ELKHORN SLOUGH

TECHNICAL REPORT SERIES 2005: 2

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The effects of grazing on native and exotic seed banks at Elkhorn Slough National Estuarine Research Reserve

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May 2005

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The appropriate citation for this document is:
Orre, K.J., Hufft, R.A., and Parker I.M. 2005. The effects of grazing on native and exotic seed banks at Elkhorn Slough National Estuarine Research Reserve. Elkhorn Slough Technical Report Series 2005:2.

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Abstract: Grazing has been suggested as a technique to maintain or even promote native success in California's heavily invaded grasslands. Varying responses of different plant species to this approach may translate into differences in seed bank species composition. These seed banks provide a long-term signature of historical grazing, and stimulation of this soil seed bank has been suggested as a restoration technique when native seeds are present. In May and September of 2004, soil samples were collected to determine if a native seed bank still persists in the heavily invaded grassland of Elkhorn Slough National Estuarine Research Reserve. In addition, I determined if the seed bank differed between historically different grazed areas. I hypothesized that species shown to respond positively to grazing would have higher abundance in regions of historically higher grazing intensity, and species known to respond positively to the absence of grazing would have higher abundance in regions of historically lower grazing intensity. The seed banks of both grazed regions were dominated by non-natives and showed no significant difference in individual abundances, except for one species (*Lolium multiflorum*). However, there were differences between the two collection dates for total species richness, species diversity, graminoid (grass, sedges, and rushes) richness, evenness, and four of eight species abundances analyzed. All were found to be significantly higher in September. This study emphasizes the importance of species level analysis, and consideration of sampling time when analyzing soil seed banks.

Introduction

Rates of biological invasion have been dramatically amplified as a result of increased human travel and commerce worldwide (Vitousek 1997; Huenneke 1998). Extensive examples of floral and faunal invasions (from deliberate or unintentional introductions) can be cited globally. Such examples include the grass *Cortaderia jubata* in California (Lambrinos 2000), the exotic bumble bee *Bombus terrestris* in Tasmania (Hingston et al 2002), and *Acacia saligna* in the fynbos of South Africa (Holmes and Cowling 1997), to name a few. As populations of these exotics grow, some native species are becoming rare and endangered**.** Consequently, because of the threat to native biodiversity by exotics, some native species are now recognized for their conservational importance (Huenneke & Thomson 1994).

For roughly the last 250 years since the beginning of the Spanish missions, California has undergone a change in species composition dominated largely by Mediterranean annuals (1999 Mensing & Byrne 1998, Hatch et al.). Whether or not this change was due solely to the competitive nature of the exotics or was initiated by human made disturbance is still debated (Mensing & Byrne 1998, Dull 1999, Sax and Brown 2000**)**. Introduced species may have out-competed the natives (Mensing & Byrne 1998). Pollen evidence from the exotic annual *Erodium cicutarium* shows that it was well established in the Santa Barbara region long before the first missions were built in modern day California, supporting the competitive hypothesis (Mensing & Byrne 1998). However, it is thought that intact natural communities consisting of established native perennials would have been able to prevent the establishment of exotic annuals (Corbin & D'Antonio 2004). This has led many to believe that disturbance has played a key role in the success of invasions in California historically and today (Hektner & Foin 1977, Stromberg & Griffin 1996, Sax & Brown 2000, Hatch et al. 1999, Corbin & D'Antonio 2004).

Grassland disturbance results from fire, grazing, vegetative removal by humans, cultivation, and gopher activity, either combined or independently (Hatch et al. 1999, Dyer 2002). Herbivory by mammals (in addition to other faunal groups) is undoubtedly a common occurrence in all terrestrial habitats and occurred naturally at unknown intensities and frequencies long before exotic plant species were introduced (Painter 1995). The highest natural intensities are believed to be from native ungulates such as elk (Tule, Roosevelt, and Rocky Mountain), mule deer, and pronghorn antelope (Painter 1995). However what is unnatural is the introduction of livestock (cattle, sheep, goats, pigs, etc.) to California starting in the early 1800's (Silberstein et al. 2002**).** Based on the temporal concurrence of non-native plant and animal introductions, some have suggested a causal link between introduced grazers and invasion (Dull 1999).

Today exclusion of grazing from coastal grasslands is used as a means to promote native grass success (Hatch 1999). However, this strategy is often founded on observation and hearsay (Dyer 2003) or short-term studies yielding unreliable data (Hamilton et al. 2002). Furthermore, it is difficult to apply generalities in management strategies to different sites (such as inland vs. coastal grasslands), because of variation in moisture and disturbance histories. Studies have produced mixed results on effects of grazing on native and exotic species (Bartolome et al. 1986, Hatch 1999, Hayes & Holl 2003a). For example, Hayes and Holl (2003b) found that annual forbs (native and exotic together) responded positively to grazing, whereas perennial native forbs showed a higher species richness in ungrazed areas. However, they were unable to find a clear trend on the effects of grasses lumped as guilds. Perhaps more interestingly, when looking at the species level, the native *Danthonia californica* has been shown to respond positively to grazing (Hatch 1999, Hayes & Holl 2003b). Yet Hamilton et al. (2002) found that in the absence of grazing, the native *Nassella* sp. responded positively by colonizing new areas. This suggests that perhaps generalities about native and non-native species cannot be made, demanding further study at a species-specific level. If grazing benefits certain native species but is detrimental to others, restoration strategies could be complicated and very specific to geographical location and species composition.

The unique life history of plants also complicates management strategies because many plants disperse not only through space, but also via their seed bank. Seeds of annual and perennials of all different guilds become deposited (either on the surface or in the soil) and become known as the soil seed bank (Goodson 2001). Here viable seeds may remain buried within the soil for many years (Warr et al. 1993**,** Bekker et al. 1998), and their regenerative success and longevity may be correlated with their size and shape (Bekker et al. 1998). These seed banks may reflect the species above ground (Chang et al 2001, Figueroa et al 2004), however it has been observed that there is often dissimilarity between surface vegetation and the seed bank (Bekker et al. 1997, Chang et al 2001, Holmes 2002, Maccherini & De Dominicis 2003). Floristic dissimilarity may arise between vegetation and soil seed banks based on historical changes in species composition (Bekker et al. 1997), as well as differences in reproductive strategies (Goodson 2001). It is this dissimilarity that gives the seed bank its potential value for restoration of native habitats. After a site has been disturbed, and the sediment is mixed, dormant seeds that become freshly exposed can play a major role in the regeneration of the disturbed habitat (Warr et al. 1993). This idea has been suggested as a potential recruitment approach in regeneration of surface vegetation that is no longer represented (Warr, et al. 1993, Chang et al. 2001, Zhang et al. 2001).

One location where management techniques could be applied to restore native vegetation is the Mediterranean grassland at Elkhorn Slough. Opening into the Monterey Bay at Moss Landing, Elkhorn Slough is located 145 kilometers south of San Francisco and 32 kilometers north of Monterey. Elkhorn Slough National Estuarine Research Reserve (ESNERR) is a 583-hectare reserve on the eastern shore of the slough. Grasslands of the central coast of California (including what is now ESNERR) that are presumed to have previously been dominated by native bunchgrasses, such as *Danthonia californica*, *Deschampsia cespitosa,* and *Nassella* spp., have been heavily invaded and replaced by exotics, such as *Vulpia myuros myuros*, *Bromus* spp., *Aira caryophyllea, Briza* spp., and *Avena* spp. (Stromberg et al. 2001). Historically, grazing in the area began at low numbers at the end of the 18th and beginning of the 19th centuries. In 1825, what is now ESNERR was part of a land grant that by the early 1830's had over 6000 cattle and 500 horses. This land grant extended from Moro Cojo Slough to Elkhorn Slough, and east to San Miguel Canyon. Approximately 30 years later the land grant began to be subdivided and fenced into parcels. From about 1875 to the early 1970's, the land of present day ESNERR was developed into dairies (Silberstein et al 2002, Andrea Woolfolk, pers. comm.). By 1980, the California Department of Fish and Game purchased large parcels of land and designated it as ESNERR. Within two years of its initiation, ESNERR was free of all livestock (Silberstein et al. 2002). Interestingly, two fence lines dating back to the subdivision of parcels in late 1860's to early 1870's are still visible today. These fences persisted through various management techniques for about 100 years. Aerial photos taken in 1931, 1937, 1949, 1956, 1966, 1971, and 1980 show the two fences appearing to have restricted livestock access (figure 1). The area to the far north was operated as a dairy for about 100 years with a gap between 1905-1915 when the land was used as a hunting reserve and was cattle free. Similarly the area to the far south was also operated as a dairy for the same 100-year period (Andrea Woolfolk, pers. comm.). Historically the area bound by the fences has likely been subjected to a difference in intensity and duration of grazing compared to the far north and south areas. A clear differential pattern of vegetation is easily seen in the photos (figure 1), showing differences in management techniques. Generally, the areas to the far north and far south that appear in the photos to have higher grazing intensity can be referred to as areas of "historically higher grazing intensity." The area bound by the two fences having been grazed less intensely, and possibly more sporadic, can be referred to as area of “historically lower grazing intensity” (figure 2).

This study investigates two central questions: 1) Is there still a native seed bank at ESNERR? and 2) Are the seed banks of both native and exotic species different in historically higher grazing intensity vs. historically lower grazing intensity? I will compare the impacts of historical grazing on the diversity, richness, and evenness for forbs, graminoids (grasses, sedges, and rushes), and total species. In addition I will evaluate abundances at a species-specific level for specific native and exotic species. I predict that native species, such as *D. californica,* that have been shown to respond positively to grazing will have higher abundances in sites of historically higher grazing intensity. Furthermore, species known to respond positively to the absence of grazing, such as *N. pulchra* and native perennial forbs, will be more abundant in the historically lower grazing intensity.

Materials and Methods

Study Site

A short walk from the visitors’ center at ESNERR lay two historically important fence lines, indicated only by the occasional fence post, approximately three-meter wide line of *Carduus pycnocephalus* (Asteraceae), or raised line in the terrain (Andrea Woolfolk, pers. comm., per. obs.). Each fence line runs roughly east west (see figure 1) and is no longer than 200 meters. The two fence lines are 150 meters apart at their closest measurement, enclosing an area of approximately 1.75 ha. These fences are believed to have extended farther east and west historically, however a lack of historical information on the extent of their distance covered could not be certain.

Sampling

Sampling took place twice (May and September 2004), taking into consideration sampling prior to and after seed rain of that year's growing season. This was done only along portions of fence line known with historical certainty. Random points were picked along each fence line at least 4 m apart from each other (five each in May, four each in September). At each point a 4 m quadrat was placed 10 meters from the fence on both sides of the fence (figure 3). Within the quadrat, I used a slide hammer to take a soil core 15 cm deep and 5 cm wide at each meter intersection (25 samples total). The 25 samples were mixed together into two and a half gallon Ziploc bags. Bags were sealed and stored at room temperature in the Parker lab at UC Santa Cruz.

Greenhouse

Starting in November 2004, soil cores from each respective quadrat were sifted to remove large debris included in the cores. I then layered approximately 1 cm of soil on top of 3 cm of potting soil in a 25 x 50 cm tray (1250 cm^3 field soil). Thirty-six trays (one for each quadrat) were then randomized into three rows of twelve inside a greenhouse at UC Santa Cruz. Temperatures in the greenhouse varied between 7° C at night to 21° C during the day. Soil was kept moist, and light intensity was approximately 70% of direct sunlight. Within each tray, total area was split in two (each 25 x 25 cm). Each half was randomly assigned for use in measuring the diversity of either graminoids or forbs. A random quarter of each half tray (12.5 x 12.5 cm) was used to measure abundance. Once a week forbs were weeded from graminoid plots (12.5 x 12.5 cm) and graminoids from the forb plots.

Each individual seedling was marked with a uniquely numbered toothpick within each abundance plot, and germination was scored weekly. Photos of seedlings were taken to establish a seedling guide for identifying (Appendix 1). Several weeks after germination, the seedlings were grouped by morphological types (“morpho-types”). As densities began to get thick enough that competition for light and nutrients was becoming a factor, individuals were either transplanted or pulled (if they had been identified). Transplanted individuals were placed into growth chambers to help accelerate the time between germination and flowering. As individuals were identified to species (Hickman 1993), they were recorded and then removed. A herbarium of species germinated can be found at the natural history museum at UCSC.

Statistical Analyses

Diversity was measured using the Shannon diversity index (H’), where $H' = -\Sigma p_i \log p_i$ and p_i is the proportion of all individuals that are individuals of that species (Brower et al. 1997). Evenness (J’) was calculated based on the Shannon diversity ($J' = H' / H_{max}'$) where H’ is diversity, H_{max}' is the maximum possible diversity per plot ($H_{max}' = \log s$), and s is the total number of species per plot (Brower et al. 1997). Species richness (total species, forb, and graminoid), native richness, H’, and J’, were each analyzed between the two historical grazing intensities and two dates of sampling as main effects using a two-way ANOVA. Abundance was analyzed for species considered invasive, dominant in above ground vegetation at ESNERR (Hayes & Holl 2003b, personal observation), and present in 5 or more plots. Species abundances were also analyzed using a two way ANOVA for date and intensity. These species included *Lolium multiflorum, Vulpia bromoides, Geranium dissectum, Phalaris aquatica, Sonchus asper, Stellaria media,* and *Anagallis arvensis*. In addition, species found to have high abundances that are not considered invasive or dominant in above ground vegetation were also analyzed. Total species richness and all abundances were log transformed (log (1+x)), where x is species richness per plot or abundance per plot) for ANOVA analyses.

Results

I recorded a total of 50 species, 36 forbs, 12 grasses, one sedge, and one rush (Table 1). By and large, native species were dramatically underrepresented in the soil seed bank. With the exception of the rush *Juncus bufonius*, natives were found in fewer than three plots for any given effect (Table 1). Additional evidence of the low native presence was the rarity of the clover *Trifolium microdon*, which was so rare that only one individual was present in the entire study. Some exotic forbs such as *Silybum marianum*, also had very low presences, while other exotic forbs such as *Anagallis arvensis* had very high presence across effects.

The number of forbs, graminoids, and total species showed no difference between grazing durations (Table 2a-c, Figure 4a). However, total species richness and graminoid richness were significantly higher in September than in May (Table 2a-b, Figure 4a). Unlike graminoids, forbs showed no difference between sample dates. Of the species which germinated, only seven were native, resulting in very low native to exotic ratios across both sampling dates and grazing histories (Table 2d, Figure 5a), but no significant difference between sampling times or locations.

The Shannon diversity index showed no significant difference between grazing intensities (Table 2e, Figure 4b). However, like total species richness, diversity and evenness did differ between sampling dates (Table 2e-f). The seed bank in September had higher diversity than the seed bank of May (Figure 4b).

These species (matching my above invasive criteria) *L. multiflorum, V. bromoides, G. dissectum, P. aquatica, S. asper, S. media,* and *A. arvensis,* were analyzed for differences in abundance between historical grazing intensities and sampling date. All were well represented in the soil seed bank across both historically different grazing intensities, and showed no significant difference in abundance except for *L. multiflorum* (Table 2g-n, Figure 5). In addition to no significant difference between grazing intensities, *P. aquatica, S. asper, S. media*, and *A. arvensis* showed no differences between sampling dates (Table 2k-n, Figure 5).

The exotic grass *L. multiflorum* had significant main effects and a significant interaction term (Table 2g, Figure 5a). Abundance was extremely low in all of May's samples. Only one individual was found in the region of historically lower grazing intensity, and none in the region of historically higher grazing intensity. Conversely for September, abundance was significantly higher in the region of historically higher grazing intensity than the region of historically lower grazing intensity. Overall, *L. multiflorum's* abundance was higher in September (Figure 5a). Another exotic grass, *V. bromoides,* also had a significant interaction term (Table 2h, Figure 5b). Total abundance of *V. bromoides* was significantly less in May than September. Within May's seed bank, abundance was higher for the region of historically higher grazing intensity. However, within September's seed bank abundance was higher for the region of historically lower grazing intensity (Figure 5b).

G. dissectum showed a significant interaction term (Table 2i, Figure 5c). In May, the abundance of *G. dissectum* was higher in the region of historically higher grazing intensity than the region of historically lower grazing intensity. However, for September's seed bank the abundance was higher in the region of historically lower grazing intensity. For all individuals of *G. dissectum,* abundance was higher in September (Figure 6b).

Despite low presence of native species, the native rush *J. bufonius* exhibited very high abundance compared to other species (Figures 5d). *J. bufonius* showed a significant interaction term (Table 2j, Figure 5d). In May, there was statistically no difference between either grazed regions. However, in September abundance was significantly less for the region of historically lower grazing intensity than the region of historically higher grazing intensity (Figure 5d).

Discussion:

Native Seed Bank

The seven native species present in this study were *Baccharis pilularis, Cyperus* cf *esculentus* (sedge)*, Trifolium microdon, J. bufonius* (rush)*, Oxalis albicans ssp pilosa, Calandrinia ciliata,* and *Claytonia perfoliata.* It is interesting to consider why these species, a small subset of all species native to ESNERR, are present in this study. Based on ESNERR's history of grazing for the last 200+ years, grasslands at ESNERR can be considered disturbed habitat. Many exotic species found in this study (e.g., *S. asper, A. arvensis, S. media,* etc) are known to be common in disturbed habitats (Hickman 1993). *C. esculentus, T. microdon, J. bufonius,* and *C. perfoliata*, although native, are also common among disturbed habitats. In fact, *C. esculentus* is considered a weed worldwide, and *J. bufonius* is also found throughout the world (Hickman 1993). Although not considered to be characteristic of disturbed habitats, *B. pilularis* (coyote brush), is a common shrub found in chaparral and coastal-sage scrub. *C. ciliata* is typically found in grassy areas and cultivated fields, similar to the habitat of much of ESNERR (Hickman 1993). The presence of only widely disturbed or disturbance-prone species suggests that these areas of ESNERR might be too degraded to consider disturbance as a restoration technique.

Despite the near absence of natives in this study, and the complete absence of native grasses altogether, native species do still exist at ESNERR. Remnant native patches of *D. californica*, *N. pulchra*, *Elymus glaucus* and *Bromus carinatus* are still found in the greater Elkhorn Slough watershed, however with lower percent cover compared to exotic grasses (eg. *V.*

bromoides and *L. multiflorum*) (Hayes & Holl 2003a). Since this study did not compare above ground species composition to below ground composition, I cannot say whether or not patches of native vegetation existed within my sample area. However, since no native grasses were found in this study, it is likely that no native above ground patches exist within sampled plots, but could be elsewhere at ESNERR. Since seed density generally decreases as distance increases from parents (Bustamante & Simonetti 2000), and the availability of seeds may constrain recruitment (Seabloom et al. 2003a), native seeds are probably going be concentrated around native patches. Therefore, despite no native grass seed bank found in this study, it is highly likely that a native seed bank does still exist at ESNERR, and can be found in isolated "hot spots" throughout the reserve. In order to capitalize on these hot spots in the seed bank, patches of natives will first need to be visually identified in the aboveground community, and then the seed bank around these patches explored.

Differences between historical grazing intensities

The fact that forbs, graminoids, total species richness, H', and J' showed no significant differences between historical intensities is noteworthy. Historical differences in grazing around the fence lines at ESNERR created no difference in below ground species composition. Based on historical photos (figure 1), above ground vegetation differed as a result of varying historical intensities. However, this difference in intensity did not translate into differences in the soil seed bank. Perhaps the historical signature of grazing intensity has faded in the 25 years since grazing completely ceased at ESNERR.

These results may give more insight into the invasion history at ESNERR. It is possible that, despite differences in grazing on the different sides of the fences for the 100 years prior to initiation of ESNERR, exotic invasion and subsequent dominance may predate varying grazing regimes inflicted by the dairy farmers. This implies that the varying historical grazing intensities during the 100-year period created no difference in below ground species composition. Exotic dominance may have been maintained not by varying intensities, but possibly because rare natives are recruitment-limited (Seabloom et al. 2003). Data from this study suggests that we cannot necessarily rely on historically different grazing regimes to reflect differences in below ground species composition.

At the species level, historical grazing regimes also had little to no effect.   Similarly to no significance found in forbs and graminoids lumped into groups, the analysis at the species level also showed no significance (except *L. multiflorum*). This data suggests that for *V. bromoides*, *G. dissectum*, *J. bufonius*, *P. aquatica*, S. *asper*, *S. media,* and *A. arvensis* individually, differences in abundance between historical grazing intensities are not displayed in the soil seed bank. Different historical grazing intensities may alter species abundance for certain species (e.g., *L. multiflorum*), but this conclusion can not be applied to all species. This further emphasizes the importance of analyzing effects of historical grazing at the species level.

The exotic grass *L. multiflorum*, was more abundant in the regions of historically higher grazing intensity, although this was only evident in September (Figure 5a). Grazing has been suggested as providing a key role its seed germination (Deregibus et al. 1994). The ecological benefit to L. multiflorum of grazing could be a result of reduced competition by neighboring species, however more interestingly, it is suggested that control over seed germination by phytochrome in this species may be an adaptation to disturbance (Deregibus et al. 1994). This provides a possible mechanism for the higher abundance of *L. multiflorum*'s in the region of historically higher grazing intensity (Fig 5a).

This study has shown that when analyzing a soil seed bank, date of sampling should strongly be considered. Generally, if there were significant differences between sampling dates, September yielded higher measurements in richness, H’, J’, and abundance. Higher richness in late summer has also been observed in other studies of Mediterranean grasslands (Jimenez & Armesto 1992, Figueroa et al. 2004). The grassland at ESNERR is a winter grassland, in which germination typically starts during the months of November or December, grows throughout the winter, and then sets seed in June. It is not surprising to see that September would usually yield higher abundances, richness, or diversity because by May many seeds deposited from the previous year’s seed set will have germinated in the fall (Russi et al. 1992). Other possible mechanisms include granivory (Russi et al. 1992, Folgarait & Sala 2002) or failed seed emergence (Russi et al. 1992).

The very high abundance of *J. bufonius* found in this study is similar to results of other seed bank studies (Jutila et al. 1998, Staniforth et al. 1998). Interestingly, despite no difference in abundance between grazing intensities from samples collected in May, there was a significant difference between grazing intensities in September. Abundance was significantly less in the region of historically lower grazing intensity (Figure 5d). *J. bufonius* might therefore, respond positively to historically higher grazing intensity, however it has been observed that in the absence of grazing its seed bank is actually higher in abundance (Jutila 1998). Thus suggesting that the low abundance found in that region may be attributable to random sampling variation.

Abundances of *V. bromoides*, *L. multiflorum*, and *G. dissectum* were all significant for a main effect (date) and an interaction effect. For both *V. bromoides* and *G. dissectum,* September’s seed bank abundance was significantly higher in regions of historically lower grazing intensity. This further suggests that September yields a more complete portrayal of the soil seed bank. *L. multiflorum,* in September, had higher abundance in regions of historically higher grazing intensity. Its high abundance in the region of historically higher grazing intensity may be attributable to *L. multiflorum's* preference for higher grazing intensity (Deregibus et al. 1994). It is not clear why *V. bromoides* and *G. dissectum* were significantly higher in regions of historically lower grazing intensity, or why the eight species I analyzed individually was so abundant. Life history is one explanation, as annuals often have higher seed production than perennials (Lambers et al. 1998). Six of the species (*S. asper, S. media, A. arvensis, J. bufonius, V. bromoides, L. multiflorum,* and *G. dissectum*) are annuals, but two (*P. aquatica,* and *S. media)* are perennials. It is possible that these perennials have especially high seed production each year of a long-lived seed bank.

Suggestions for Restoration via Seed Bank

If looking to apply revegetation via seed bank disturbance, it is important to look at the species composition of the seed bank first. For ESNERR, a native seed bank was not shown to be persistent within my sample area; however isolated patches of natives do still exist. Since a widespread native seed bank was non-existent within my sample area, I cannot recommend revegetatation of native species via disturbance of the soil seed bank around those fences. This approach would only promote more exotic success, especially if disturbance was initiated shortly after seed set of a given growing season. However, it is important to note that these fence lines might not be representative of the entire ESNERR, and that further study of the soil seed bank throughout the reserve is critical before excluding stimulation of the soil seed bank as possible restoration technique.

This study suggests that persistent native seed banks may be rare in highly invaded grasslands similar to ESNERR. Also, historically different grazing intensities and durations do not necessarily translate into differences in species composition in the seed bank. Positive response to historically higher grazing intensity was found in only one species, further suggesting that analysis at the species level is important in better understanding responses to grazing. Species abundance in the seed bank is likely to be the highest soon after seed set. However, this is not universal across all species. Some species show no significant difference between sampling dates, and therefore depending on the species represented in the seed bank, timing of disturbance should be applied when exotic abundance is lowest and native abundance is highest (if possible).

Acknowledgments

I would like to thank Rebecca Hufft and Ingrid Parker for their tremendous support with this project from start to finish. Thank you to Jim Velzy and Linda Locatelli for their help in the greenhouse, and Andrea Woolfolk at ESNERR for her help with developing the history of the fence lines. Also thank you to the California Native Plant Society Santa Cruz Chapter (Dr. Patrick Elvander Memorial Scholarship) and The Nature Conservancy (Oren Pollack Grassland Research Grant) for their financial assistance.

Literature Cited

Bartolome, J.W., S.E. Kluekert, and W.J. Barry. 1986. Opal phytoliths as evidence for displacement of native grasslands. Madrono 33:217-222.

Bekker, R.M., G.L. Verweij, R.E.N. Smith, R. Reine, J.P. Bakker, and S. Schneider. 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? Journal of Applied Ecology 34: 1293-1310.

Bekker, R.M., J.P. Bakker, U. Grandin, R. Kalamees, P. Milberg, P. Poschlod; K. Thompson, and J.H. Willems. 1998. Seed Size, Shape, and Vertical Distribution in the Soil: Indicators of Seed Longevity. Functional Ecology 12(5) 834-842.

Bustamante, Ramiro O. and Javier A. Simonetti. 2000. Seed predation and seedling recruitment in plants: the effect of the distance between parents. Plant Ecology 147: 173-183.

Brower, James E., J.H Zar, and C.N. vonEnde. *Field and Laboratory Methods for General Ecology.* Boston, MA. WCB/McGraw-Hill 1997.

Chang, E.R., R.L. Jefferies, and T.J. Carleton. 2001. Relationship between vegetation and soil seed banks in an arctic coastal marsh. Journal of Applied Ecology 89: 367-384.

Corbin, J.D. and C.M. D'Antonio. 2004. Competition Between Perennial and Exotic Annual Grasses: Implications for an Historical Invasion. Ecology 85(5): 1273-1283.

Deregibus, V.A., J.J. Casal, E.J. Jacob, D. Gibson, M. Kauffman, and A.M. Rodriguez. 1994. Evidence that heavy grazing may promote the germination of *Lolium multiflorum* seeds via phytochrome-mediated perception of high red/far-red ratios. Functional Ecology 8, 536-542.

Dull, Robert A. 1999. Palynological evidence for 19th century grazing-induced vegetation change in the southern Sierra Nevada, California, U.S.A. Journal of Biogeography 26: 899-912.

Dyer, A. R.. 2002. Burning and Grazing Management in a California Grassland: Effect on Burning on Bunchgrass Seed Viability. Society for Ecological Restoration 10(1): 107-111.

Dyer, A.R. 2003. Burning and Grazing Management in a California Grassland: Growth, Mortality, and Recruitment of *Nassella pulchra*. Restoration Ecology 11(3): 291-296.

Figueroa, J.A., S. Teillier, and F.M. Jaksic. 2004. Composition, size and dynamics of the seed bank in a Mediterranean shrubland of Chile. Austral Ecology 29: 574-584.

Folgarit, P.J. and O.E. Sala 2002. Granivory rates by rodents, insects, and birds at different microsites in the Patagonian steppe. Ecography 25:417-427.

Funes, G., S. Basconcelo, S. Diaz, and M. Cabido. 2001. Edaphic patchiness influences grassland regeneration from the soil seed-bank in mountain grasslands of central Argentina. Austral Ecology 26: 205-212.

Goodson, J.M., A.M. Gurnell, P.G. Angold, and I.P. Morrissey. 2001. Riparian seed banks: structure, process and implication for riparian management. Progress in Physical Geography 25: 301-325.

Hamilton, J.G., J.R. Griffin, and M.R. Stromberg. 2002. Long-Term Population dynamics of native *Nassella* (Poaceae) Bunchgrasses in Central California. Madrono 49: 274-284.

Hatch, D.A., J.W. Bartolome, J.S. Fehmi, and D.S. Hillyard. 1999. The Effects of Burning and Grazing on a Coastal California Grassland. Restoration Ecology 7: 376-381.

Hayes, G.F. and K.D. Holl 2003(A). Site-Specific responses to native and exotic species to disturbances in a mesic grassland community. Applied Vegetation Science 6: 235-244.

Hayes, G.F. and K.D. Holl. 2003(B). Cattle Grazing Impacts on Annual Forbs and Vegetation Composition of Mesic Grasslands in California. Conservation Biology 17: 1694-1702.

Hektner, M.M. and T.C. Foin. 1977. Vegetation Analysis of a Northern California Coastal Prairie: Sea Ranch, Sonoma County, California. Madrono 24: 83-103.

Holmes, P.A. 2002. Depth distribution and composition of seed-banks in alien invaded and uninvaded fynbos vegetation. Austral Ecology 27: 110-120.

Hickman, James C. Ed. *The Jepson Manual: Higher Plants of California,* Berkeley, CA: University of California Press, 1993.

Huenneke, L., D. Glick, F.W. Waweru, R.L. Brownell, Jr., and R. Goodland. 1988. SCOPE Program on Biological Invasions: A Status Report. Conservation Biology 2(1): 8-10.

Huenneke, L.F. and J.K. Thomson. 1994. Potential Interference Between a Threatened Endemic Thistle and an Invasive Nonnative Plant. Conservation Biology 9(2): 416-425.

Jimenez H. E. and J. J. Armesto 1992. Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. Journal of Vegetation Science. 3: 579-586.

Jutila, H. M. 1998. Seed banks of grazed and ungrazed Baltic seashore meadows. Journal of Vegetation Science. 9 (3), 395-408.

Lambers, H., F. S. Chapin III, T. L. Pons. *Plant Physiological Ecology,* New York, Springer, 1998 313-314.

Maccherini, S. and Vincenzo De Dominicis. 2003. Germinable soil seed-bank of former grassland converted to coniferous plantation. Ecological Research 18: 739-751.

Mensing, S. and R. Byrne. 1998. Pre-mission invasion of *Erodium cicutarium* in California. Journal of Biogeography 25: 757-762.

Middleton, B.A. 2003. Soil seed banks and the potential restoration of forested wetlands after farming. Journal of Applied Ecology 40: 1025-1034.

Noy-Meir, M., M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean Grassland Plants to Grazing and Protection. Journal of Ecology 77: 290-310.

Painter, E.L. 1995. Threats to the California Flora: Ungulate Grazers and Browsers. Madrono 42: 180-188.

Russi, L., P. S. Cocks, and E.H. Roberts (1992). Seed bank dynamics in a Mediterranean grassland. Journal of Applied Ecology 29: 763-771.

Sax, D.F. and J.H. Brown. 2000. The Paradox of Invasion. Global Ecology and Biogeography 9: 363-371.

Silberstein, M., C. Zabin, L. Newberry, D. Mountjoy, L. Strnad, and J. Caffrey 2002. History of Land Use 93-115. In Caffrey, J., M. Brown, W.B. Tyler, and M. Silberstein (Eds.), *Changes in a California Estuary: A Profile of Elkhorn Slough*. Hong Kong: Elkhorn Slough Foundation.

Staniforth, R. J., N. Griller, C. Lajzerwicz. 1998 Soil seed banks from coastal subarctic ecosystems of Bird Cove, Hudson Bay. 5(2), 241-249.

Stromberg, M. R., P. Kephart, and V. Yadon. 2001. Composition, invasibility, and diversity in coastal California grasslands. Madrono 48:236-252

Stromberg, M.R. and J.R. Griffin. 1996. Long-Term Patterns in Coastal California Grasslands in Relation to Cultivation, Gophers, and Grazing. Ecological Applications 6(4): 1189-1211.

Vitousek, P.M., H.A. Mooney, J. Lubchenco, and J.M. Melillo. 1997. Human Domination of Earth’s Ecosystems. Science 277: 494-499.

Warr, S. J., K. Thompson, and M. Kent. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. Progress in Physical Geography 17(3): 329-347.

Zimmerman, R.C. and J.M. Caffrey 2002. History of Land Use 118-130. In Caffery, J., M. Brown, W.B. Tyler, and M. Silberstein (Eds.), *Changes in a California Estuary: A Profile of Elkhorn Slough*. Hong Kong: Elkhorn Slough Foundation.

Zhang, Z.Q., W.S. Shu, C.Y. Lan, and M.H. Wong. 2001. Soil Seed Bank as an Input Seed Source in Revegetation of Lead/ Zinc Mine Tailings. Restoration Ecology 9 (4): 378-385.

Table 1: Species list showing family, species, status (native vs exotic), and date/plots found.
M =may, S = September, h = high historical grazing intensity, l = low historical grazing intensity

Family	**Species**	**Status**	**M-h**	**M-l**	**S-h**	**S-l**
Apiaceae	*Conium maculatum*	Exotic	5	2	1	2
Asteraceae	*Baccharis pilularis*	Native	0	1	2	1
Asteraceae	*Conyza* sp.	?	0	0	2	0
Asteraceae	*Gnaphalium luteo-album*	Exotic	1	0	0	0
Asteraceae	*Silybum marianum*	Exotic	0	0	1	0
Asteraceae	*Soliva sessilis*	Exotic	0	1	1	1
Asteraceae	*Sonchus asper*	Exotic	4	2	3	2
Asteraceae	*Sonchus oleraceus*	Exotic	0	1	0	1
Brassicaceae	*Cardamine hirsuta*	Exotic	1	2	2	2
Brassicaceae	*Hirschfeldia incana*	Exotic	6	2	0	2
Caryophyllacea	*Cerastium glomeratum*	Exotic	3	3	2	3
Caryophyllacea	*Silene gallica*	Exotic	0	3	4	3
Caryophyllacea	*Spergula arvensis* ssp *arvensis*	Exotic	0	1	0	1
Caryophyllacea	*Spergularia bocconei*	Exotic	1	0	0	0
Caryophyllacea	*Stellaria media*	Exotic	3	2	1	2
Chenopodiaceae	*Atriplex triangularis*	Exotic	3	3	1	3
Crassulaceae	*Crassula tillaea*	Exotic	0	0	1	0
Cyperaceae	*Cyperus* cf *esculentus*	Native	2	1	1	1
Fabaceae	*Lotus* cf *corniculatus*	Exotic	1	3	1	3
Fabaceae	*Medicago polymorpha*	Exotic	3	2	1	2
Fabaceae	*Trifolium microdon*	Native	0	0	1	0
Fabaceae	*Trifolium repens*	Exotic	3	1	1	1
Fabaceae	*Trifolium subterraneum*	Exotic	2	0	1	0
Geraniaceae	*Erodium moschatum*	Exotic	1	1	1	1
Geraniaceae	*Geranium dissectum*	Exotic	5	4	4	4
Juncaceae	*Juncus bufonius*	Native	10	9	8	9
Lythraceae	*Lythrum hyssopifolium*	Exotic	7	8	7	8
Malvaceae	*Malva* cf *parviflora*	Exotic	1	0	0	0
Oxalidaceae	*Oxalis albicans ssp pilosa*	Native	1	2	0	2
Plantaginaceae	*Plantago coronopus*	Exotic	1	1	1	1
Plantaginaceae	*Plantago lanceolata*	Exotic	0	0	1	0
Poaceae	*Aira caryophyllea*	Exotic	0	0	1	0
Poaceae	*Avena barbata*	Exotic	1	0	1	0
Poaceae	*Briza minor*	Exotic	2	3	2	3
Poaceae	*Bromus hordeaceus*	Exotic	1	0	1	0
Poaceae	*Bromus stamineus*	Exotic	0	0	3	0
Poaceae	*Lolium multiflorum*	Exotic	1	0	4	0
Poaceae	*Phalaris aquatica*	Exotic	5	5	4	5
Poaceae	*Poa annua*	Exotic	2	1	1	1
Poaceae	*Polypogon monspeliensis*	Exotic	5	1	3	1

Poaceae	*Vulpia bromoides*	Exotic	2	1	5	1
Poaceae	*Vulpia myuros*	Exotic	1	0	1	0
Polygonaceae	*Polygonum arenastrum*	Exotic	3	4	3	4
Polygonaceae	*Rumex acetosella*	Exotic	0	2	2	2
Polygonaceae	*Rumex pulcher*	Exotic	0	1	2	1
Portulicaceae	*Calandrinia ciliata*	Native	0	2	0	2
Portulicaceae	*Claytonia perfoliata*	Native	0	3	1	3
Primulaceae	*Anagallis arvensis*	Exotic	10	7	4	7
Rubiaceae	*Galium aparine*	Exotic	0	0	1	0
Solanaceae	*Solanum nigrum*	Exotic	1	2	0	2

Table 2: ANOVA results for a) total richness, b) graminoid richness c) forb richness d) percent natives, e) H' -diversity, f) J'- evenness, and abundance for g) *Lolium multiflorum* h) *Vulpia bromoides* i) *Geranium dissectum* j) *Juncus bufonius* k) *Phalaris aquatica* l) *Sonchus asper* m) *Stellaria media*, and n) *Anagalis arvensis*.

a) Total Richness

Source	D.F.	S.S.	F Ratio	P
Date	1	0.0790209	7.7206	0.0090
Grazing	1	0.0188321	1.8429	0.1841
Grazing x Date	1	0.0034207	0.3342	0.5672
Error	32	0.3275207		

b) Graminoid Richness

Source	D.F.	S.S.	F Ratio	P
Date	1	44.0055560	25.2136	<.0001
Grazing	1	0.2000000	0.1146	0.7372
Grazing x Date	1	6.4222220	3.6797	0.0640
Error	32	55.8500000		

c) Forb Richness

Source	D.F.	S.S.	F Ratio	P
Date	1	0.0125000	0.0026	0.9598
Grazing	1	6.2347222	1.2874	0.2650
Grazing x Date	1	1.9013889	0.3926	0.5354
Error	32	154.9750000		

d) Percent Natives

Source	D.F.	S.S.	F Ratio	P
Date	1	0.0043372	0.8664	0.3589
Grazing	1	0.0037655	0.7522	0.3922
Grazing x Date	1	0.0099195	1.9815	0.1689
Error	32	0.1601943		

e) Diversity (H')

Source	D.F.	S.S.	F Ratio	P
Date	1	0.9991139	6.8262	0.0136
Grazing	1	0.1234655	0.8435	0.3653
Grazing x Date	1	0.0290915	0.1988	0.6587
Error	32	4.6836781		

f) Evenness (J')

	D.F.	S.S.	F Ratio	P
Date	1	0.5468916	4.8436	0.0351
Grazing	1	0.0426497	0.3777	0.5432
Grazing x Date	1	0.0618218	0.5475	0.4647
Error	32	3.6109550		

g) *Lolium multiflorum*

	D.F.	S.S.	F Ratio	P
Date	1	1.168696	7.3256	0.011
Grazing	1	0.676904	4.243	0.048
Grazing x Date	1	1.0596609	6.6422	0.015
Error	32	5.105139		

h) *Vulpia bromoides*

	D.F.	S.S.	F Ratio	P
Date	1	14.043718	19.2409	1E-04
Grazing	1	2.634439	3.6094	0.067
Grazing x Date	1	4.146961	5.6816	0.023
Error	32	23.356489		

i) *Geranium dissectum*

	D.F.	S.S.	F Ratio	P
Date	1	0.95596411	5.8585	0.021
Grazing	1	0.21260654	1.3029	0.262
Grazing x Date	1	0.76458566	4.6856	0.038
Error	32	5.2216398		

j) *Juncus bufonius*

	D.F.	S.S.	F Ratio	P
Date	1	0.0038721	0.0068	0.9347
Grazing	1	0.6873514	1.2088	0.2798
Grazing x Date	1	0.8402603	4.9948	0.0325
Error	32	18.1964950		

k) ***Phalaris aquatica***

Source	D.F.	S.S.	F Ratio	P
Date	1	0.3695955	1.5841	0.2173
Grazing	1	0.1367450	0.5861	0.4496
Grazing x Date	1	0.0018942	0.0081	0.9288
Error	32	7.4663246		

l) ***Sonchus asper***

Source	D.F.	S.S.	F Ratio	P
Date	1	0.10640388	0.6597	0.4227
Grazing	1	0.09525743	0.5906	0.4478
Grazing x Date	1	0.00253183	0.0157	0.9011
Error	32	5.1611929		

m) ***Stellaria media***

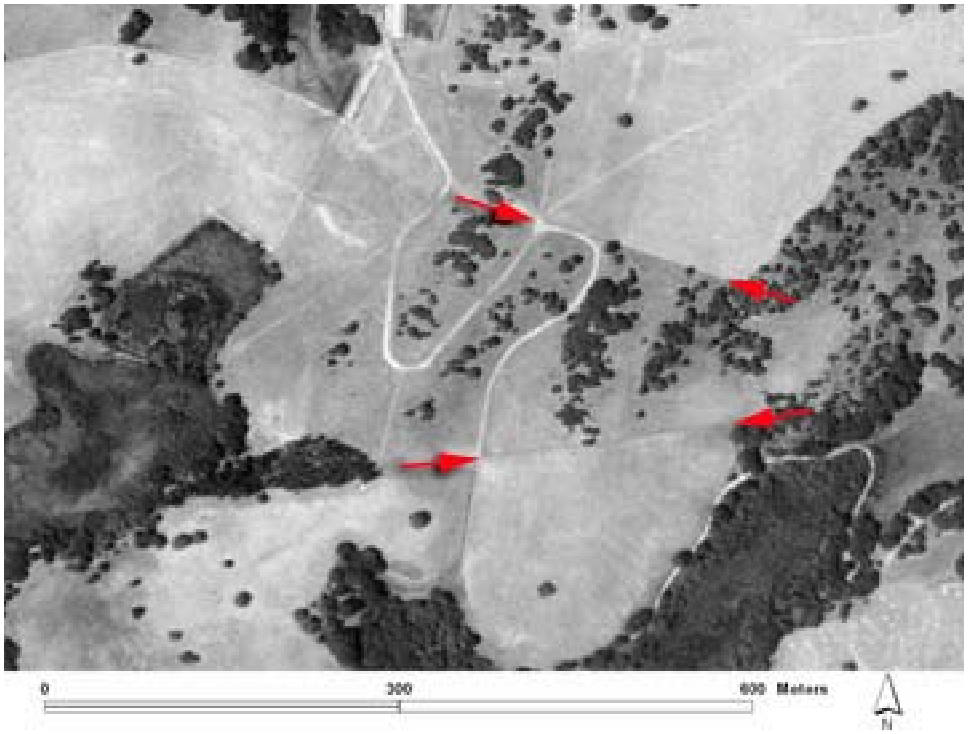
Source	D.F.	S.S.	F Ratio	P
Date	1	0.19131263	0.7406	0.3959
Grazing	1	0.13978332	0.5411	0.4673
Grazing x Date	1	0.07110932	0.2753	0.6034
Error	32	8.2664492		

n) ***Anagalis arvensis***

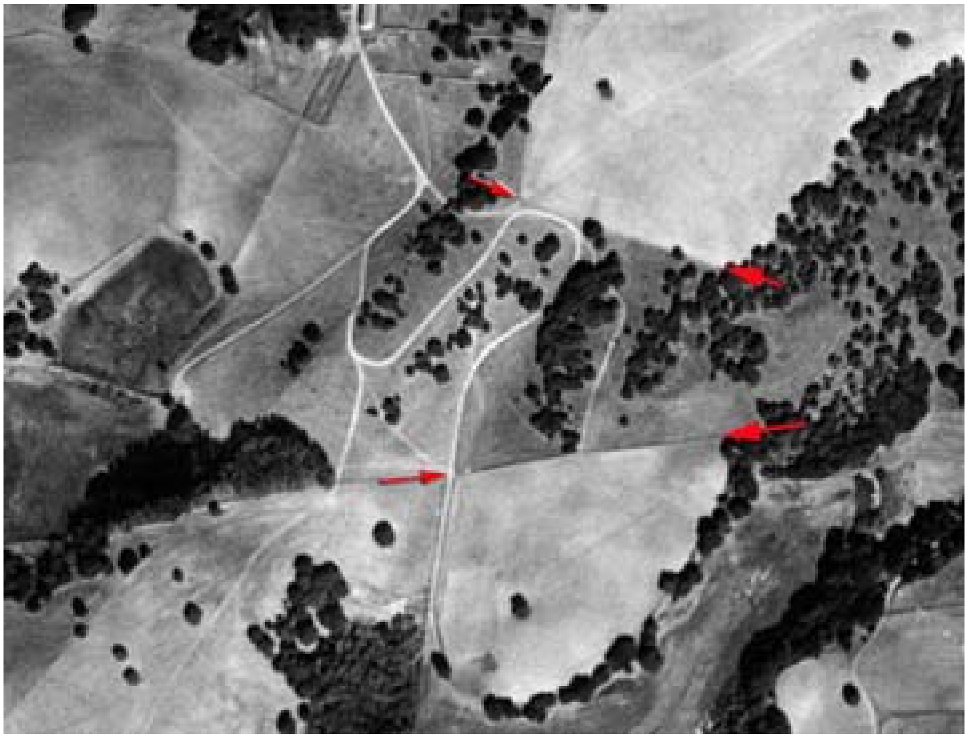
Source	D.F.	S.S.	F Ratio	P
Date	1	0.34452679	1.107	0.3006
Grazing	1	0.0012395	0.004	0.9501
Grazing x Date	1	0.19770042	0.6352	0.4313
Error	32	9.959653		

Figure 1: Aerial photos of present day ESNERR taken in a) 1931 b) 1937 c)1949 d) 1956 e)1966 f)1971 g)1980 (post removal of grazing). Note east-west fences separating historically higher grazing intensity (far north and far south) from historically lower grazing intensity (area bound between fence and road). Arrows indicate portion of fence sampled.

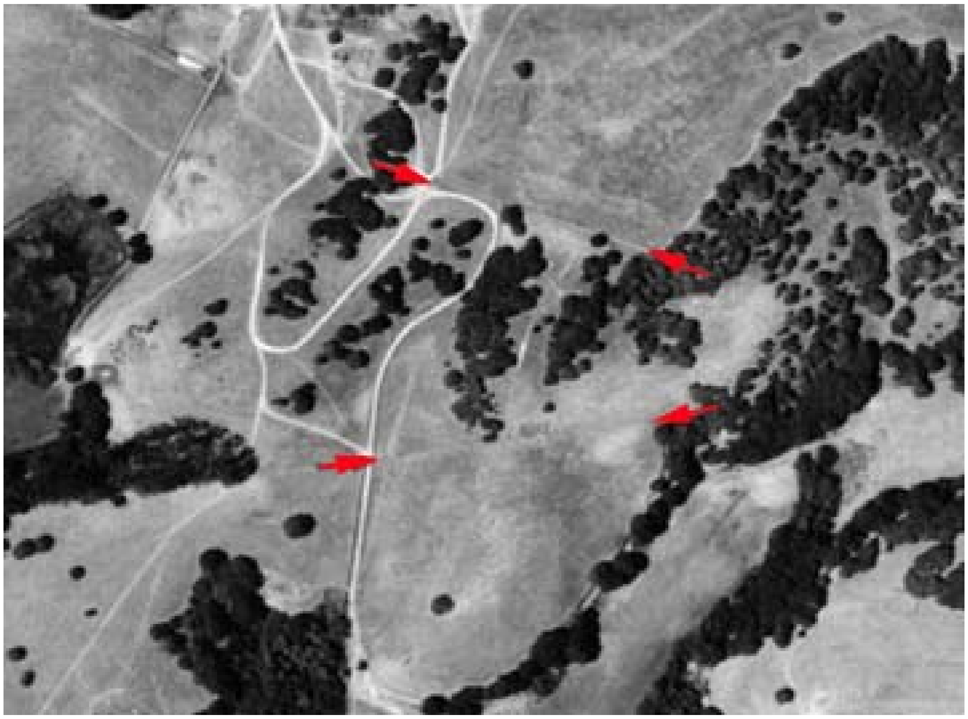
a)



b)



c)



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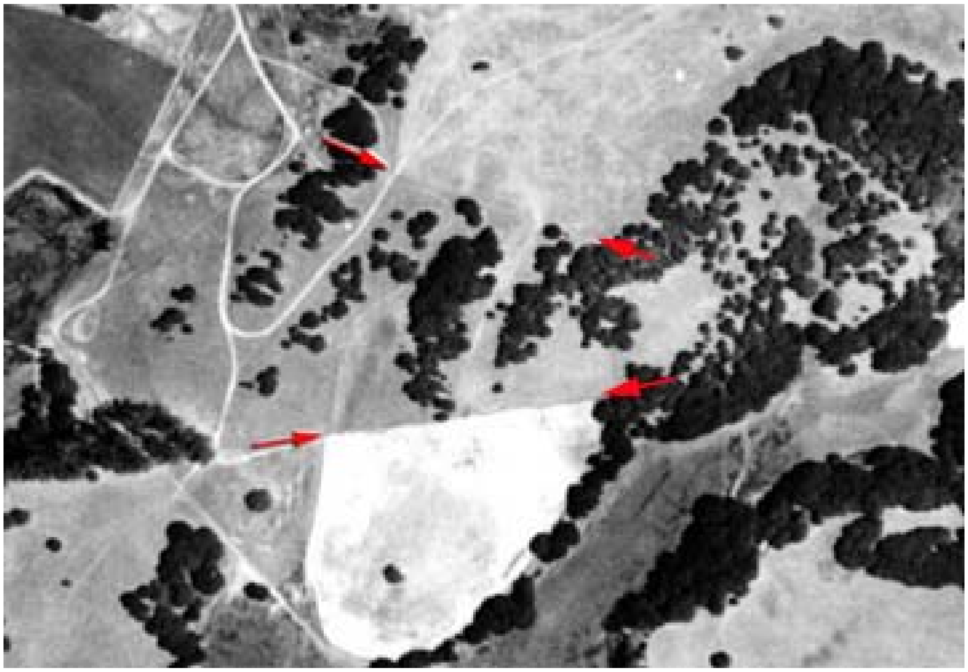
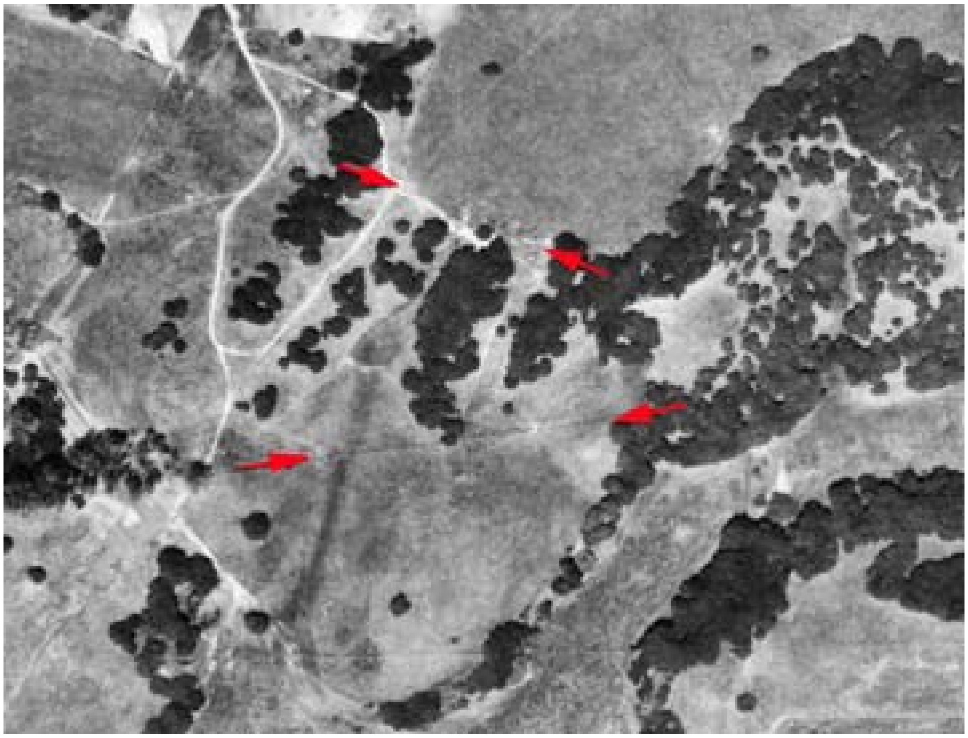


e)

f)



g)

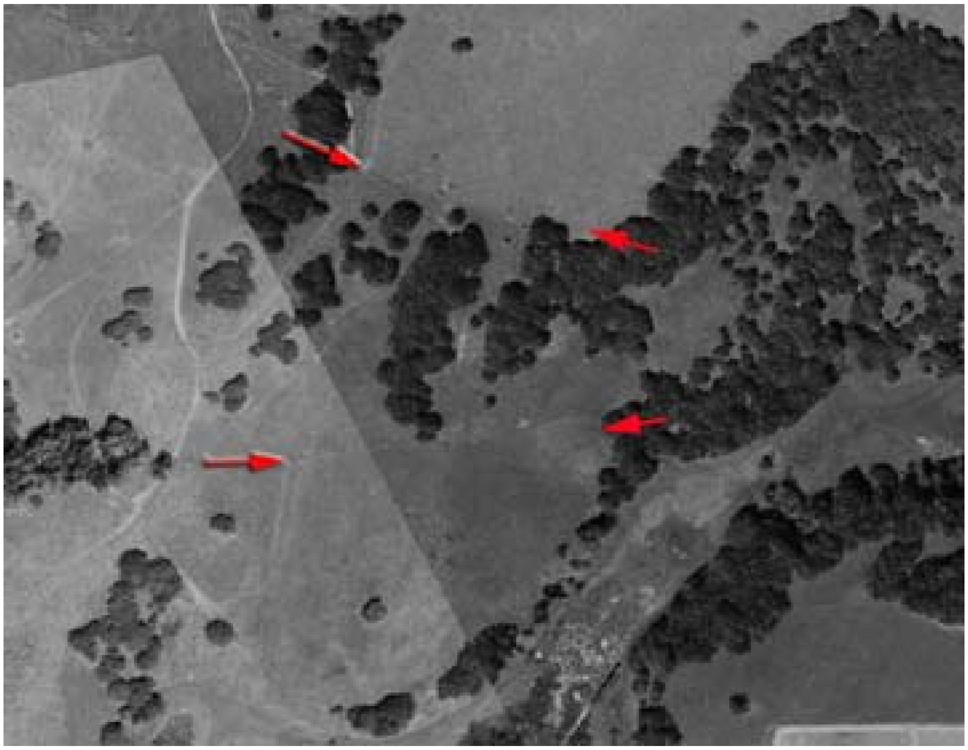


Figure 2: Schematic of 2 fence lines with each square representing a random point along the line.

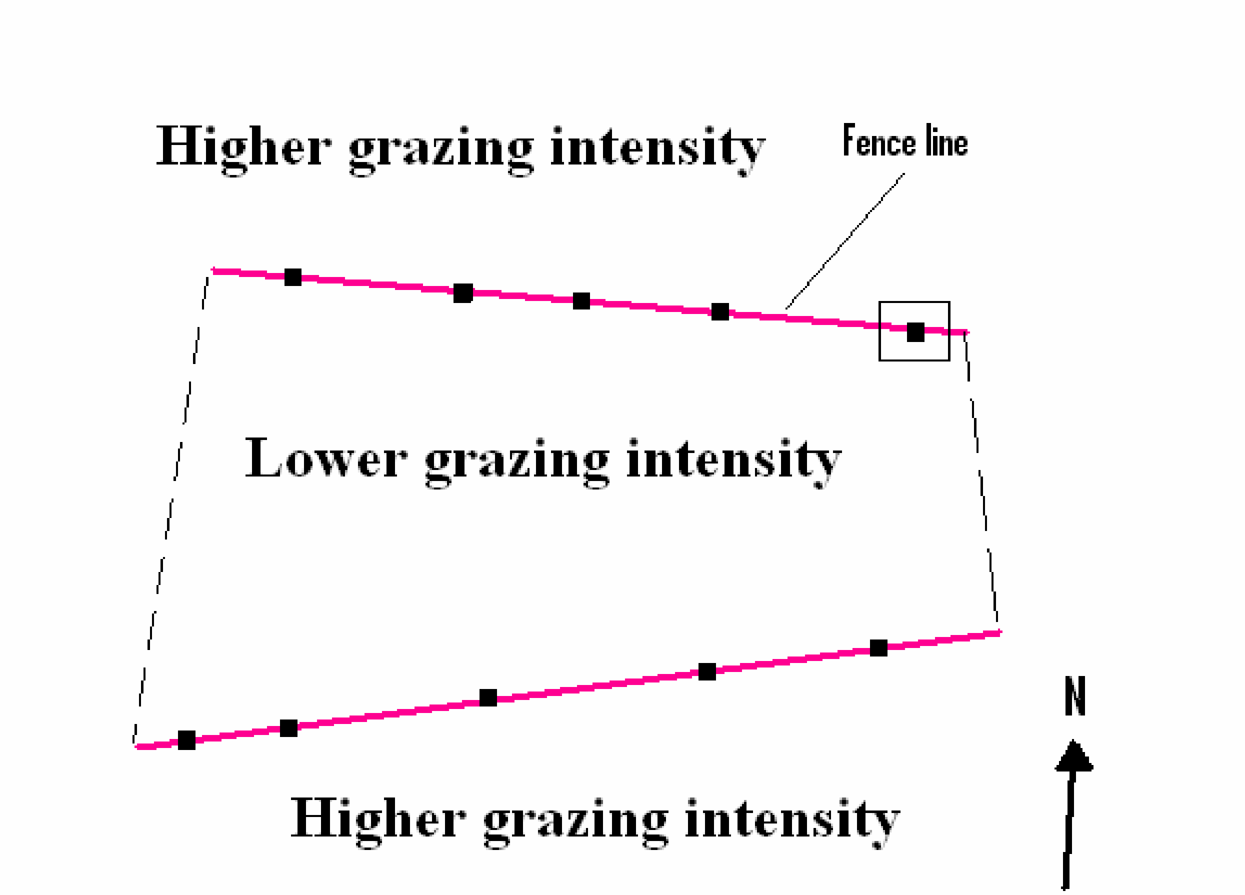


Figure 3: Expanded view of random point along fence line showing quadrats. Soil cores taken at each intersecting meter (25 total samples per quadrat).

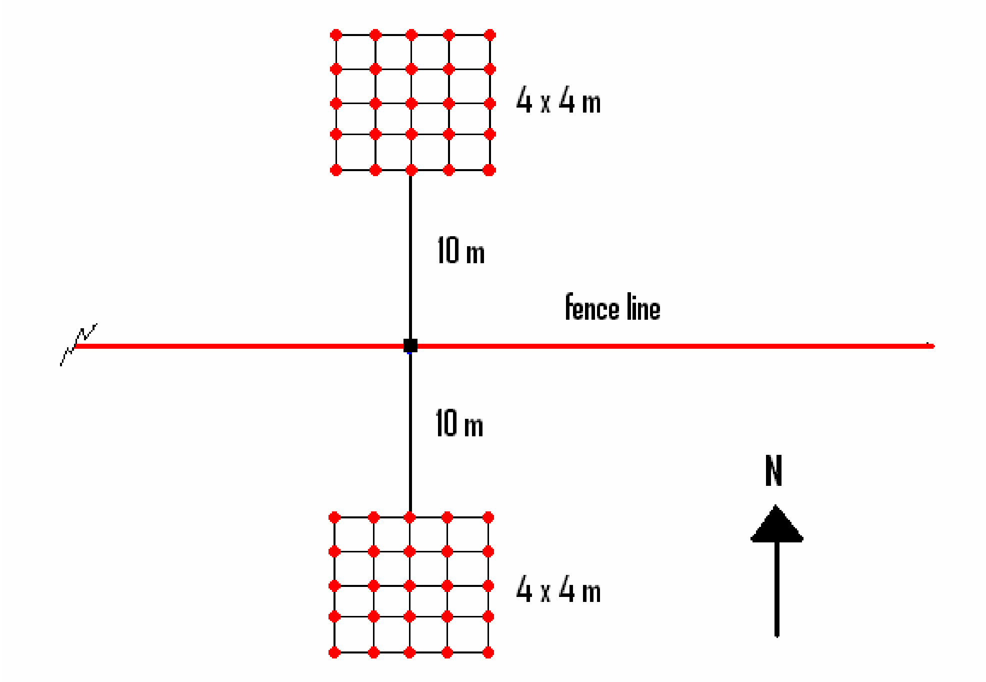
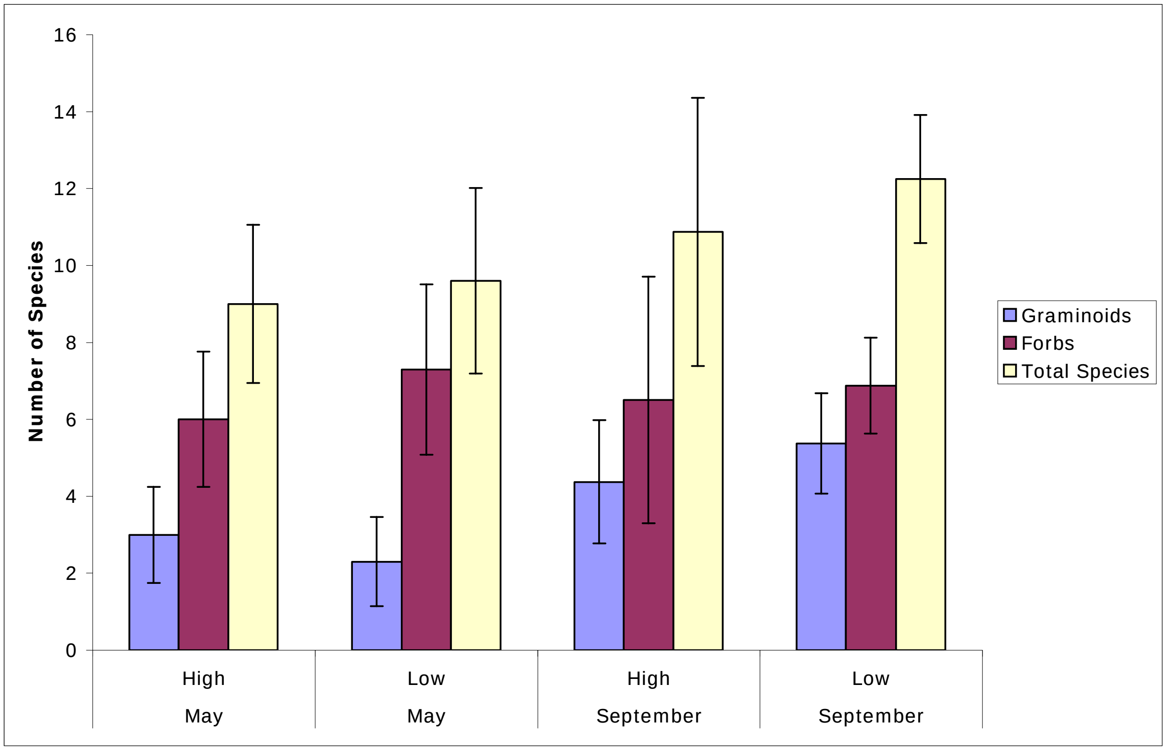
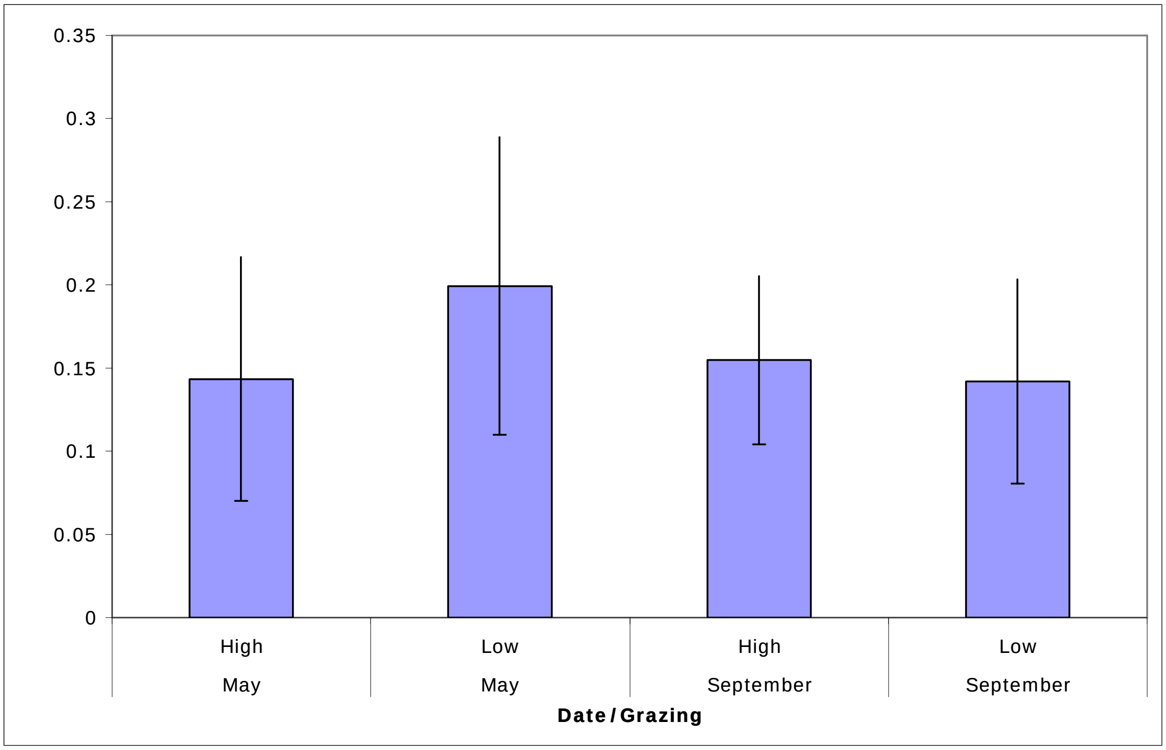


Figure 4: a) Number of graminoids, forbs, and total species by date and grazing intensity with +/- 1 standard deviation b) percent of species that were native, with +/- 1 standard deviation c) diversity (H') and evenness (J'), with +/- 1 standard deviation.

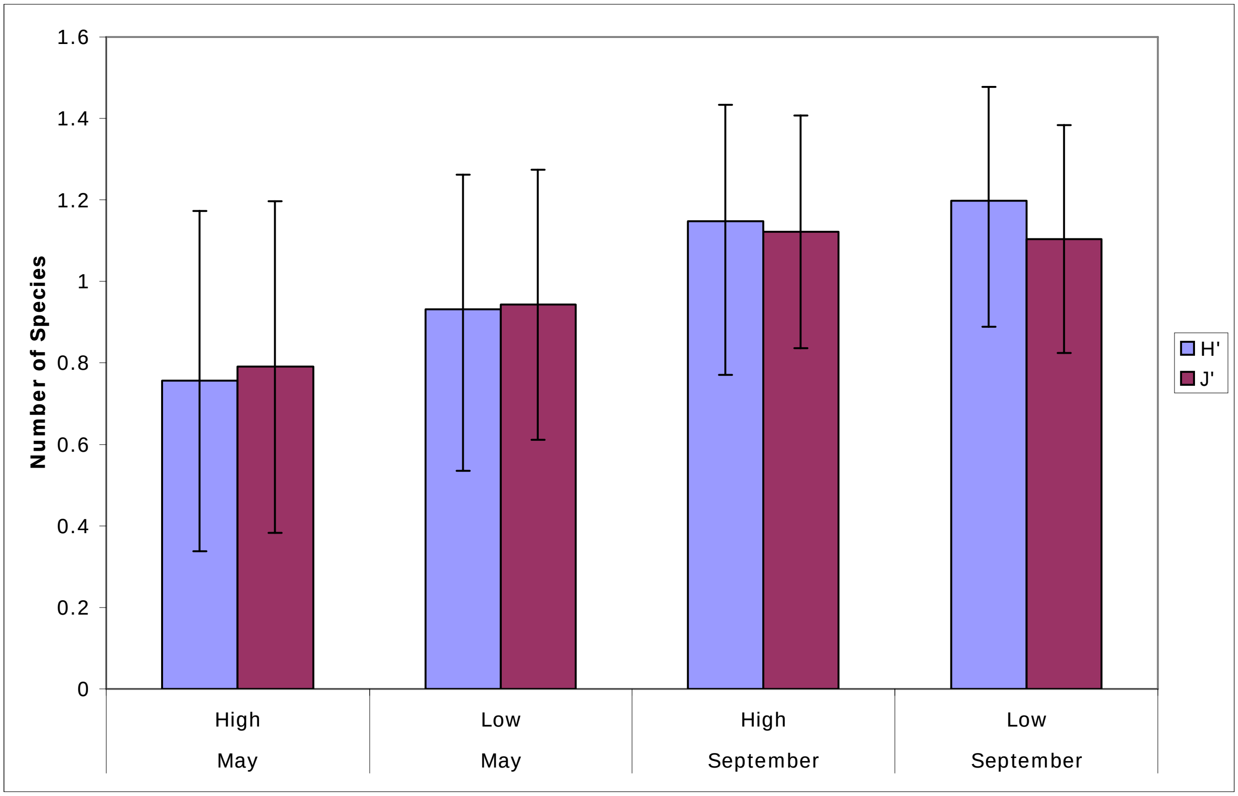
a)



b)



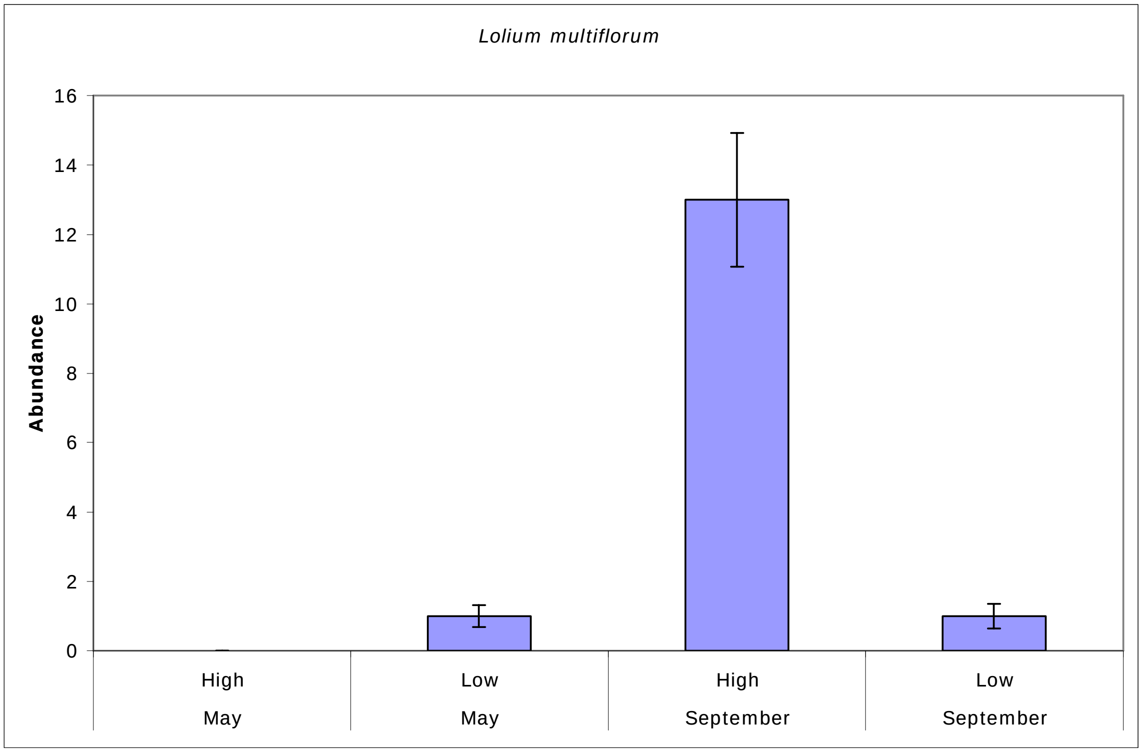
c)



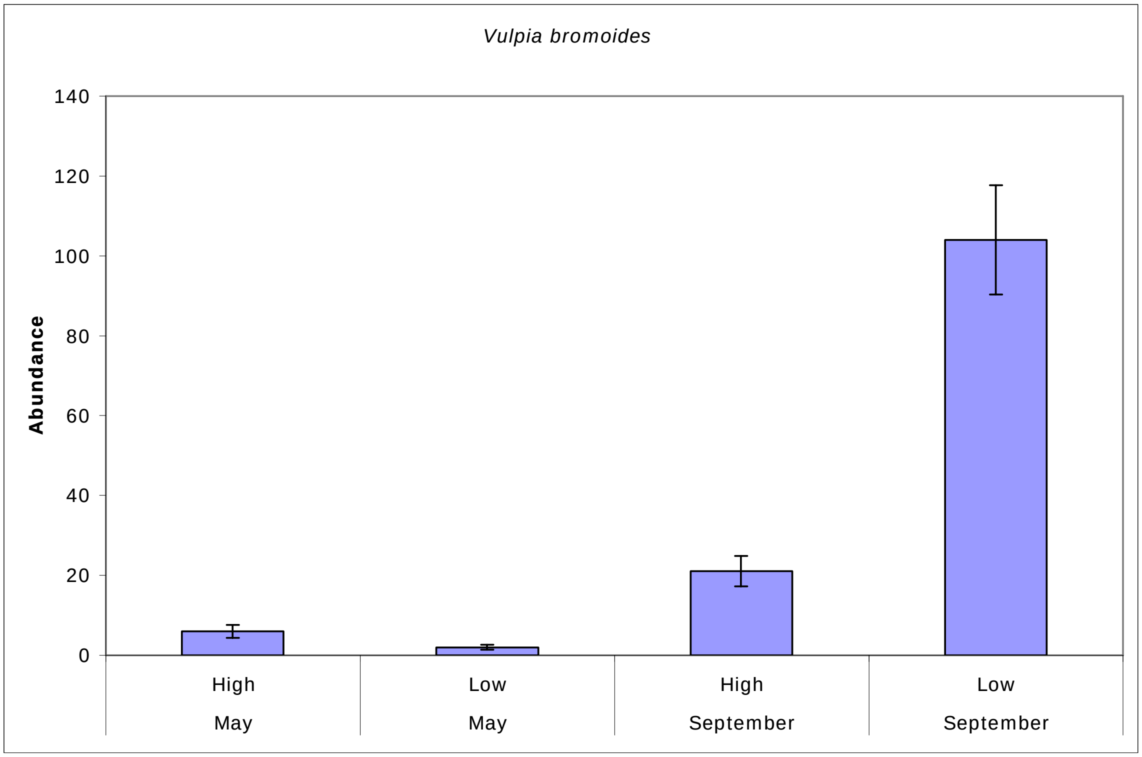
Number of Species
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
High
May
Low
May
High
September
Low
September
H'
J'

Figure 5: Abundance of a) *Lolium multiflorum* b) *Vulpia bromoides* c) *Geranium dissectum* d) *Juncus bufonius* (native) e) *Phalaris aquatica* f) *Sonchus asper* g) *Stellaria media* h) *Anagallis arvensis* by date and grazing intensity with +/- 1 standard deviation.

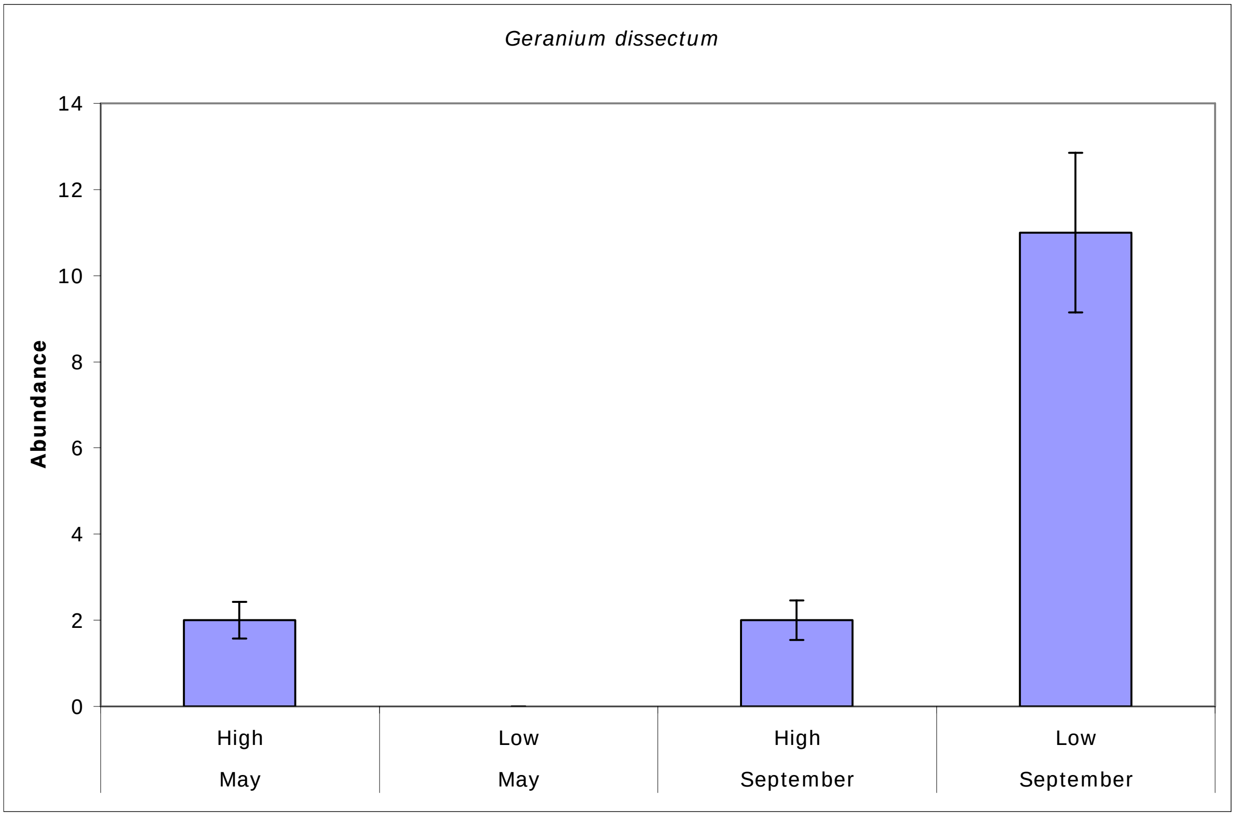
a)



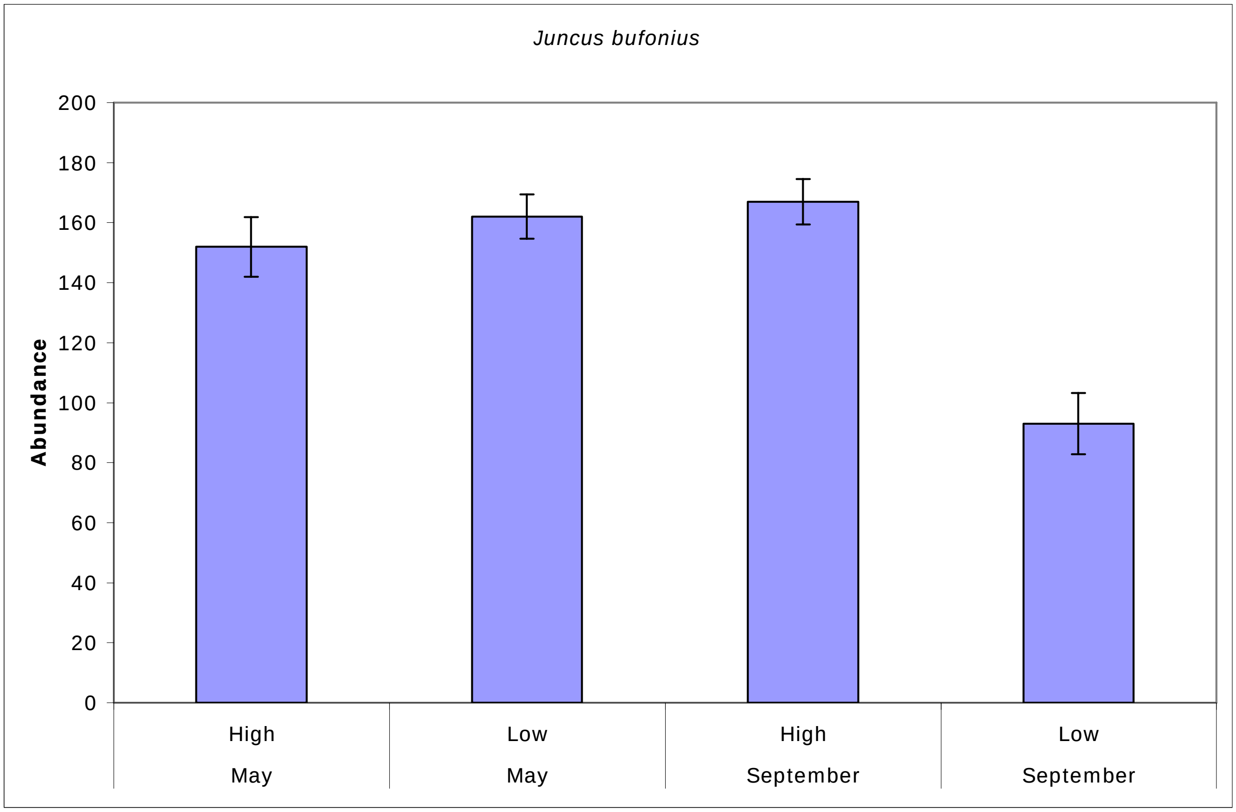
b)



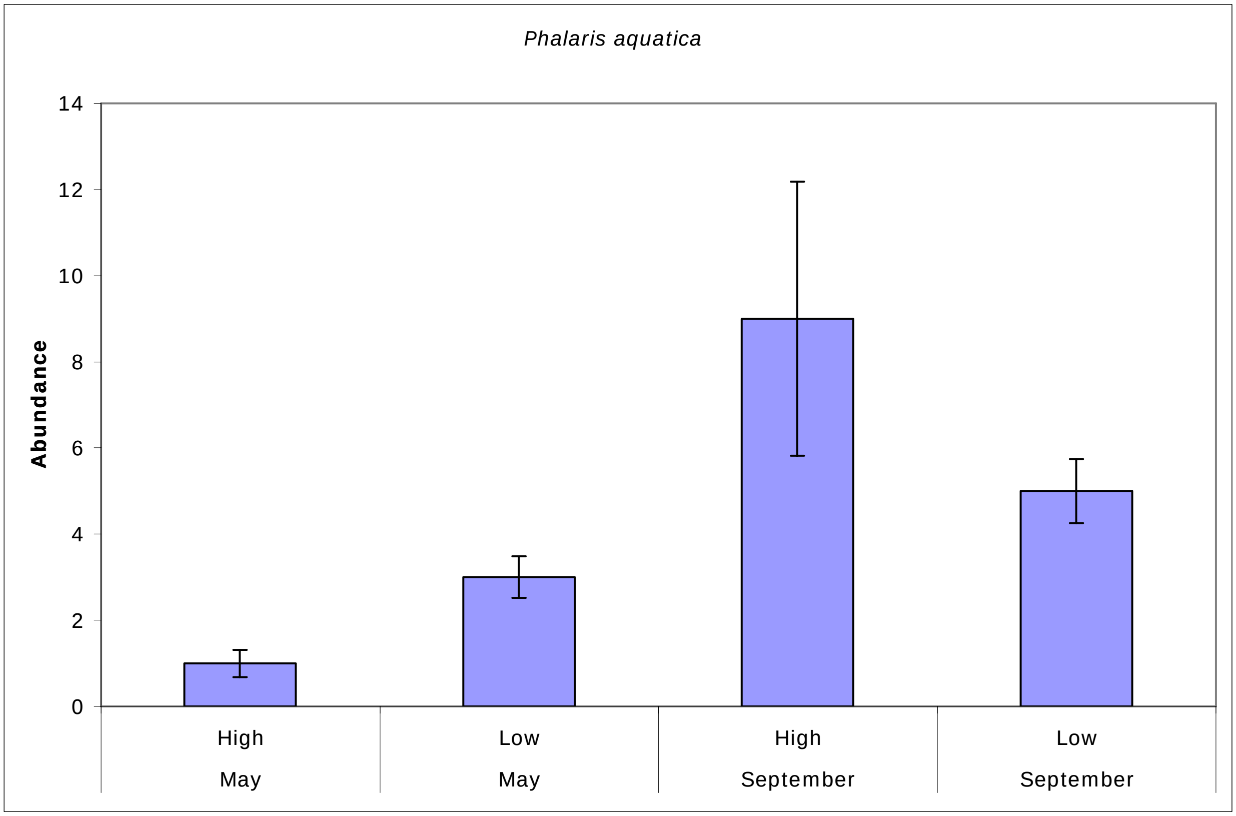
c)


Geranium dissectum
Abundance
0
2
4
6
8
10
12
14
High
May
Low
May
High
September
Low
September

d)

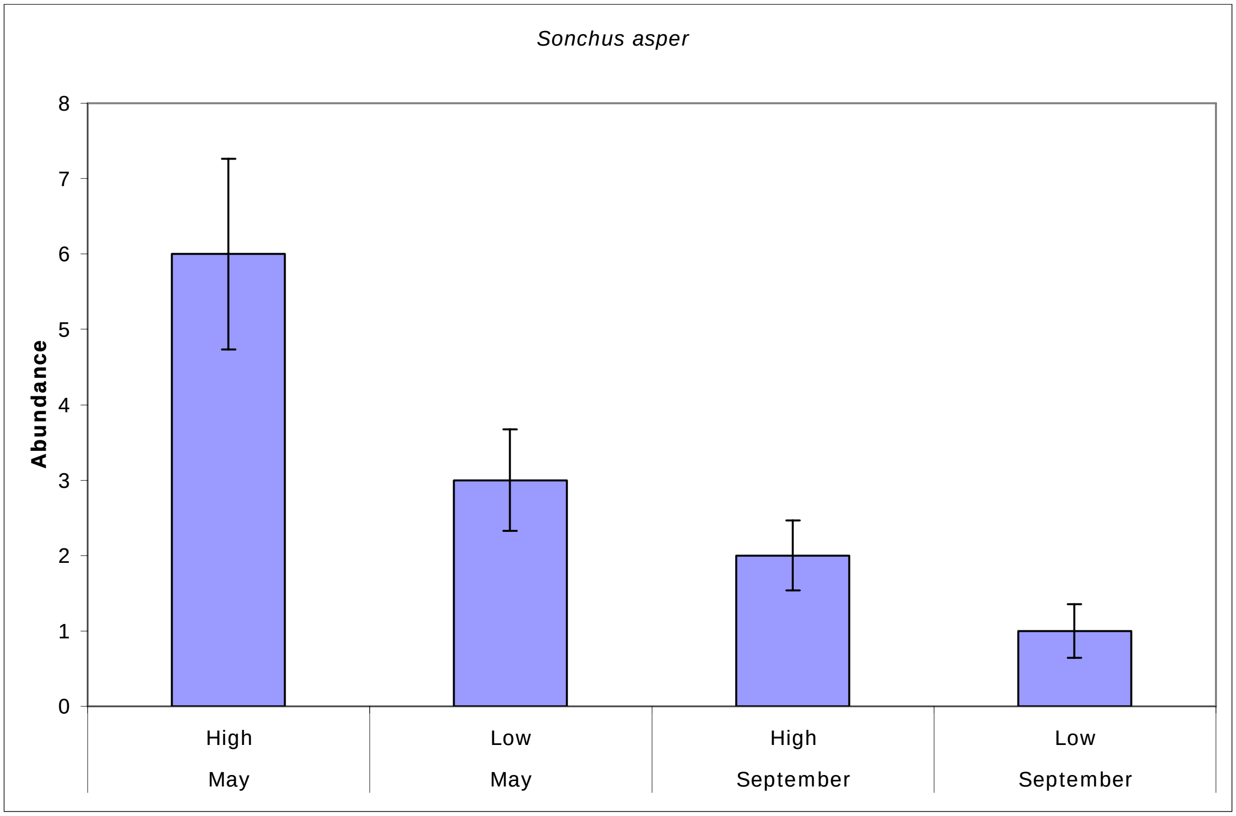

Juncus bufonius
Abundance
0
20
40
60
80
100
120
140
160
180
200
High
May
Low
May
High
September
Low
September

e)



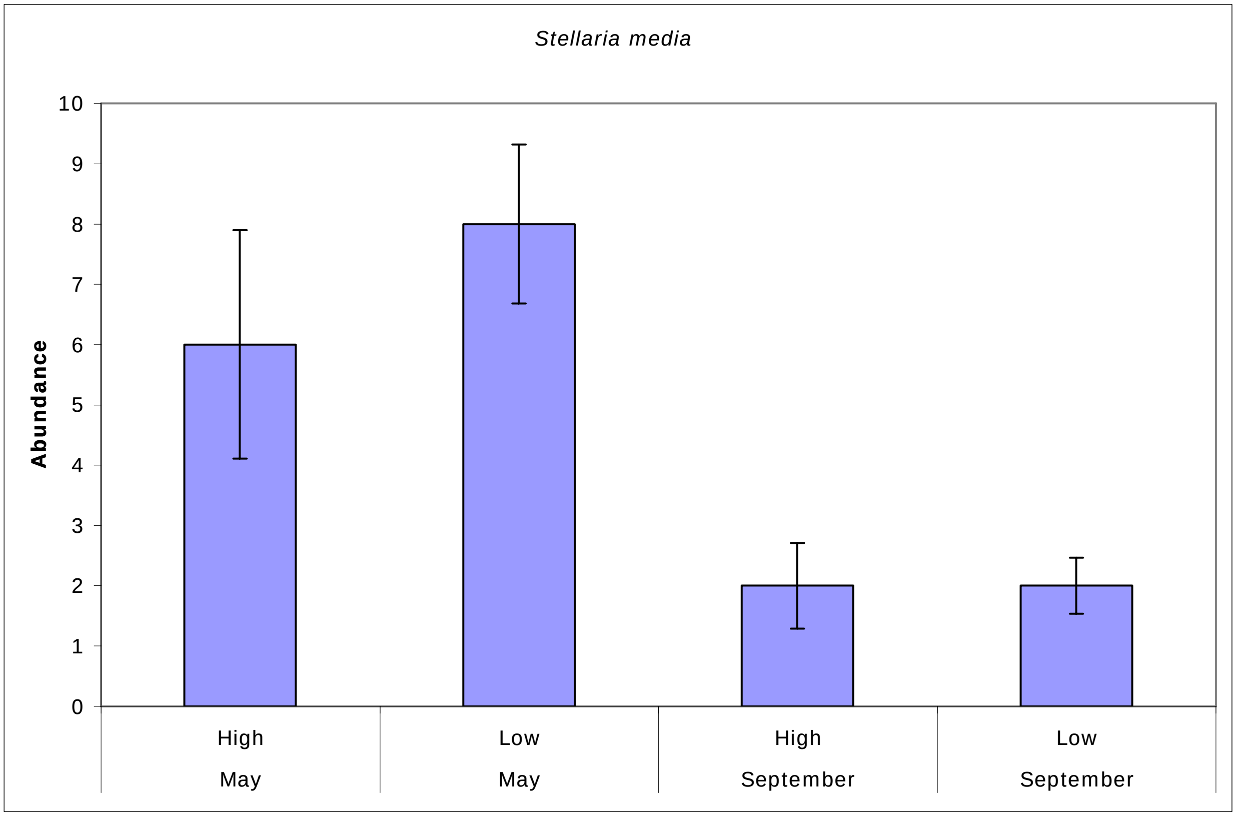
Phalaris aquatica
Abundance
14
12
10
8
6
4
2
0
High
May
Low
May
High
September
Low
September

f)



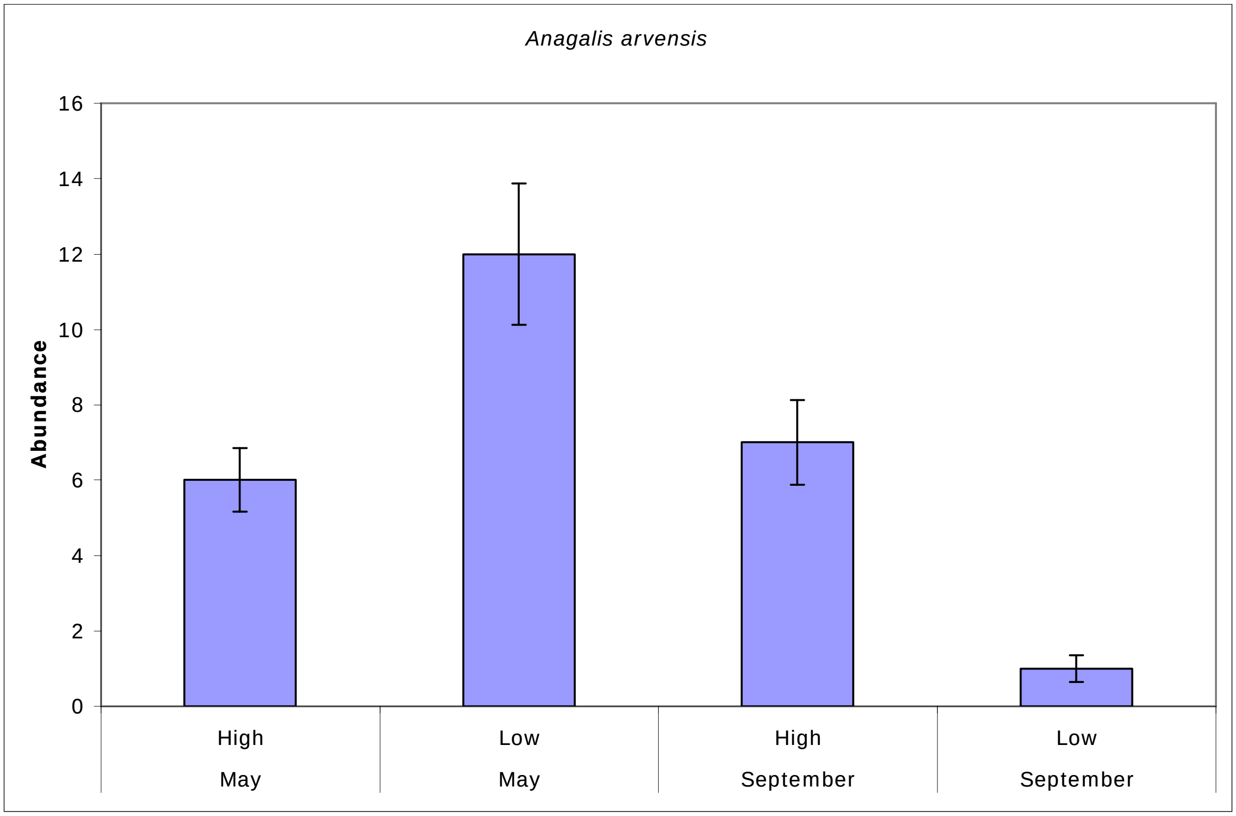
Sonchus asper
Abundance
8
7
6
5
4
3
2
1
0
High
May
Low
May
High
September
Low
September

g)



Stellaria media
Abundance
10
9
8
7
6
5
4
3
2
1
0
High
May
Low
May
High
September
Low
September

h)



Anagalis arvensis
Abundance
16
14
12
10
8
6
4
2
0
High
May
Low
May
High
September
Low
September