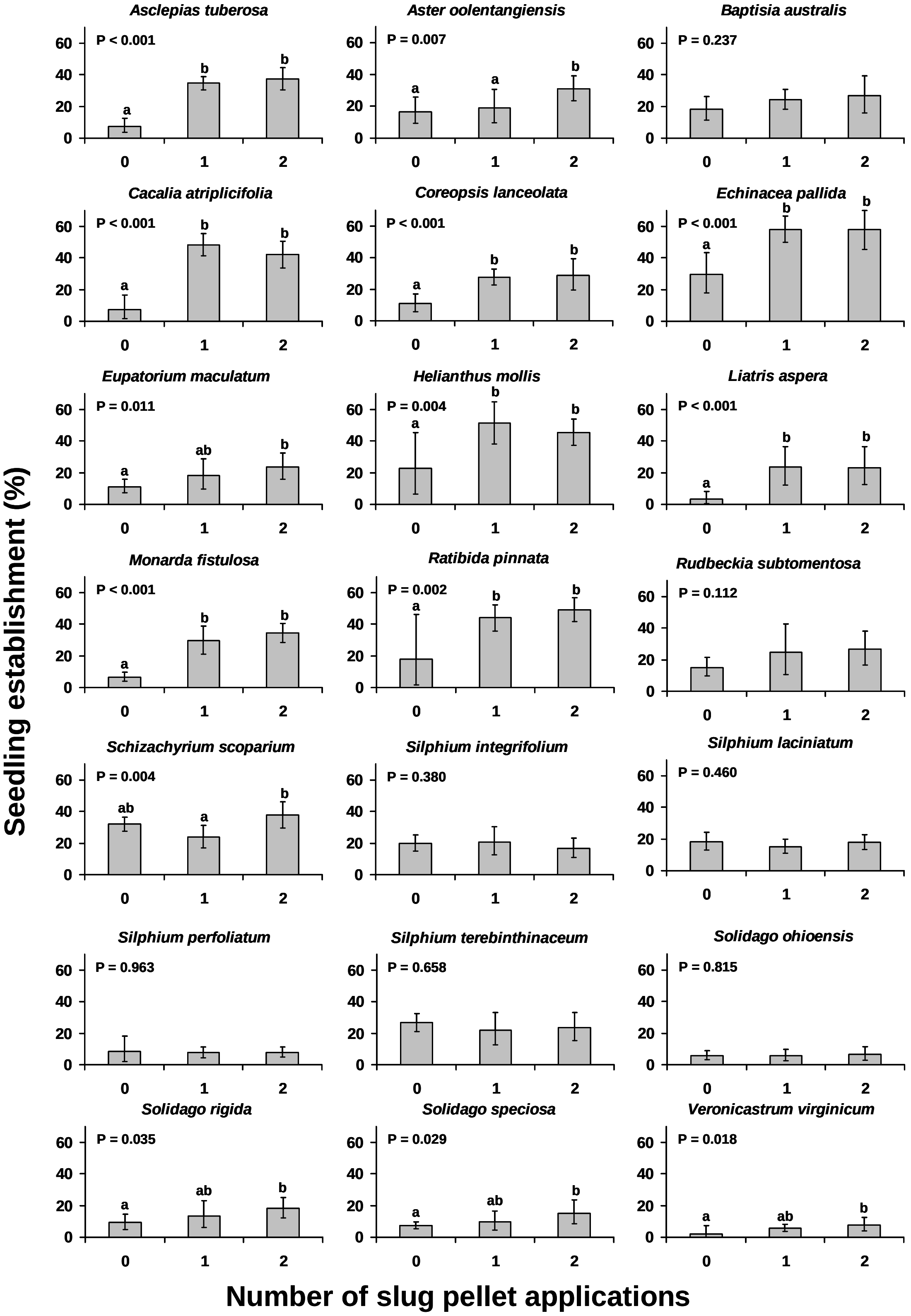
Figure 7. Phenology diagram showing the relative timing of emergence of plants in year 2 of the experiment. The diagram is based on phonological census data collected in the field between 17 March 2000 and 31 May 2000. It shows for 24 of the sown test species which of the four phenological stages were present at a particular census date, but does provide an indication of the actual percentage of shoots falling into a particular category.

Figure 8. Effects of slug baiting on spring defoliation levels in spring in 18 prairie plant species one year after sowing. Values represent the percentage of emergent shoots with a defoliation >10%. In five species, defoliation never exceeded 10% of any shoot.

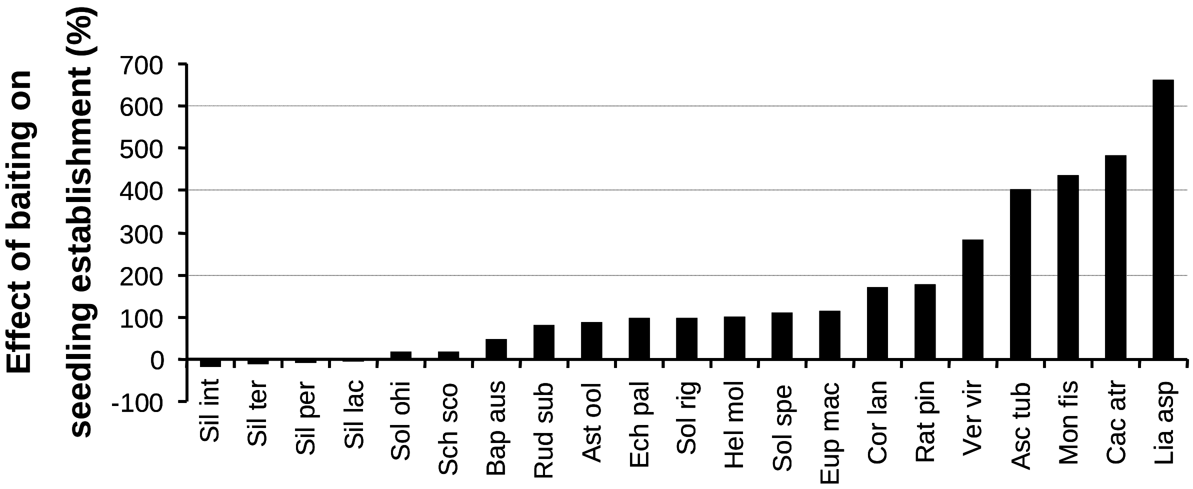
(Figure 1)


1999
Slug numbers per station
0
5
10
15
20
Not baited (strip A)
1x baited (strip B)
2x baited (strips C+D)
1 2 3 4 5 6 7
1 2 3 4 5 6 7
1 2 3 4 5 6 7
Slug census

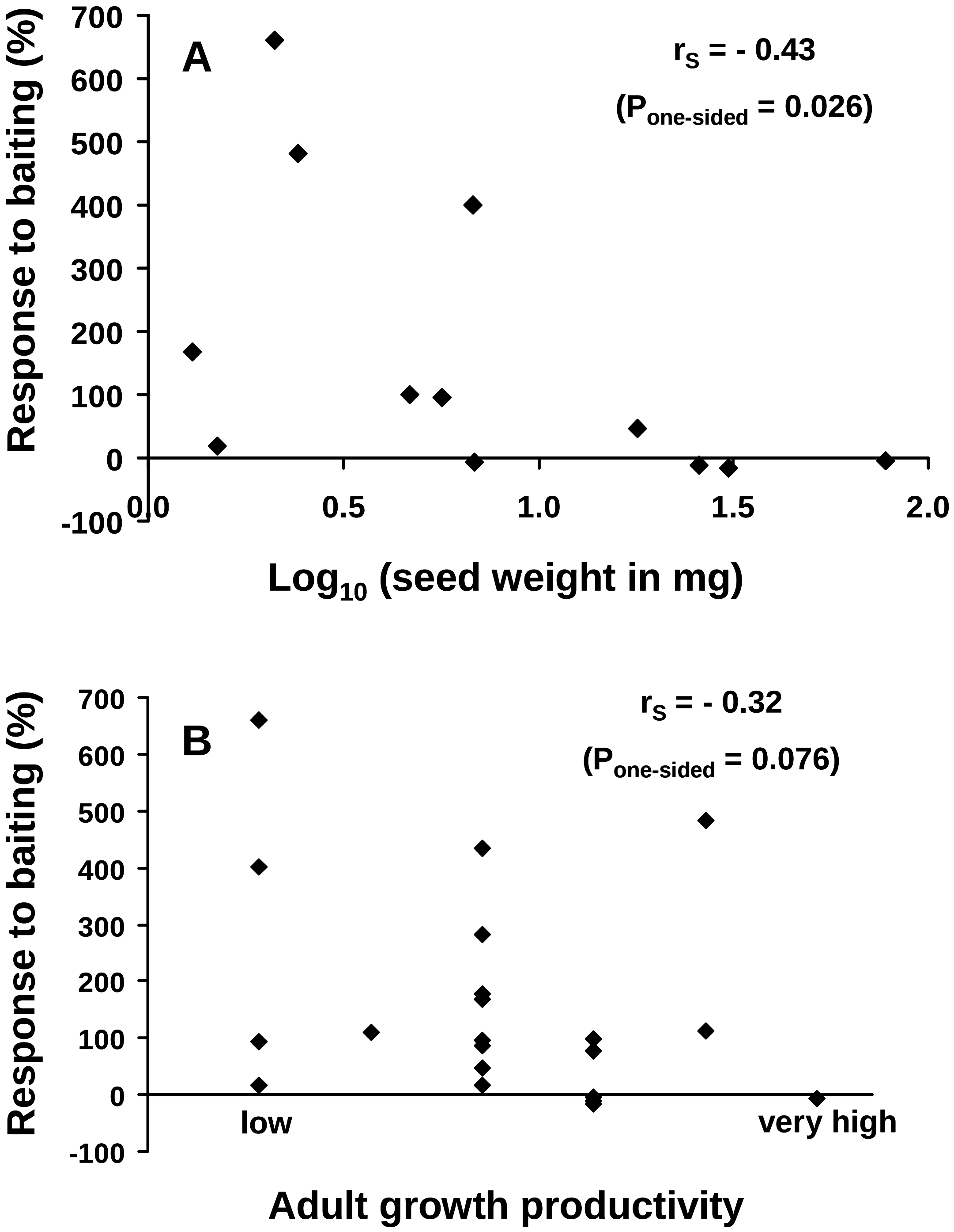
(Figure 2)


Seedling establishment (%)
Number of slug pellet applications
0
20
40
60
0
1
2
Asclepias tuberosa
P < 0.001
a
b
b
Aster oolentangiensis
P = 0.007
a
a
b
Baptisia australis
P = 0.237
Cacalia atriplicifolia
P < 0.001
a
b
b
Coreopsis lanceolata
P < 0.001
a
b
b
Echinacea pallida
P < 0.001
a
b
b
Eupatorium maculatum
P = 0.011
a
ab
b
Helianthus mollis
P = 0.004
a
b
b
Liatris aspera
P < 0.001
a
b
b
Monarda fistulosa
P < 0.001
a
b
b
Ratibida pinnata
P = 0.002
a
b
b
Rudbeckia subtomentosa
P = 0.112
Schizachyrium scoparium
P = 0.004
ab
a
b
Silphium integrifolium
P = 0.380
Silphium laciniatum
P = 0.460
Silphium perfoliatum
P = 0.963
Silphium terebinthinaceum
P = 0.658
Solidago ohioensis
P = 0.815
Solidago rigida
P = 0.035
a
ab
b
Solidago speciosa
P = 0.029
a
ab
b
Veronicastrum virginicum
P = 0.018
a
ab
b

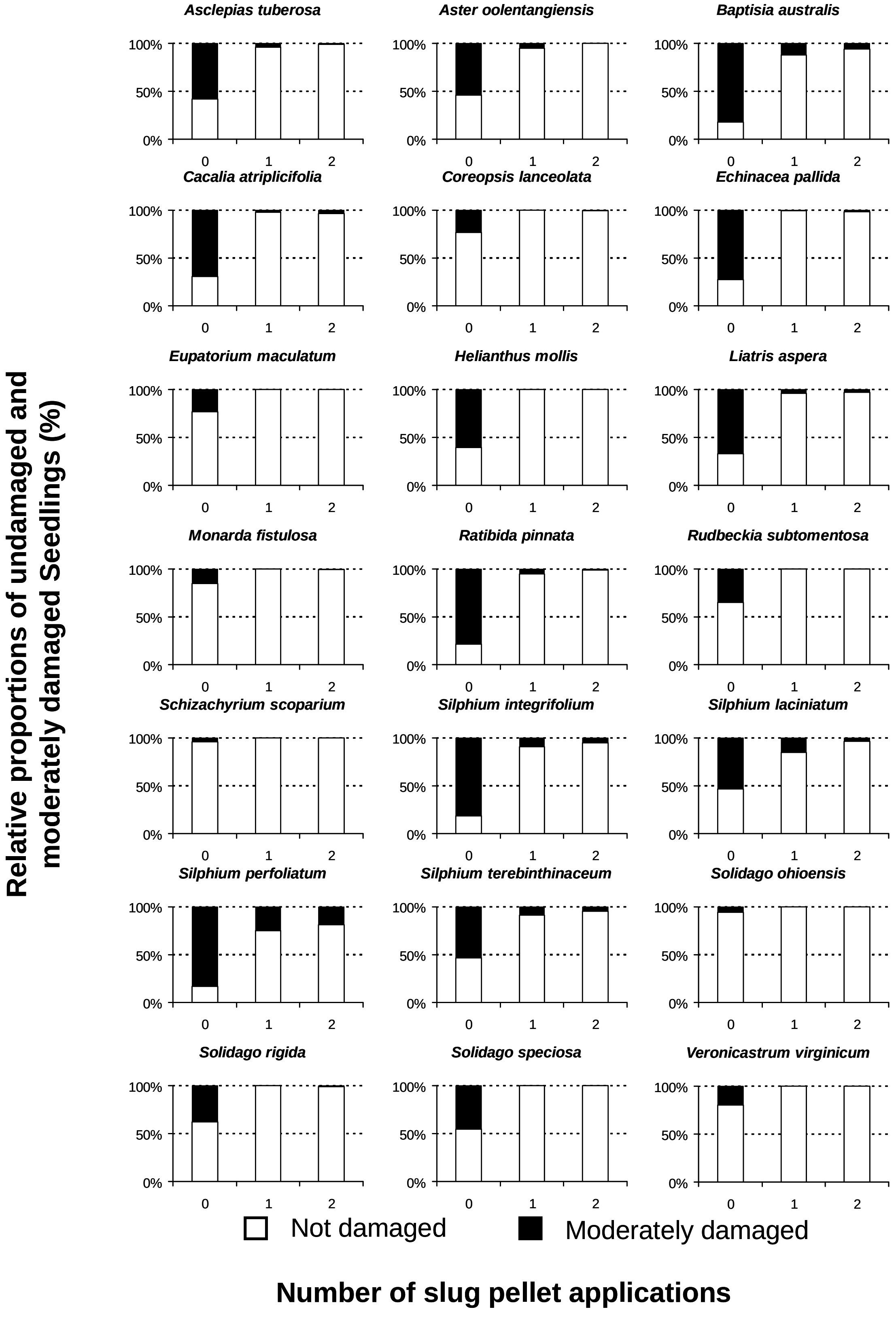
(Figure 3)


Effect of baiting on seedling establishment (%)
700
600
500
400
300
200
100
0
-100
Sil int
Sil ter
Sil per
Sil lac
Sol ohi
Sch sco
Bap aus
Rud sub
Ast ool
Ech pal
Sol rig
Hel mol
Sol spe
Eup mac
Cor lan
Rat pin
Ver vir
Asc tub
Mon fis
Cac atr
Lia asp

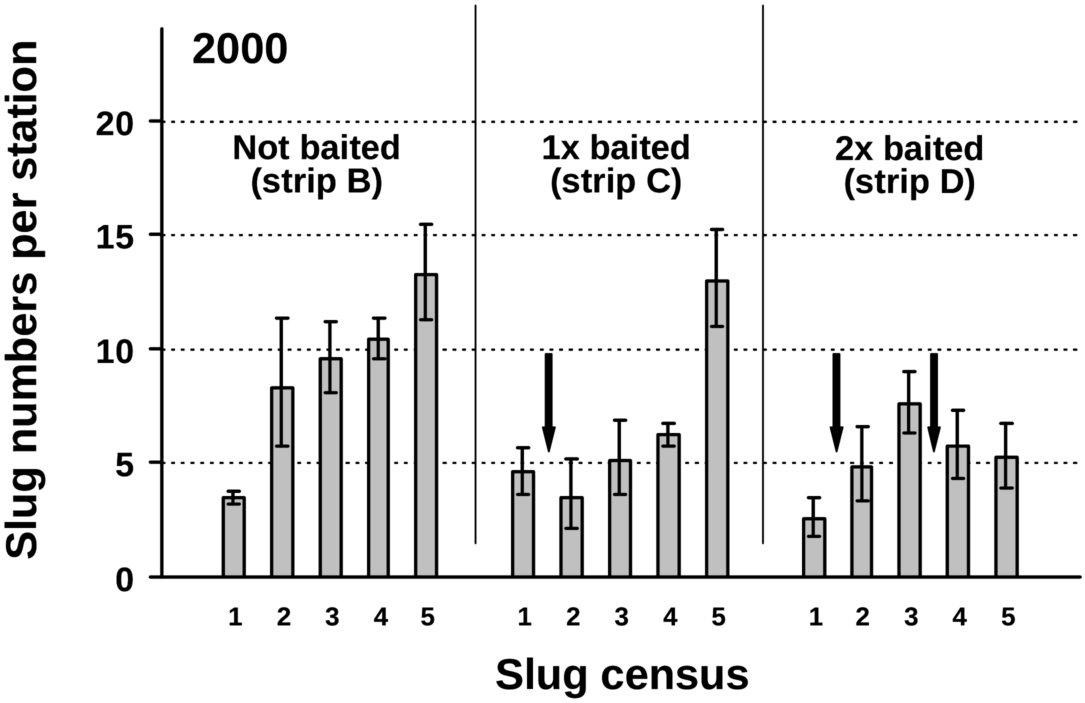
(Figure 4)


A
Response to baiting (%)
700
600
500
400
300
200
100
0
-100
0.0
0.5
1.0
1.5
2.0
Log10 (seed weight in mg)
rS = - 0.43
(Pone-sided = 0.026)
B
Response to baiting (%)
700
600
500
400
300
200
100
0
-100
low
very high
Adult growth productivity
rS = - 0.32
(Pone-sided = 0.076)

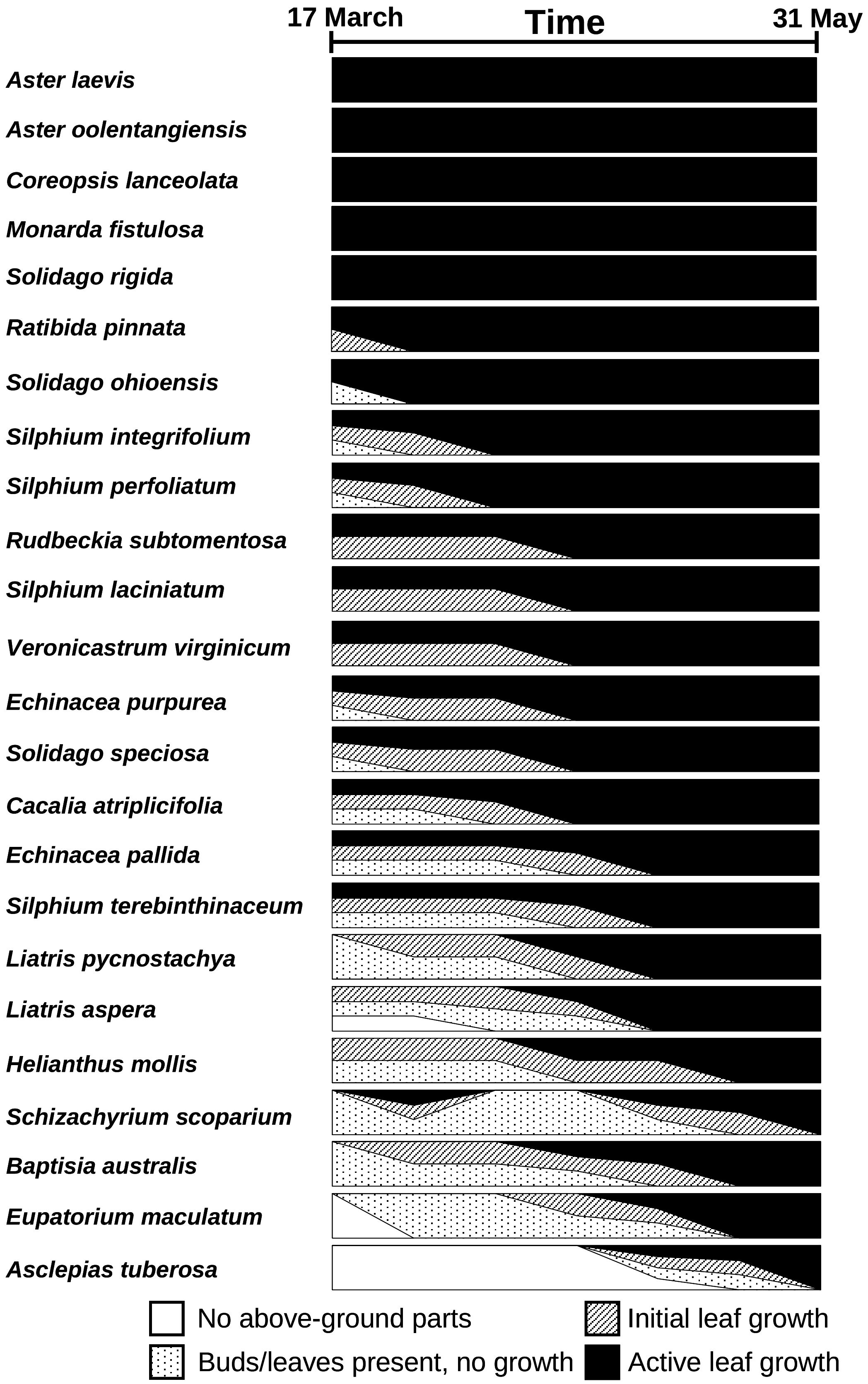
(Figure 5)


Asclepias tuberosa
Aster oolentangiensis
Baptisia australis
Cacalia atriplicifolia
Coreopsis lanceolata
Echinacea pallida
Eupatorium maculatum
Helianthus mollis
Liatris aspera
Monarda fistulosa
Ratibida pinnata
Rudbeckia subtomentosa
Schizachyrium scoparium
Silphium integrifolium
Silphium laciniatum
Silphium perfoliatum
Silphium terebinthinaceum
Solidago ohioensis
Solidago rigida
Solidago speciosa
Veronicastrum virginicum
100%
50%
0%
0
1
2
Relative proportions of undamaged and moderately damaged Seedlings (%)
☐ Not damaged
■ Moderately damaged
Number of slug pellet applications

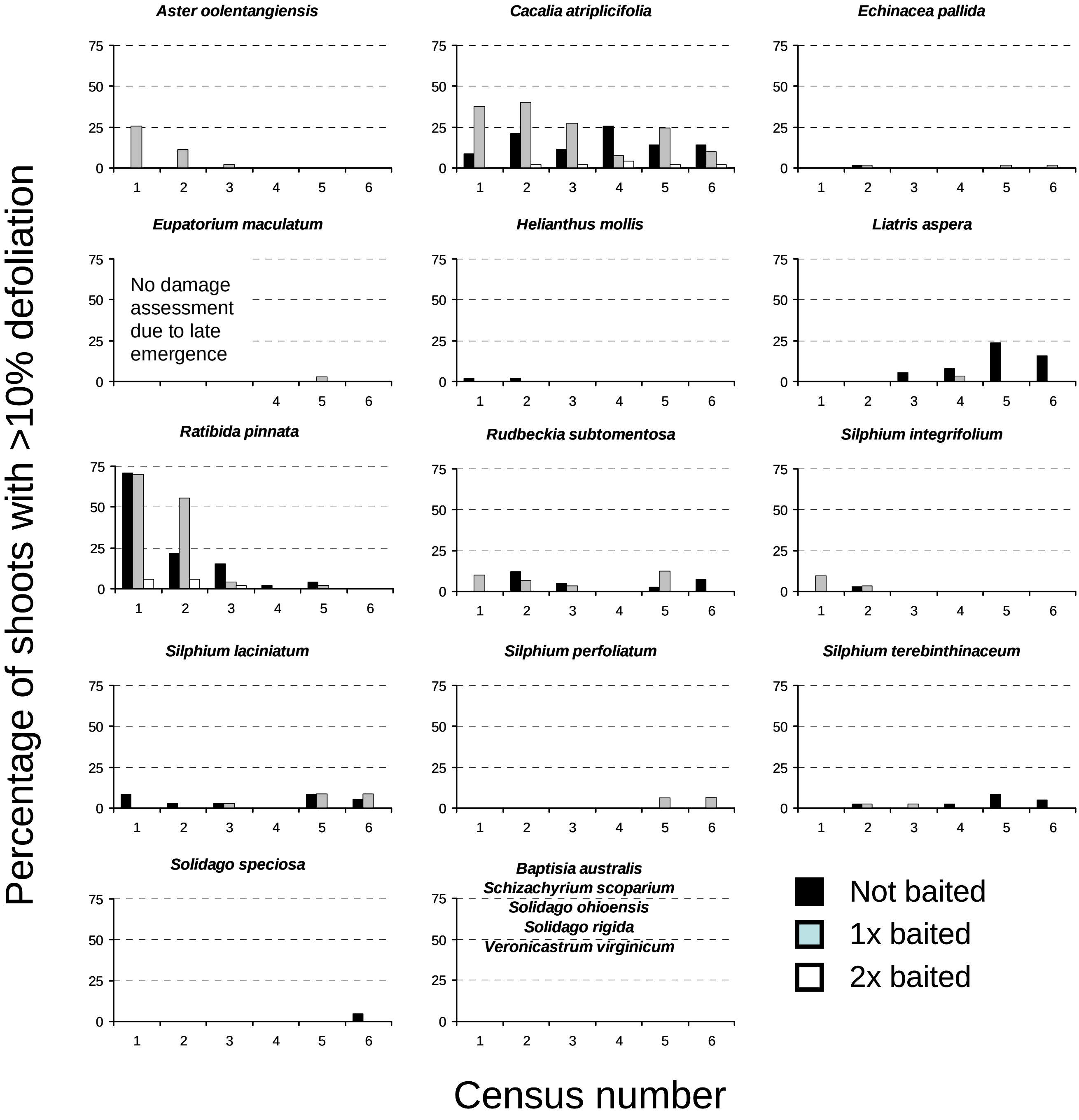
(Figure 6)


2000
Slug numbers per station
0
5
10
15
20
Not baited
(strip B)
1x baited
(strip C)
2x baited
(strip D)
1
2
3
4
5
Slug census

(Figure 7)


17 March
Time
31 May
Aster laevis
Aster oolentangiensis
Coreopsis lanceolata
Monarda fistulosa
Solidago rigida
Ratibida pinnata
Solidago ohioensis
Silphium integrifolium
Silphium perfoliatum
Rudbeckia subtomentosa
Silphium laciniatum
Veronicastrum virginicum
Echinacea purpurea
Solidago speciosa
Cacalia atriplicifolia
Echinacea pallida
Silphium terebinthinaceum
Liatris pycnostachya
Liatris aspera
Helianthus mollis
Schizachyrium scoparium
Baptisia australis
Eupatorium maculatum
Asclepias tuberosa
☐ No above-ground parts
▨ Initial leaf growth
⬚ Buds/leaves present, no growth
■ Active leaf growth

(Figure 8)


Aster oolentangiensis
Cacalia atriplicifolia
Echinacea pallida
Eupatorium maculatum
No damage assessment due to late emergence
Helianthus mollis
Liatris aspera
Ratibida pinnata
Rudbeckia subtomentosa
Silphium integrifolium
Silphium laciniatum
Silphium perfoliatum
Silphium terebinthinaceum
Solidago speciosa
Baptisia australis
Schizachyrium scoparium
Solidago ohioensis
Solidago rigida
Veronicastrum virginicum
0
25
50
75
1
2
3
4
5
6
Percentage of shoots with >10% defoliation
Census number
Not baited
1x baited
2x baited