Effects of disturbance and microhabitat on the growth and invasive potential of *Matricaria perforata* in a sub-alpine meadow

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Effects of Disturbance and Microhabitat on the Growth and Invasive Potential of *Matricaria perforata* in a Sub-alpine Meadow

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This study evaluated the effects of disturbance and microhabitat on the success of a recently introduced, potentially invasive plant species, scentless chamomile (*Matricaria perforata*). We attempted to determine whether the species is capable of moving from its current roadside "strongholds," and invading more pristine sub-alpine meadows near Rocky Mountain Biological Laboratory in Gothic, Colorado. A documentary component of this study evaluated the local distribution of *M. perforata* and its coincidence with disturbances. A manipulative study involved introducing seeds and seedlings of *M. perforata* into three types of microhabitats comprising both anthropogenic and naturally occurring disturbances. Performance of individuals was evaluated during the growing season using relative growth rates and total shoot biomass. Results of the documentary study indicated that *M. perforata* is capable of colonizing meadow disturbances, and of growing in areas with little disturbance, yet some factor is limiting its proliferation from roadside into meadow. Results of the manipulative introduction point to herbivory as a major limiting factor in the establishment and spread of M. *perforata*. Further research is necessary to determine how important herbivory may be as a natural biological control that restricts the species to more anthropogenically disturbed areas.

INTRODUCTION

Studying the rapid proliferation of a species into a novel habitat has a justifiedly distinguished history (Elton, 1958). Biological invasions are particularly rich sources of ecological insight. In recent years there has been an increasing amount of scientific attention focused on the ecological threats of biological invasions. Biological invasions occur when an organism arrives in a locale beyond its previous range (Williamson, 1996). Such organisms can be referred to as exotics or aliens, yet they are not necessarily invaders. Although it is relatively easy to label a species as an exotic, it is much more difficult to determine whether a species can be considered truly invasive. Two important questions which are frequently asked by biologists are: (1) What attributes of communities make them more likely to be invaded? and (2) What attributes of individual species make them more likely to be successful invaders? (Crawley, 1987; Burke and Grime, 1996).

One important characteristic of invasive species that distinguishes them from exotic species which are merely extant in a given environment is their ability to proliferate, even in more "pristine" areas which have been relatively unaltered by human activity. Although many invaders can be considered "weeds" or "colonizers," a species does not necessarily have to possess the characteristics of either to be an invader (Williamson, 1996). In the end, the perceived consequences of a species' presence often play a defining role in labeling a species as invasive. Invasive species can pose a global threat to biodiversity and ecological integrity, act as vectors for disease, promote extinction of native species, and inhibit human economic activities (Vitousek et al., 1996).

Despite the critical problems that invasive species pose for the conservation and management of many natural ecosystems, surprisingly little is known about the determinants of the distribution and abundance of invading species (Thébaud et al., 1996). There may be very few valid generalizations about invasive species, and it may only be possible to make weak, probabilistic predictions about which species are capable of becoming invasive (Crawley, 1987; Blossey and Nötzold, 1995). The inability to effectively predict whether a particular introduction will proliferate or whether it will become locally extinct seems to be largely a result of the complex interactions between a species and its target community, and the fact that biological invasions are fundamentally context-specific situations (Crawley, 1987; Thébaud et al., 1996). In order to better assess the risk of biological invasions, it is necessary to consider the characteristics of the "target" community, as well as the functional characteristics of the species likely to invade (Burke and Grime, 1996). As Bazazz (1986) described, “the colonizer and the colonized are partners in the process.”

A study of the success of exotic plant species in the British Isles indicated that the more invasible plant communities were characterized by low levels of plant cover (Crawley, 1987). This assertion is consistent with the observation that a closed cover of established indigenous species has been cited as the major factor reducing the probability of successful invasion (Burke and Grime, 1996). Although it has been difficult for biologists to determine universal characteristics of invaders or invasible communities, it seems clear that biological invasions in plant communities are frequently facilitated by disturbance, which tends to result in low levels of plant cover (Burke and Grime, 1996; Kotanen, 1997). Disturbance can be generally defined as a discrete punctuated killing, displacement or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established (Sousa, 1984). Crawley (1987) suggested that it may be possible to rank plant communities in terms of their invasibility according to the frequency and intensity of soil disturbance. However, all soil disturbances are unlikely to be equivalent; different types of disturbance can have significantly different effects on the ability of an introduced species to proliferate (Kotanen, 1997).

Pocket gopher (*Thomomys talpoides*) throws are significant sites of disturbance in sub-alpine meadows (Langenheim, 1962). The microhabitat provided by a gopher throw -- reduced cover and a churned, aerated substrate -- may be particularly favorable for the proliferation of an invader. For example, Reichman (1988) reported that gopher throws provide important sites for seed germination, and may enhance the success of annuals in crowded abandoned fields of intermediate age. Freedom from aboveground competition for light, which may be the major limiting factor in plant growth, could afford plants growing on gopher mounds an advantage (Reichman, 1988).

Although disturbance can play a major role in the establishment of an introduced species, a species must possess characteristics which enable it to take advantage of such disturbance for an invasion to progress. Experimental studies by Burke and Grime (1996) demonstrated that invading species differ in their ability to exploit disturbance and that the invasive success of certain species could be explained through the identification of functional characteristics conducive to establishment. Characteristics such as an enhanced ability to capture elevated quantities of light and mineral nutrient resources, as well as inherently faster growth rates, contributed to the relative success of certain introduced species over indigenous species in disturbed areas (Burke and Grime, 1996). Species able to germinate at lower temperatures and in a wide range of light conditions were most likely to produce a high density of established plants, lending support to the idea that a “highly plastic response to environmental variation” is an attribute marking successful invaders (Burke and Grime, 1996).

When considering the attributes of individual species that make them successful invaders, it is important to keep in mind that a successful biological invasion is relatively rare (Williamson, 1996). According to the “tens rule,” only ten percent of all introductions or “escaped” taxa become established and self-sustaining (Williamson, 1996). Furthermore, of those species that become established, only ten percent become pests. Williamson (1996) distinguished between organisms that are merely extant in a habitat and those that could proliferate and thus cause detriment.

In this study, we attempted to determine the role of disturbance and microhabitat on the success of a particular potentially invasive species, scentless chamomile (*Matricaria perforata* Merát).). Originally native to Europe, *M. perforata* has become a well established invader in Canada and is slowly spreading southwards in North America (Kay, 1994; Blackshaw and Harker, 1997). It has been reported as a major agricultural pest in both its native and non-native range, and is resistant to some common chemical herbicides (Kay, 1994; Blackshaw and Harker, 1997). This work addressed several questions. Are particular types of microhabitats more conducive to invasion? Is *M. perforata* capable of moving from its current roadside "strongholds" and invading more pristine sub-alpine meadows? Can gopher throws or other unvegetated microsites facilitate this invasion? Comparison of the performance of this introduced species in various types of disturbance and microhabitats allows an examination of these questions.

METHODOLOGY

Scentless chamomile is typically a seed-producing winter or summer annual, but it is also capable of existing as a short-lived perennial (Kay, 1994; Bowes et al., 1995). Anecdotal observations of dead flowering stems (apparently from last year's growing season) attached to the current year's flowering individuals *M. perforata* indicate that it may be capable not only of perennation, but iterocarpy as well. *M. perforata* is highly phenotypically plastic, varying greatly in size and life history, and is a hardy plant which can tolerate poorly drained soils and a wide range of environmental conditions (Kay, 1994; Blackshaw and Harker, 1997

Along Colorado's western slope, *M. perforata* can reach high densities in disturbed areas, especially along roadsides (Weber and Wittman, 1996). It is common along the road to Gothic, Colorado (County Road 317), north of the town of Mt. Crested Butte. The species is a very recent arrival; the consensus is that it has been observed in the Upper East River Valley for less than 15 years (e.g., B. Frase, K. Darrow, pers. comm.). A recent study at the Rocky Mountain Biological Laboratory has shown that the species has a competitive advantage when grown with showy daisy (*Erigeron speciosa*), a native perennial (Sheikh and Kelrick, unpublished). Individuals of *M. perforata* have been observed growing on gopher disturbances in a relatively "pristine" meadow in the Mt. Crested Butte area. It seems that *M. perforata* may be on the "threshold" of being considered invasive, and knowledge about its ability to grow in less disturbed areas could help clarify its status.

Documentary Study

A documentary study was conducted to provide information regarding the current local distribution of *M. perforata* in the Mt. Crested Butte area, as well as its dispersal capabilities, that could influence its colonization of nearby meadows. This study also examined the level of disturbance within the study area in an effort to determine whether there is a relationship between the attributes of "colonizable" microsites and the presence and abundance of *M. perforata*. The study site was located on a downhill slope extending west from

Gothic Road, adjacent to the entrance of the Mt. Snodgrass trailhead, where *M. perforata* is abundant along the roadside and parking area. Twenty transects which extended 100 m parallel to Gothic Road were established at 3-m intervals. Fifty-cm X 50-cm quadrats were placed at 5-m intervals on the down-slope side of the transects. Presence or absence of *M. perforata* within each quadrat was noted, and its percent cover was classified into one of four categories: 0%, 1-10%, 10-50%, or 50-100%.

Following the completion of quadrat sampling along each transect, a pair of researchers walked along the 3-m band between the newly completed and previous transect lines and conducted an extensive visual survey. The number of groups of *M. perforata*, number of disturbances, number of gopher disturbances, and whether or not the *M. perforata* occurred on a disturbance were recorded. Stands of *M. perforata* greater than 50 cm in extent parallel to the length of the 3-m band were assessed as independent groups at 50-cm intervals. For the purposes of this study, an area which lacked significant vegetative cover and which had exposed substrate was considered a disturbance. Disturbances with signs of recent gopher activity, such as mounds or tunnels, were classified as gopher disturbances, while unvegetated, relatively smooth substrate was classified as non-gopher disturbance. Heavy disturbance along the roadside was more or less continuous for the entire 100-

m band, and thus it was not possible to record the incidence of non-gopher disturbances free of *M. perforata* in the three 3-m bands closest to the road. In bands further from the roadside, non-gopher disturbances greater than 50 cm in extent parallel to the length of the band were assessed as independent disturbances at 50-cm intervals along the band. Transect sampling and visual surveys of the 3-m bands extended downslope into the meadow until two consecutive bands were found to be free of *M. perforata*.

Combining sampling (areal, using quadrats) and census (non-areal) approaches provided more comprehensive information regarding the distribution of *M. perforata*. It could also serve to assess the reliability of the quadrat sampling protocol, which could be useful for future monitoring. In addition, recording both the frequency of disturbances (with and without *M. perforata*) and groups of *M. perforata* (on or off disturbed substrate) allows a two-way analysis of these conditions. Thus, the probability of the plant occurring on a disturbance, and the probability of any disturbance supporting *M. perforata*, can both be determined.

Manipulative Introduction Study

A manipulative field study is one means to evaluate the ability of *M. perforata* to colonize gopher throws and other microsites within a sub-alpine meadow. By comparing the performance of scentless chamomile in different, apparently favorable contexts, it may be possible to determine whether certain microhabitats favor this potential invader and whether anthropogenic disturbance is necessary for its proliferation. *M. perforata* seedlings were introduced into microhabitats that varied in abiotic conditions and freedom from shoot-shoot interactions.

Three types of microsites were studied: gopher-disturbed, roadside disturbance (i.e. anthropogenic), and gaps (open spaces) within existing meadow vegetation. Gopher-disturbed sites (henceforth GT) were existing natural gopher throws within the study area that appeared to be relatively recent and were within a size range that could accommodate introduced plants. Roadside microsites (RD) were located on the margins of an unpaved gravel road which runs along the study area; these served as the "baseline" for evaluating the performance of *M. perforata*, since this is the habitat where currently the species is most commonly encountered. The last category of microsite comprised meadow gaps of roughly equal area that might allow for the germination of annuals' seeds, but which could potentially become canopy-covered by adjacent perennials' above-ground growth as the growing season proceeds. This open microsite category was further manipulated by clipping, or not clipping, overhanging perennials' tissues during the course of the experiment (henceforth, subdivided into "clipped" and "unclipped" gap microsites, CG and UG, respectively). Physical parameters, including soil bulk density and water-holding capacity, were determined for each of the microsites. There were seven replicates of each of the four categories of microsites, and ten transplant locations were established at each replicate, with approximately 8 cm between transplant locations. Seedlings were gathered from the roadside at the Mt. Crested Butte study site on June 27, transplanted into flats, and then re-transplanted at the Gothic study site on the first of July. Transplants were monitored, watered as needed, and protected from direct sunlight using shade devices constructed of nylon window screen in order to facilitate their establishment. Protection of seedlings, and replacement if necessary, lasted for 9 days from the initiation of transplanting. Three seedlings were initially planted at each of the ten seedling locations at each replicate; these were thinned to one individual per location on July 12.

Performance of individuals was measured three times after seedling establishment -- number of leaves and midvein lengths of all leaves on each plant were recorded. Each leaf greater than 5 mm was counted; if a leaf had experienced herbivory, yet still had some of the blade portion of the leaf remaining, it was represented in the count as half a leaf. Leaves of *M. perforata* are highly dissected, which can make the determination of the end of midveins difficult. In this study, midvein lengths were measured from the base of the petiole to the base of the last fork of leaflets at the end of the leaf. Leaves which had experienced herbivory, and still had some of the blade remaining, were measured to the end of the remaining midvein. Midvein measurements were taken on July 13, July 23, and August 3. There were 10 days between first and second measurements, and 11 days between the second and third measurements. Thus there were a total of three weeks between the first and third midvein length measurements. These measurements allowed the calculation of relative growth rates (RGR's) non-destructively during the growing season. Total shoot biomass of individuals was determined destructively at the end of the experiment, by harvesting plants on August 4, 35 days after initiation of transplanting.

In addition to seedlings, seeds of *M. perforata* were introduced at each replicate of the four microsite categories. These seeds were collected from capitula of at least 12 individuals growing along the road at the Mt. Crested Butte site during the summer of 1998. In order to localize the plants which might arise from these seeds, a round plastic collar, approximately 15 cm in diameter and 3 cm high, was inserted into the soil to contain the seeds. In order to promote the germination of a sufficient number of plants, 50 seeds were introduced at each replicate microsite on July 12. These seeds were watered for five days, and germination was first observed on July 21, after four days of rain following the initial watering period. Numbers of seedlings were recorded on July 21. Replicates with more than 15 seedlings on July 22 were thinned to 15 seedlings, those with less than 15 seedlings were left unthinned. Positions of seedlings were mapped on July 22 and 23 to enable collection of demographic data and recognition of continued subsequent germination. Further demographic counts were conducted on July 27, August 1, and August 11 to determine survivorship and any subsequent germination. Numbers of true leaves per plant were recorded on August 1 and August 11.

RESULTS

Documentary Study

The abundance and cover of *M. perforata* decreased with distance from the road (Fig. 1). In order to analyze the quadrat-sampled data, goodness-of-fit tests comparing pairs of transects were performed on the frequencies of the four cover class categories to determine whether the distributions were consistent as distance from the road increased (Sokal and

Rohlf, 1995). For each such test, frequencies from a previous transect closer to the roadside stand of *M. perforata* were used as expected values for the frequencies observed from the immediately adjacent transect, more distant from the roadside. Statistically significant differences in frequency distributions were found between transects 1 and 2 (0 and 3 m from the road respectively; $G = 16.7$; $P < 0.001$), and transects 3 and 4 (9 and 12 m from the road respectively; $G = 16.70$; $P < 0.025$).

Data from the survey portion of the study were also analyzed using a replicated goodness- of-fit test that allowed identification of which bands (replicates) were significant contributors to lack of fit (heterogeneity chi-square; Sokal and Rohlf, 1995). Since *M. perforata* is reported to occur mainly on disturbed substrate (a ruderal species), the assumption that nearly all observed instances (369 out of 370) would occur on disturbed substrate was used for the expected values necessary to perform the test. The pooled *G* results were highly significant (G=374.785; $P << 0.0001$); the study site as a whole (3300 m^2 sampled) was not consistent with expected frequencies, because significantly more *M. perforata* plants than expected were encountered in undisturbed sites. Results of the heterogeneity chi-square test were also highly significant (heterogeneity $G = 75.77$; $P << 0.001$), indicating differences among replicate bands in their distributions of *M. perforata* on versus off disturbed substrate (Fig. 2). Partitioning the total G into contributions due to individual bands' data revealed significantly larger than expected frequencies of *M. perforata* on undisturbed substrate for bands 2, 3, 4, and 5 ($G = 229.410$, 115.125, 41.131, and 59.808 respectively; for all, $P < 0.0001$). A significant number of individuals growing in the midst of established vegetation (i.e., undisturbed substrate) was found in each of these bands (Fig. 2).

Although the majority of observations of *M. perforata* did occur on disturbed substrate (Fig. 2), most gaps and gopher throws/tunnels were not occupied by *M. perforata*, especially further than 6 m from the road (Fig. 3). The frequency of available disturbances not occupied by *M. perforata* was lowest near the roadside (1 gopher disturbance, 0 non-gopher disturbances), and highest in band 4 (79 gopher disturbances, 54 non-gopher disturbances). Beyond 6 m from the road, the large majority of disturbed microsites were unoccupied by *M. perforata*, and thus "available for colonization" (Fig. 3).

Tests for heterogeneity were conducted using BIOMstat software (Rohlf and Slice, 1997); all other statistical analyses used PC-SAS6.0 (SAS Institute, Inc. 1989).

Manipulative Introduction Study

Herbivory

From the beginning of the study, herbivory was an unanticipated factor which affected the performance of individuals. Insect herbivory, most likely the result of some species of grasshopper (e.g., Melanoplus), was noted during the establishment period of introduced seedlings, subsequent to establishment, and immediately upon the germination of introduced seeds. Incidence of herbivory was recorded during the monitoring of both the transplanted individuals and plants arising from introduced seeds. It appears that herbivory played a major role in determining the growth rates and survival of individuals, especially those in the meadow replicates.

Soil Characteristics

Analysis of variance indicated that there was no significant difference between the soil bulk densities (g/cm^3) of the meadow sites (mean [S.E.] for gaps, 1.0336 [1.076] versus for gopher throws, 0.891 [0.072]; RD sites could not be tested due to the rocky nature of the soil). However, there was a significant difference ($F = 49.03$; $P < 0.0002$) among water holding capacities of soils from different locations. Mean relative water content (at field saturation) of RD samples was significantly lower than those collected from gaps and gopher throws (mean [S.E.] for RD, 0.1856 [0.0203]; for gap, 0.3627 [0.0139]; for GT, 0.3817 [0.0104]). The difference between means of the meadow sites was not statistically significant.

Transplant Experiment

Analysis of variance of oven-dry shoot biomass among the four treatment categories indicated a highly significant treatment effect (Table 1), with RD plants producing the greatest mean shoot biomass (mean = 0.0579; standard error = 0.0023), nearly six times that of the UG treatment (mean = 0.099; standard error = 0.0017). Nonetheless, Tukey's means comparison test showed no significant difference in the means of the four treatment levels. Not only is this test rather conservative, but the design of the study required accounting for variation among the replicates treated alike, as well as variation among individual plants within each replicate (subsamples). Highly unbalanced subsample sizes resulted from high mortality, apparently due to herbivory; this contributed to the lack of resolution among treatment level means.

An analysis of RGR's for the entire course of the experiment (calculated using differences between first and third midvein length measurements) showed a significant treatment effect which corroborated the biomass data (Table 1). Mean (S.E.) RGR of plants at RD sites (0.0821 [0.0037]) was significantly higher than that for plants at the GT (0.0278[0.0119]), CG (0.0279 [0.0066]), and UG (0.0202 [0.0055]) sites. There were no significant differences among means for the meadow sites. Analyses of variance were also performed for RGR's calculated between the first and second, and second and third, midvein length measurements; both resulted in statistically significant treatment effects (Table 1). RGR's between the first and second midvein measurements indicated that RD replicates grew fastest (0.0706; [0.0052]), several times that of UG replicates (0.014 [0.0056]), yet Tukey's test showed no significant difference among these means (for reasons already presented). Although there were no statistically significant differences between the mean RGR's of the meadow treatment levels, the rank of lower values changed between first and second, and second and third midvein length measurements. Between the first and second length measurements, the mean of GT replicates was higher, but that of the CG replicates was higher between the second and third midvein length measurements. The effect of treatment on change in total number of leaves produced by plants during the experiment did not yield a statistically significant *F*-value (Table 1). However, the mean (S.E.) leaf production during the 3-week measurement period for RD replicates (6.1865 [0.8605]) was several times that of the meadow replicates (mean [S.E.] for GT, 2.4687 [0.5448]; for CG, 1.1211 [0.4558]; for UG, 1.0161 [0.3140]).

Seed Introduction

During the process of mapping germinants from experimentally introduced seeds, germination of indigenous *M. perforata* seedlings was also observed along the roadside adjacent to the study site. The fact that introduced seeds in this study germinated, was not artifact of initial watering; seeds were also observed germinating during the same time period, along the roadside (Highway 135) between Gunnison and Crested Butte, CO (Michael Kelrick, pers. comm.) An analysis of variance indicated that there was no difference in the total number of seeds which germinated at each of the microsites (*F* = 0.35; *P* = 0.78). Proportional germination of the 50 introduced seeds at each site was generally high across the different treatments (mean [S.E.] for RD, 0.637 [0.080]; for GT, 0.614 [0.113]; for CG, 0.726 [0.104]; for

UG, 0.57 [0.126]). However, the percentage of survival across the four treatments varied markedly (F = 16.06; P = 0.0001). Most meadow plants had died by August 11, the final demographic monitoring date. Tukey's test indicated a significantly higher mean percent survival for RD sites than for the other three sites (Fig. 4).

DISCUSSION

Results of the documentary study indicated that *M. perforata* is capable of growing within a meadow environment, and that it is even capable of growing in areas with little disturbance. The fact that individuals were present on undisturbed substrate in greater than expected frequencies makes it clear that the plant should not be relegated to strictly ruderal status. Presence of *M. perforata* approximately 30 m from the road is evidence that the species is capable of dispersal across some considerable distance. Seeds of *M. perforata* lack anatomical features for specialized dispersal, and it seems that the extent of their movement is largely determined after landing on the ground. It is likely that the dispersal of individuals into the meadow is a result of water movement downhill, carrying seeds from sources along the roadside.

In addition, survey data indicated that there are numerous disturbances, both gopher and non-gopher, which are unoccupied. The survey was completed during a time in the growing season when vegetative cover was likely near its maximum, thus the assessment of “colonizable” substrate is a conservative estimate; it is likely that there is even more “available” substrate in the fall or spring, when *M. perforata* seeds are known to germinate. However, there is a notable gap in the pattern of distribution of *M. perforata* in the meadow after approximately 6 m from the roadside (Figs. 2 and 3). Beyond this distance, the presence of *M. perforata* is much less frequent, despite the abundance of disturbances, indicating that its penetration further into the meadow may be seed-limited. Although results reported here indicate that *M. perforata* possesses the necessary dispersal and growth capabilities to establish and persist in the meadow, and that there are abundant unoccupied disturbances that the species could potentially colonize, anecdotal observations maintain that *M. perforata* is generally not prevalent in sub-alpine meadows in the Crested Butte area, and that it does not seem to be moving effectively from its roadside “strongholds” (M. Kelrick, pers. comm.). This begs the question of what factors can prevent or limit the proliferation of *M. perforata* into more pristine meadow environments?

Herbivory is one biotic factor which can affect plant performance, particularly in the case of an introduced species. Michael Crawley (1983) explains, “While herbivores normally have only a slight influence on the death rate of mature plants, their killing potential is illustrated by those cases where an alien insect has ravaged a native plant.” Although such cases are rare, they demonstrate the extreme nature of ecological relationships involving exotics, whether the alien taxon is the plant or the herbivore (M. Kelrick, pers. comm.). Furthermore, it is notable that if herbivores have a significant effect in regulating plant numbers via mortality it is likely that it is expressed through the deaths of seedlings rather than of mature individuals (Crawley, 1986). The plant is most vulnerable to suppression or defoliation when its seed’s reserves have run out and it begins to rely on the products of its own photosynthesis for growth and survival.

Results of the introduction study point to herbivory as a major limiting factor in the spread and establishment of *M. perforata*. Although herbivory was not a controlled variable, and thus it is not possible to conclusively determine the extent to which it affected survival and performance, there is some direct, and substantial indirect, evidence that herbivory was the important contributor to differences among the treatment levels. Although the RD soils had significantly lower water holding capacity than the meadow sites, there was unusually high precipitation during the course of the experiment (35 days of rain; 13 cm total), which minimized any potential effects of this difference (U.S. Natural Resources Conservation Service website, August 8, 1999). Similarly, there were no significant differences in the ability of *M. perforata* seeds to germinate at any of the microsites. Thus rather than differences in abiotic conditions constraining the local distribution of *M. perforata*, it seems that biotic factors, primarily herbivory, were more important determinants of the survival and performance of individuals. Analyses of variance of accumulated shoot biomass and relative growth rates indicated that there were significant differences among individual performances, across both treatments and replicate levels. The fact that the mean proportion of germinant survival was significantly higher among RD replicates than meadow replicates, and that the proportions of seedlings that survived in the meadow sites were so low, demonstrated the dramatic effect of herbivory on individual survival. Also, though there were not significant differences in the performance of the plants in CG and UG treatments, the mean biomass accumulation and growth rates of CG replicates tended to be higher than that of UG. This trend may indicate that competition is another biotic factor that could limit the establishment and survival of *M. perforata*. In a different, more typical summer with less precipitation, drought may become a more pronounced influence in sub-alpine meadow plant communities, emphasizing the roles of such biotic interactions (Del Moral, 1983).

Although many studies have examined *M. perforata* as an agricultural pest, the particular characteristics which may allow it to be considered an invasive species, and the potential implications of its presence in the United States, have not been studied extensively. This study has provided evidence that *M. perforata* possesses characteristics which are conducive to invasion, yet the species may not be capable of invading more pristine habitats due to the behavior of insects within these areas. Further research is necessary to determine the extent to which herbivory serves as a natural biological control, largely excluding *M. perforata* from meadow communities, and whether the species is limited to more anthropogenically disturbed areas. To understand the nature of effects of herbivory, knowledge of which insects are responsible, as well as of the ability of the plant to tolerate and recover from such herbivory, will be required. It is also important to determine if the herbivory observed at the Gothic study site is characteristic of sub-alpine meadows in the area, or whether it is unique to particular meadows or growing seasons. A study involving controlled herbivory (e.g., using screen enclosures) at a number of different study sites across an altitudinal gradient could provide more definitive information regarding the interaction between *M. perforata* and the sub-alpine meadow environment.

Statistical analysis of the data obtained in this study will continue on the transplant and seed introduction components of this study. Such analysis will allow more definitive conclusions regarding the extent to which herbivory affected performance, and more sensitive analysis may allow further distinctions between the performances of individuals located in different meadow sites. Maps of introduced seedlings will allow continued demographic monitoring during next year's field season, and this demographic study may provide insight into the longer-term effects of different microhabitats and herbivory on individual's performance and life histories. Understanding how *M. perforata* grows in habitats with minimal disturbance will clarify whether the species has invasive potential, and whether any management actions are necessary to curtail the spread of *M. perforata* in the East River valley.

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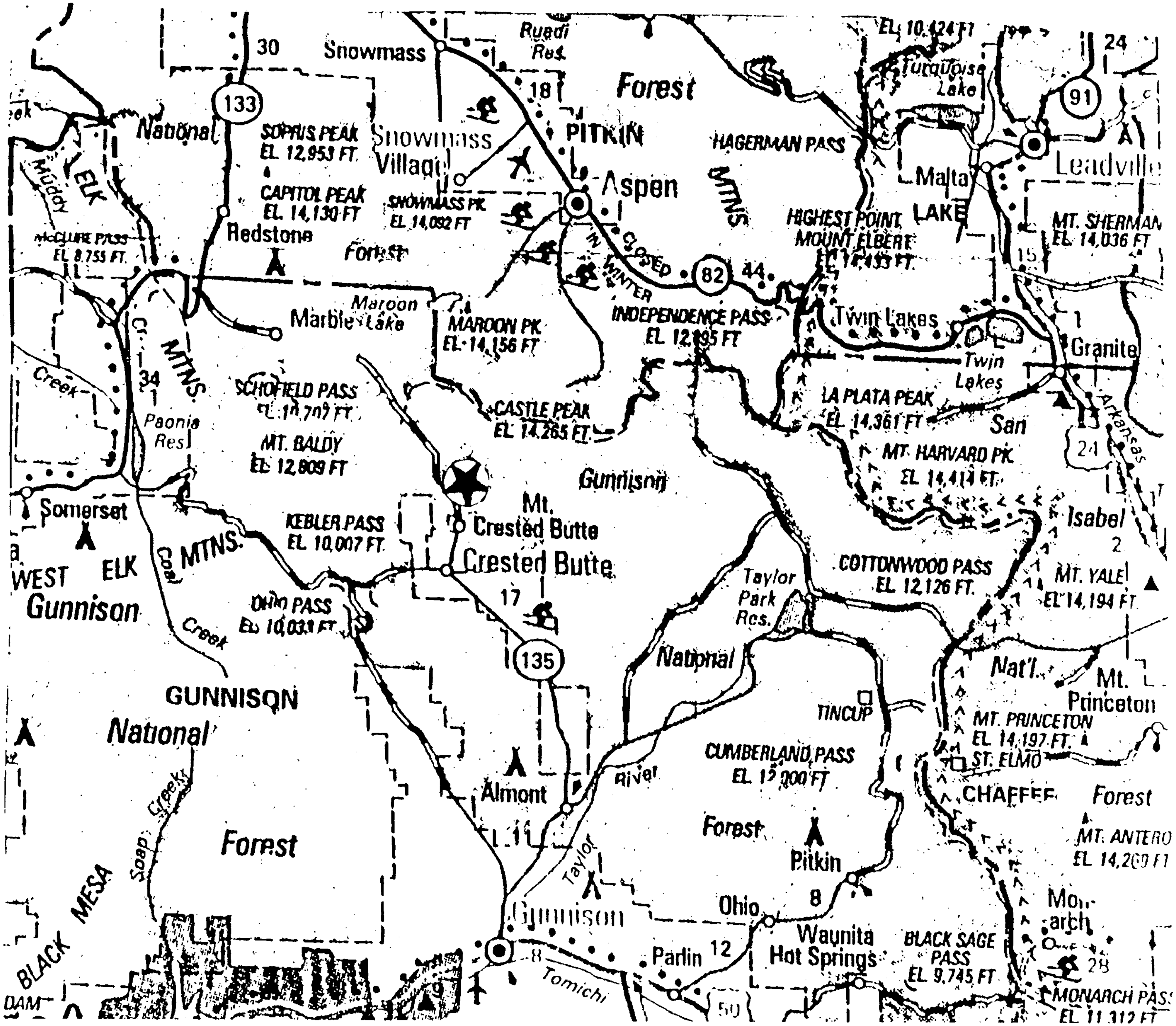
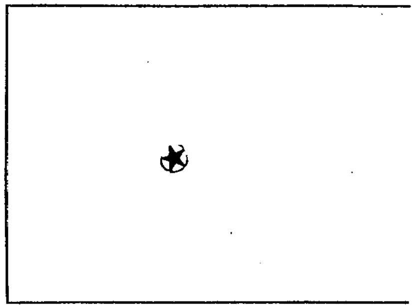

30
Snowmass
Ruedi Res.
18
Forest
EL 10,424 FT
24
Turquoise Lake
91
133
National
SOPRIS PEAK EL 12,953 FT
Snowmass Village
PITKIN
HAGERMAN PASS
Malta
Leadville
ELK
Muddy
CAPITOL PEAK EL 14,130 FT
SNOWMASS PK EL 14,092 FT
Aspen
MTNS
LAKE
HIGHEST POINT MOUNT ELBERT EL 14,433 FT
MT. SHERMAN EL 14,036 FT
15
McCLURE PASS EL 8,755 FT
Redstone
Forest
CLOSED IN WINTER
82
44
Maroon Lake
Marble
MAROON PK EL 14,156 FT
INDEPENDENCE PASS EL 12,095 FT
Twin Lakes
1
Granite
Creek
Cr.
34
MTNS
SCHOFIELD PASS EL 10,707 FT
Twin Lakes
LA PLATA PEAK EL 14,361 FT
San
Paonia Res
MT. BALDY EL 12,809 FT
CASTLE PEAK EL 14,265 FT
Arkansas
24
Gunnison
MT. HARVARD PK EL 14,414 FT
Somerset
Mt. Crested Butte
Isabel
KEBLER PASS EL 10,007 FT
2
WEST ELK
Coal
MTNS
Crested Butte
COTTONWOOD PASS EL 12,126 FT
MT. YALE EL 14,194 FT
Gunnison
Taylor Park Res.
OHIO PASS EL 10,033 FT
Creek
17
135
National
Nat'l.
Mt. Princeton
GUNNISON
TINCUP
MT. PRINCETON EL 14,197 FT
National
CUMBERLAND PASS EL 12,000 FT
ST. ELMO
Almont
River
CHAFFEE
Forest
Soap Creek
Forest
Forest
Pitkin
MT. ANTERO EL 14,269 FT
11
Taylor
Gunnison
Ohio
8
Monarch
BLACK MESA
Waunita Hot Springs
BLACK SAGE PASS EL 9,745 FT
Parlin
12
28
8
Tomichi
50
MONARCH PASS EL 11,312 FT
DAM

Colorado



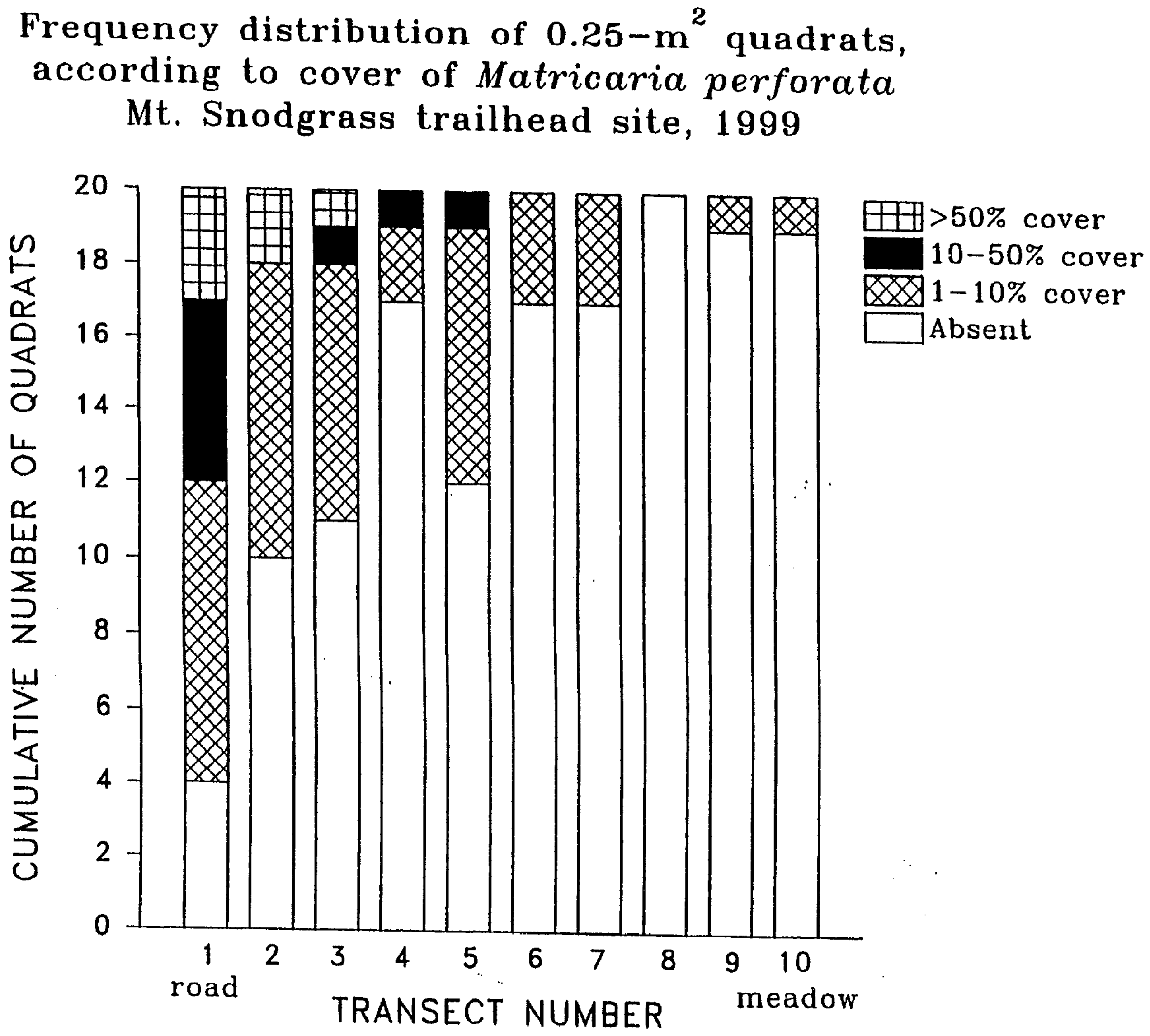


Figure 1. Frequencies of quadrats (0.25 m^2) according to cover class categories of *M. perforata*. Sampling occurred at 5-m intervals along 100-m transects (20 quadrats per transect) parallel to the road, located at 3-m intervals from the roadside into the meadow.

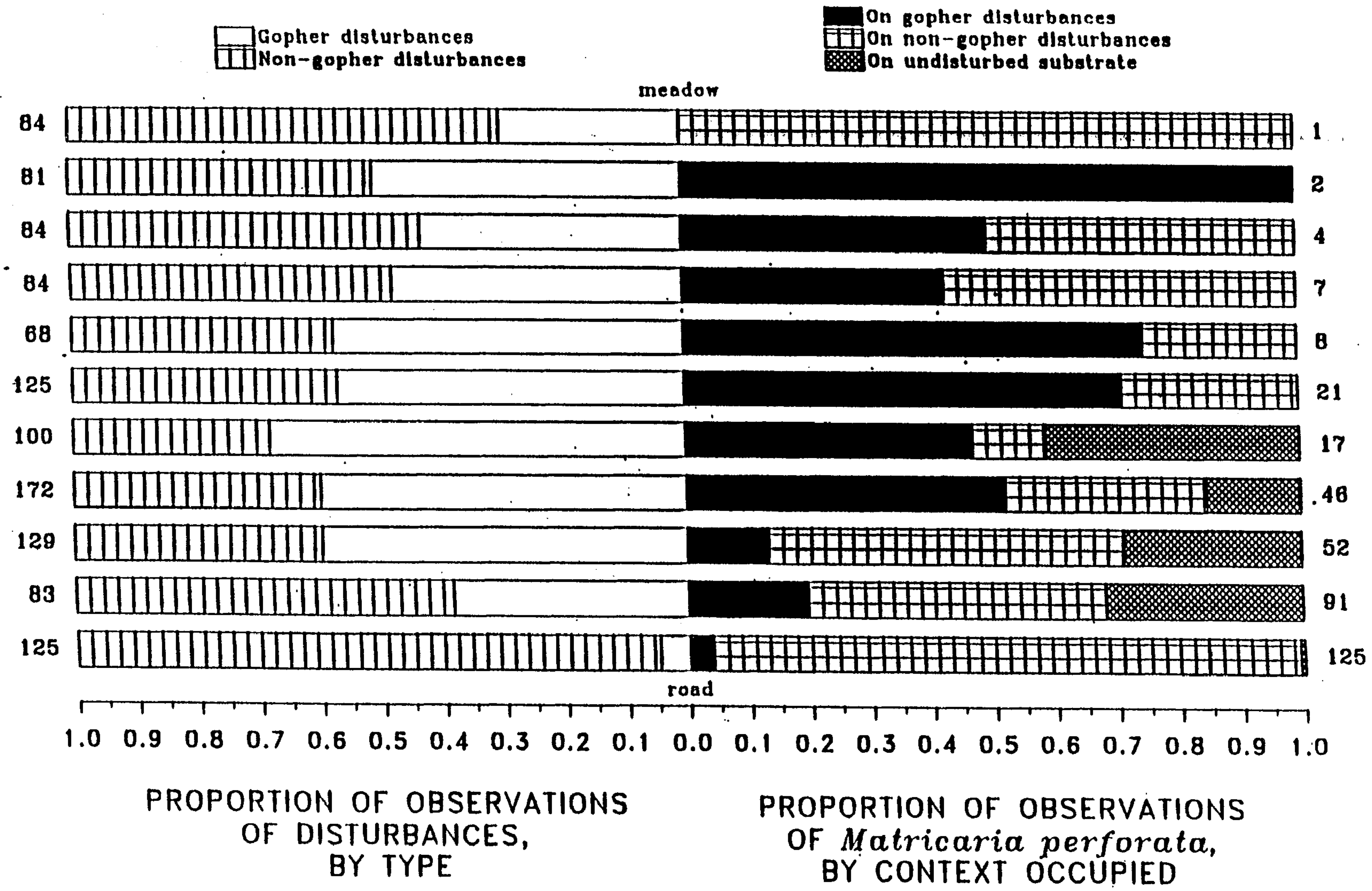


Figure 2. Proportions of observations of disturbances, by type, and of *M. perforata*, by context occupied. Numbers accompanying each histogram bar indicate the total number of relevant observations for each band surveyed. Each band was 100 m long X 3 m wide, and were contiguous, beginning adjacent and parallel to the road (bottom histogram bar). The furthest transect was located 33 m into the meadow (top bar).

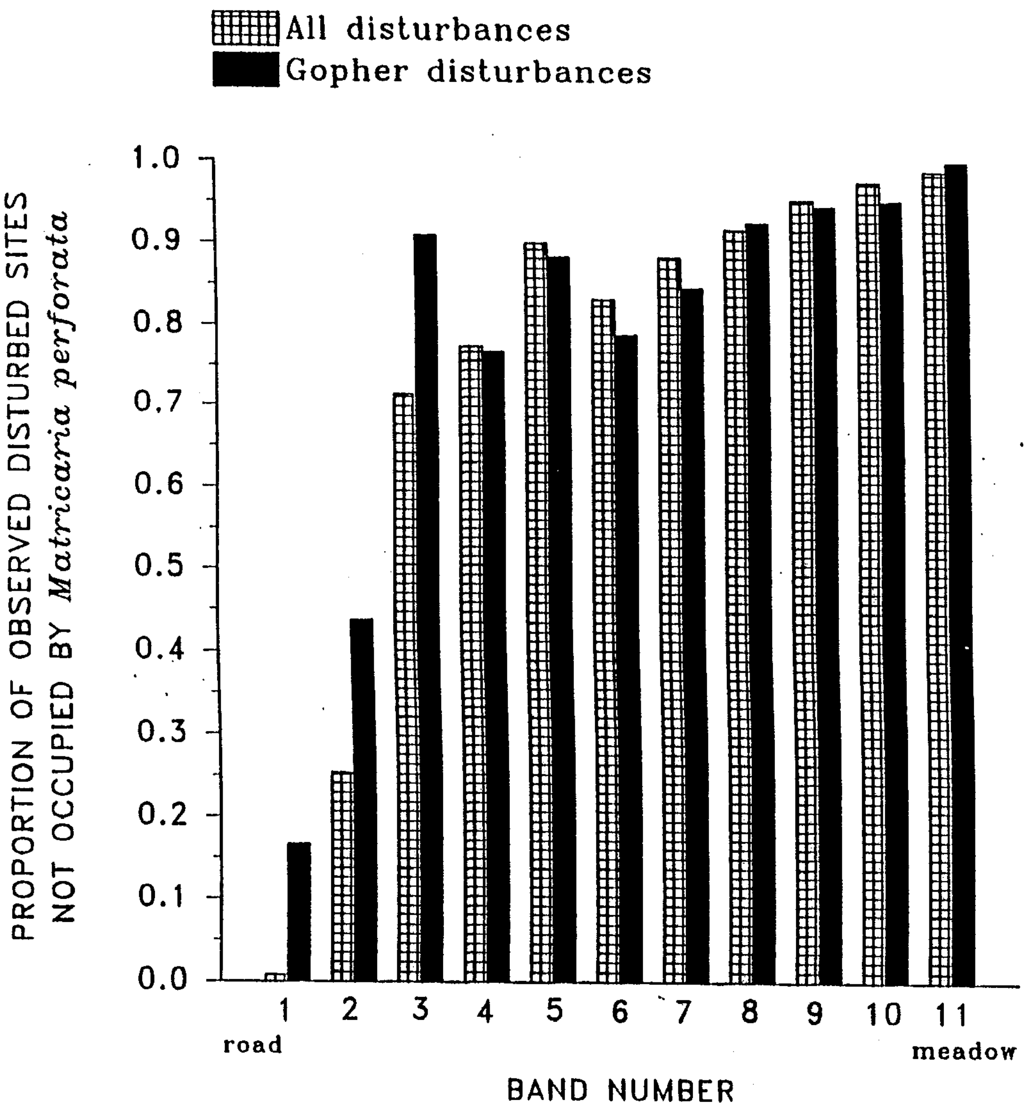


Figure 3. Proportion of disturbed sites unoccupied by *M. perforata*, portrayed by band location. Each band was 100 m long X 3 m wide, and were contiguous, beginning adjacent and parallel to the road (leftmost histogram bars). The furthest transect was located 33 m into the meadow (rightmost bars).

Table 1. Results of one-way analyses of variance for selected dependent variables from the transplant experiment. Statistical significance is ∝ ≤0.05

Dependent variable of interest	*F*-value for treatment effect	Significance
Oven-dry shoot biomass	6.87	$P < 0.006$
RGR 1 (between first and second midvein measurements)	4.40	$P < 0.029$
RGR 2 (between second and third midvein measurements)	4.49	$P < 0.024$
Total RGR (between first and third midvein measurements)	10.17	$P < 0.001$
Change in leaf number (between first and third measurements)	1.99	Not significant

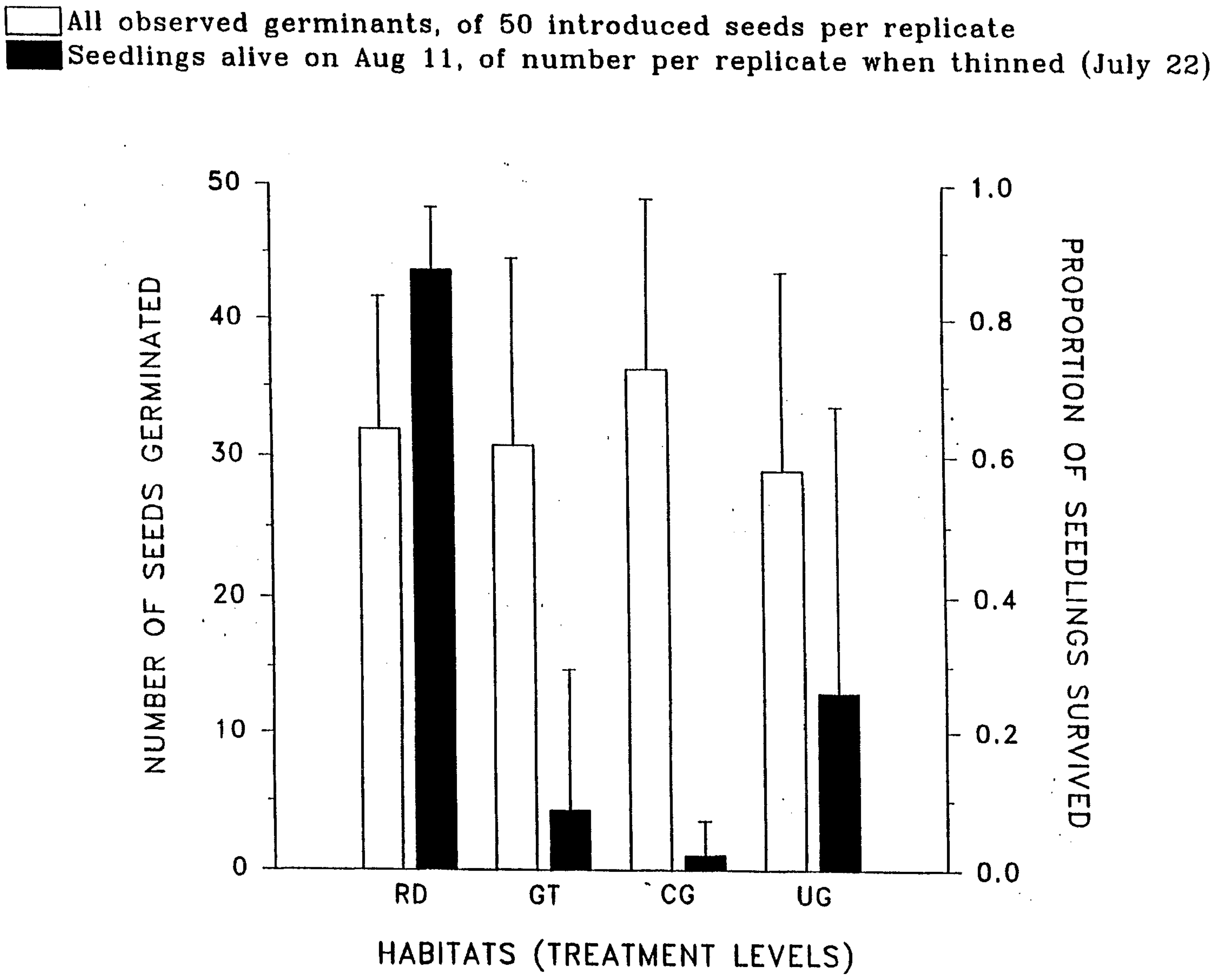


Figure 4. Mean number of seeds germinated at each microsite type, and mean proportion of seedlings surviving to the end of the study period (approximately three weeks). Proportion surviving is based on demographic maps which were started immediately after observing germination and updated four times during the three-week period. Whiskers represent half of 95% confidence intervals.