

Gastropod Herbivore Preference for Seedlings of Two Native and Two Exotic Grass Species

SARA M. MOTHERAL

Ecology, Evolution, and Marine Biology Department, University of California, Santa Barbara 93106

AND

JOHN L. ORROCK¹

Department of Biology, Washington University, Saint Louis, Missouri 63130

ABSTRACT.—Herbivores can affect the composition of grassland communities. We examined seedling herbivory by the introduced snail, *Helix aspersa*, on four grass species common in California grasslands. To assess preference, standardized tests using equal amounts of seedlings of the same age were conducted in addition to tests in which live seedlings were exposed to snail herbivory. *Helix aspersa* exhibited the greatest preference for native *Bromus carinatus*, while native *Nassella pulchra* and exotic *B. hordeaceus* were moderately preferred. Exotic *Avena fatua* was least preferred. Assessment of preference using both standardized and live seedling trials yielded consistent results, suggesting that preference is due to variation in seedling quality rather than differences in per-seedling biomass that are likely to exist under field conditions. *Avena fatua* is very common in California grasslands while *B. carinatus* is relatively rare. Our results suggest that the high level of snail preference for *B. carinatus* and aversion to *A. fatua*, coupled with severe effects on future growth due to complete defoliation of live seedlings, may reinforce patterns of establishment of these grasses observed in natural communities.

INTRODUCTION

Terrestrial gastropods can have important effects on species composition in grassland communities (Hanley *et al.*, 1995b; Hulme, 1996; Buschmann *et al.*, 2005; Cleland *et al.*, 2006; Peters, 2007), and have been shown to have a significant negative impact on the survival and overall biomass of grassland plants (Hanley *et al.*, 1995b; Hulme, 1996; Buschmann *et al.*, 2005). Although gastropods are considered to be generalist herbivores, laboratory studies have shown that certain plant species are preferred over others (Cates and Orians, 1975; Dirzo, 1980). Field studies confirm that preference for particular species can lead to changes in recruitment (*e.g.*, Hanley *et al.*, 1995b) and that gastropods can have an especially large impact on forbs (Hanley *et al.*, 1995a, 1995b; Fenner *et al.*, 1999). However, few studies specifically examine preference of gastropods for grasses. One field study that compared the acceptability of four grasses in addition to several forb species showed that grasses vary greatly in relative acceptability to gastropods (Hanley, 2004). Understanding preference for grasses is important because grasses form the bulk of biomass in grassland systems and may dictate important processes, such as fire regime (D'Antonio and Vitousek, 1992). The potential importance of snails for grassland dynamics is highlighted by work of Cottam (1985) suggesting that gastropods may play a role in affecting the abundance and persistence of rare grass species by preferentially consuming those species that are least abundant in the community. Long-term studies from Switzerland that suggest that annual grasses may benefit from gastropod herbivory due to the suppression of dominant perennial species (Buschmann *et al.*, 2005).

¹ Corresponding author: e-mail: orrock@wustl.edu; Telephone: (314) 935-5818; FAX: (314) 935-4432

Studies have shown that snails have an important role in determining the composition of California grassland communities (Cleland *et al.*, 2006; Peters *et al.*, 2006; Peters, 2007; Strauss *et al.*, 2009). However, little is known about whether this effect on species composition is a result of gastropod preference for certain California grass species. Gastropod herbivores have been shown to have a significant impact on seedling survival (Hulme, 1994; Hanley *et al.*, 1995a, 1995b; Fenner *et al.*, 1999; Cleland *et al.*, 2006), especially young seedlings (Hulme, 1994; Hanley *et al.*, 1995a). Some studies have attributed the species composition of California grasslands to the relative establishment success of different species (Seabloom *et al.*, 2003; Orrock *et al.*, 2008). Thus, gastropods may play a role in the dominance of certain grasses by reducing the ability of other species to re-establish if they show distinct preferences in diet.

Most preference trials involving gastropods have been conducted using standardized tests in which cut portions of plants are offered to gastropods and the amount consumed is quantified (Cates and Orians, 1975; Dirzo, 1980; Buschmann *et al.*, 2006). These types of trials are advantageous in that they allow for a well-controlled examination of preference. However, submitting standardized plant portions to the snails may not reflect preference of snails under natural conditions because snails are unlikely to encounter standardized portions of seedlings in nature. For example, even in situations where seedling number is controlled, seedling biomass is likely to vary due to differences in seedling growth rates, and snails may attack seedlings based on size or other characteristics (Fenner *et al.*, 1999). Moreover, excision of leaf discs for standardized trials may release attractive odors, causing the plant to be more readily consumed (Buschmann *et al.*, 2006) or may increase the possibility of inducing chemical defenses in the plant. Preference trials using entire seedlings (*e.g.*, Hanley and Lamont, 2001) provide consumers with more ecologically realistic choices, but may be limited in their ability to address whether preference was based on seedling biomass or some other seedling characteristic (*e.g.*, nutritional quality). Alternatively, garden tests and field trials allow for the examination of preference in a more natural setting, but are not easily controlled nor do they allow for precise quantification of the amount of material consumed. Buschmann *et al.* (2006) suggests that it may be advantageous to link such standardized tests with additional tests that examine herbivory of live seedlings to allow for the control of other variables that may influence herbivore choice such as differences in plant morphology.

In this study we examined whether the common introduced snail *Helix aspersa* (Muller) exhibits a preference for four grass species common to California grasslands. We used two native perennial grass species, *Nassella pulchra* (H. S. Hitchc.) and *Bromus carinatus* (Hook. and Arn.), that are thought to have been important components of California grasslands before the invasion of exotic grasses (Heady, 1977), and two of the most common exotic annual grasses, *Avena fatua* (L.) and *B. hordeaceus* (L.) (Heady, 1977). Studies of gastropod herbivory show that seedling age and size may be an important determinant of preference (Hulme, 1994; Hanley *et al.*, 1995a). Therefore, whereas most previous preference studies have compared either herbivore preference for whole seedlings (Hanley and Lamont, 2001), or preferences for standardized portions of plant material (Dirzo, 1980; Fenner *et al.*, 1999), we used both techniques to examine whether preference is determined by per-seedling biomass or differences in nutritional quality of different species.

METHODS

STUDY SPECIES, SNAIL COLLECTION AND SEEDLING PREPARATION

Helix aspersa is native to Western and Southern Europe and was introduced to Southern California in the mid-19th Century (Potts, 1975). Populations of *H. aspersa* are typically

associated with the presence of humans and cultivation; however, several populations have been documented in uncultivated areas near Santa Barbara, California (Potts, 1975). A study of four different populations of *H. aspersa* in sites of varying sizes over a 4 y period shows that populations of *H. aspersa* can be highly variable (Potts, 1975). For example: densities of different populations, calculated based on Potts' census data and the size of his study sites, range from 5.50 snails/m² to 24.76 snails/m² in Sep. 1966, from 0.53 snails/m² to 1.52 snails/m² in Nov. 1968, and from 3.0 snails/m² to 8.84 snails/m² in Jun. 1969. Densities of *H. aspersa* have also been found to be considerable in other studies in California grassland (Strauss *et al.*, 2009).

Active snails are highly susceptible to water loss via evaporation; thus, much of their activity is regulated by the availability of moisture (Perea *et al.*, 2007). California grasslands are characterized a Mediterranean climate, in which seeds lie dormant over long, dry summers and emerge shortly after autumn rains (Heady, 1977). These autumn rains also supply the moisture conducive for *Helix aspersa* activity. Thus, seedlings are likely to emerge during a period when *H. aspersa* is active. Strauss *et al.* (2009) suggest that gastropod herbivores are the primary cause of seedling mortality during winter months in California grasslands.

Twenty-five snails were collected from a local mixed grassland/coastal shrubland habitat, composed of grasses including *Avena fatua*, *Bromus diandrus* (Roth), *B. carinatus* and *B. hordeaceus*, as well as *Baccharis pilularis* (DC.) and *Raphanus sativus* (L.), located near the University of California, Santa Barbara. Most of the grass vegetation at the collection site is composed of exotic *A. fatua*, *B. diandrus* and *B. hordeaceus*, while native *B. carinatus* is very rare. Although *Nassella pulchra* is not present at the site where the snails were collected, we choose to include it in this study because *N. pulchra* is often the focus of grassland restoration efforts; thus, it is often planted in areas where it is absent or rare. To reduce possible effects of any pre-disposed preferences due to diet history, when not being used for experiments, snails were maintained exclusively on a diet of locally grown organic lettuce and fed ad lib. Although seedling consumption by *Helix aspersa* is not correlated with individual snail mass (Hanley *et al.*, 2003), we used snails of similar size in our experiment to guard against preferences that might vary with snail size (mean snail mass was 6.5 ± 1.25 g SE). Snails were housed in the lab in a large translucent container (33 × 52.1 × 43.2 cm). A florescent light with a timer was set above the container to provide a consistent photoperiod of 12 h of light per day; temperature in the container was ambient lab temperature (approximately 20 C ± 5 C). Snails were marked with a unique number on the shell to avoid using a snail more than once in each of the experiments. For each experiment, snails were randomly drawn from the large container; 16 snails were used for the standardized trials, and 20 were used in the live-seedling trials. Some snails were used for both the standardized feeding trials and the live seedling feeding trials, while others were only used in one of the two trials. Prior to all preference trials, snails were not fed for 48 h (Hanley *et al.*, 1995a). Experiments were conducted in one of five round feeding arenas made of translucent plastic. Each feeding arena measured 25.4 cm tall and 19 cm in diameter. Four holes (approximately 5 × 7.5 cm each) were cut in the top of each arena and covered with aluminum window screening to provide ventilation. For each experiment, two snails were selected and placed on opposite sides of a feeding arena, equal distances away from the food source. Hanley *et al.* (2003) have demonstrated that the use of multiple gastropods in preference trails produces less variable results than trials with single herbivores.

All seedlings used in the experiment were grown in a greenhouse at the University of California, Santa Barbara. To facilitate inspection of individual seedlings during feeding

trials and to eliminate the potentially confounding effect of root competition among seedlings, each seedling was grown in separate 25 ml test tubes filled with soil. All seeds and seedlings were watered once a day until the soil in the test tube was visually saturated.

FEEDING TRIALS WITH STANDARDIZED AMOUNTS OF PLANT MATERIAL

Standardized feeding trials were conducted by placing a 9.0 cm diameter Petri dish containing 15.5 ± 0.4 mg of each seedling species in a feeding arena with a pair of randomly selected snails. Cut portions of each species were placed equal distances apart on the Petri dish, and arranged in a random order. Seedlings used in these trials were planted prior to the experiment such that they were of equal age (3 d). The snails were allowed to eat for 24 h, after which, the Petri dishes were removed and the remaining seedlings were weighed. Petri dishes were washed between trials to remove any residual chemical cues. To account for weight loss due to drying rather than herbivory, the same procedure was conducted, but no snails were present in the feeding arenas. A total of eight standardized feeding trials were conducted on 12 Jun. and 13 Jun. 2007.

FEEDING TRIALS USING WHOLE LIVE SEEDLINGS

Feeding trials with live seedlings consisted of randomly placing ten seedlings of each species in a feeding arena with a pair of randomly selected snails. A test tube rack large enough to hold 40 25 ml test-tubes was placed inside each feeding arena and surrounded on four sides with soil approximately 10 cm deep to facilitate snail access to the seedlings (*i.e.*, seedlings were presented at soil level). Seeds were planted 10 d prior to the experiment. Seedlings emerged 5–7 d after planting; thus, the age of the seedlings ranged between 3–5 d old prior to the start of the feeding trial. Seedlings from the four species that were the same age differed in size (comparing 99 3 d old seedlings using ANOVA; $df = 3, 95, F = 8.73, P < 0.001$). *Avena fatua* was, on average, the largest of the four species with an average height of $62.08 (\pm 2.54 \text{ SE})$ mm. *Bromus carinatus* had an average height of $49.52 (\pm 2.63)$ mm, the average height of *B. hordeaceus* was $45.51 (\pm 2.93)$ mm and *Nassella pulchra* measured an average of $45.96 (\pm 2.74)$ mm tall. Across all of these species, there is a highly significant relationship between height and seedling mass (analysis of 15 1–5 d old seedlings per species using regression, all $r^2 > 0.89$, all $P < 0.001$). Variation in seedling size may be due to differences in seed size among the species, as *A. fatua* seeds were the largest and produced the largest seedlings, *B. carinatus* seeds were smaller than *A. fatua* and produced smaller seedlings, and *N. pulchra* and *B. hordeaceus* seeds were that smallest and produced the smallest seedlings.

Forty-eight hours after offering the seedlings, the number of each species that had been consumed was recorded. A longer feeding time (48 h) was allotted for the live seedling trials compared to that in the standardized trials (24 h) because a much larger amount of plant material was offered in the live seedling trails. In nearly every case in which herbivory was observed, the entire seedling was consumed (*i.e.*, 98% of the 168 seedlings attacked were completely consumed). In the few cases in which a plant was not entirely consumed, an estimate of the percentage consumed was made. Ten separate feeding trials were conducted from 9–10 May and 22–23 May 2007. Test tubes and test tube racks were washed between feeding trails.

STATISTICAL METHODS

Because foods presented within a trial are not strictly independent, we used multivariate methods to examine data from both experiments (Roa, 1992; Manly, 1993; Manly, 1995; Lockwood, 1998). We examined selection in the standardized trials by comparing the

proportion of each plant type consumed relative to the total amount of consumption in each trial (Manly, 1995; Lockwood, 1998). This approach allowed us to characterize herbivore food choice when amounts of food are identical, so herbivore choice was not confounded by differences in food quantity and availability. To accommodate weight loss due to drying over the course of the standardized trials, we followed the approach recommended by Manly (1993), which allowed us to incorporate changes in sample weight due to water loss over the course of the experiment (*i.e.*, autogenic change) and changes due to the factor of interest (*i.e.*, consumption by snails). Overall differences in consumption among seedling types were then tested by comparing the differences observed in seedlings in control (*i.e.*, no snail) and herbivore trials by using Yao's test (Yao, 1965); for full details on this procedure, *see* Manly (1993). Following this omnibus multivariate test, we evaluated relative differences in consumption among seedling species by calculating 95% confidence limits using the formula $SE \times t_{Yao}$, where SE is the standard error calculated using formulae in Manly (1995) and t_{Yao} is the t statistic calculated using Yao's (1965) method (Manly, 1993).

To compare consumption of live seedlings, we used the multivariate approach described in Lockwood (1998). Because we were interested in the relative consumption of seedlings, we used the proportion of each species consumed within a trial as the dependent variable, such that the four proportions for each trial sum to 1. Although this approach is similar to the approach used in the standardized trials, it differs in two ways. First, there is no adjustment for autogenic change of live seedlings. Second, because of differences in seedling growth rate, some seedling species were larger than others (*i.e.*, although seedlings were the same age at the time they were fed to snails, total biomass of species differed). This analysis allows us to characterize herbivore food choice under the most ecologically realistic scenario, as differences in growth rates create differences in seedling biomass under field conditions, even if seedlings germinate at the same time. As with our analyses in standardized trials, we used 95% confidence limits to evaluate differences in preference following the omnibus multivariate test.

RESULTS

FEEDING TRIALS WITH STANDARDIZED AMOUNTS OF PLANT MATERIAL

There were significant differences in selection among the four species in the standardized trials ($R = 28.75$; $F = 7.95$; $df = 3, 9.7$; $P < 0.01$). Preference for *Bromus carinatus* was significantly higher than preference for *Nassella pulchra* and *Avena fatua* (Fig. 1A). *Avena fatua* was significantly less preferred than *B. hordeaceus* and *B. carinatus*. There was no significant difference in preference between *B. carinatus* and *B. hordeaceus*, between *N. pulchra* and *B. hordeaceus*, and between *N. pulchra* and *A. fatua*. On average, the absolute consumption of *A. fatua* was $2.27 (\pm 1.34 \text{ SE})$ mg, $6.95 (\pm 1.47)$ mg of *B. carinatus*, $5.66 (\pm 1.74)$ mg of *B. hordeaceus* and $3.42 (\pm 0.87)$ mg of *N. pulchra*.

FEEDING TRIALS USING WHOLE LIVE SEEDLINGS

Overall the results for seedling consumption trials largely mirrored those of the standardized trials ($F = 49.30$; $df = 3, 7$; $P < 0.001$). *Bromus hordeaceus* was preferred over *Avena fatua* and *Nassella pulchra*. *Bromus carinatus* was also preferred over *B. hordeaceus* in these trials (Fig. 1B). To some degree, the significant preference for *B. carinatus* compared to *B. hordeaceus* seedlings is attributable to the lower variance in the seedling trials, as the magnitude of the difference between *B. carinatus* and *B. hordeaceus* was similar between standardized and seedling trials (Fig. 1). Consumption of *B. carinatus* was highest with an average number of $7.15 (\pm 1.02)$ seedlings consumed each trail. *Nassella pulchra* and *B. hordeaceus* were moderately

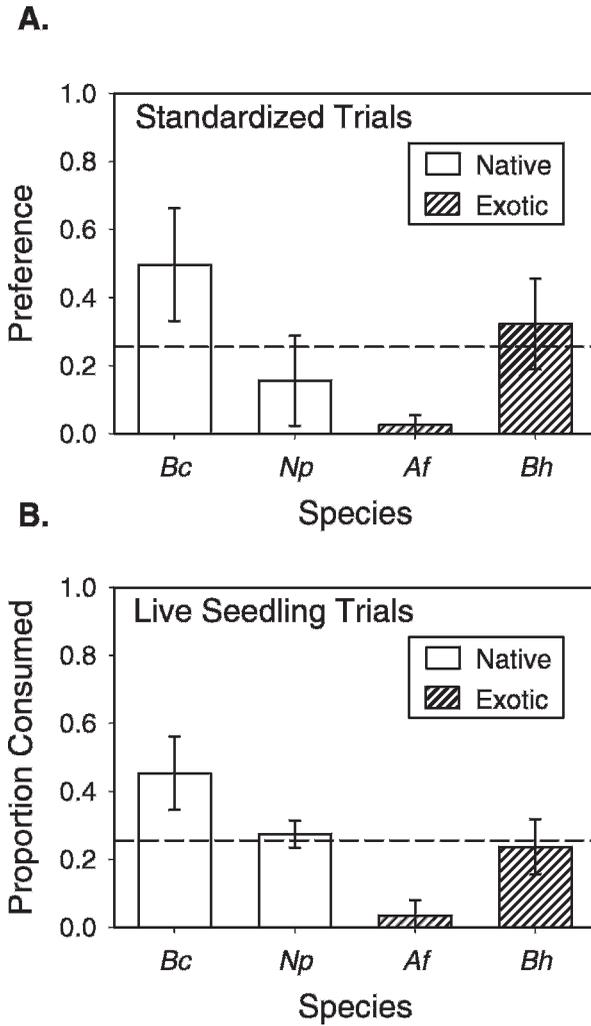


FIG. 1.—The consumption of four grass species by the exotic snail *Helix aspersa*. The dashed line represents the expectation if all species were equally preferred. Error bars represent 95% confidence limits. Bc is *Bromus carinatus*, Np is *Nassella pulchra*, Af is *Avena fatua* and Bh is *Bromus hordeaceus*. (A) Results from standardized seedling trials comparing consumption of four grass species by snail herbivores. (B) Results from trials where live seedlings were presented to snails

preferred. On average, 4.70 (± 0.93) *N. pulchra* seedlings and 4.30 (± 0.93) *B. hordeaceus* seedlings were consumed during each trial. *Avena fatua* was the least preferred of all four species with an average of only 0.5 (± 0.22) seedlings consumed per trial.

DISCUSSION

Our results demonstrate that snail preference varies among grass species (Hanley, 2004): snails exhibited a substantial preference for *Bromus carinatus* and a strong aversion to *Avena*

fatua. Our two feeding experiments revealed similar results, suggesting that herbivore choice is not affected by species-specific seedling size; thus, preference may be determined by variation in nutritional quality and/or factors affecting plant palatability rather than seedling biomass. Observations of feeding behavior during our study showed that gastropod herbivory often results in complete removal of seedling aboveground biomass, which is likely to significantly impact future plant growth and competitive ability (Hanley and Fegan, 2007). These strong effects, coupled with preference for particular species, may have important implications for grass species composition within California grasslands.

The use of both standardized and live seedling feeding experiments in this study revealed that preference is not influenced by seedling biomass: despite variation in the sizes of the different species, consumption in the live seedling trials was similar to standardized trials in which equal amounts of each species were offered. This suggests that species differences in nutritional quality and/or factors affecting plant palatability, *i.e.*, chemical properties and morphological anti-herbivore defenses such as pubescence and silica content (Hanley and Fegan, 2007), not seedling biomass, determine the preference of gastropod herbivores. While other studies have shown that gastropod preference differs greatly within mixtures of forbs and grasses (Cleland *et al.*, 2006; Peters *et al.*, 2006), our study demonstrates that herbivore choice may vary greatly within grasses. Earlier palatability studies, which focused on mature plants from various functional groups, found that gastropods tend to prefer annual plants over perennials (Grime *et al.*, 1968; Cates and Orians, 1975). We found that an annual grass (*Avena fatua*) was least preferred while a perennial (*Bromus carinatus*) was most readily consumed. Thus, we suspect that when plants are seedlings, gastropod preference may not be influenced by the life-history of plants; however, due to our limited sample size, this idea requires further investigation using a greater number of species.

Our focus on seedlings is important because seedling survival is thought to be a key factor in grassland composition (Hanley *et al.*, 1995b; Fenner *et al.*, 1999). In our feeding trials, snails consumed grass seedlings, completely removing all aboveground biomass of the plant (98% of attacked seedlings were completely defoliated). This suggests that gastropod herbivory is likely to have severe repercussions for future seedling growth and competitive ability (Hanley and Fegan, 2007). This observation further supports the claim that gastropods have the greatest impact on plants in their seedling stage (Hulme, 1994; Hanley *et al.*, 1995b; Fenner *et al.*, 1999).

Field studies have shown that gastropods have important impacts on community composition in California grasslands (Cleland *et al.*, 2006; Peters *et al.*, 2006, 2007). Such impacts have been attributed to preferences for certain plant species (Hanley *et al.*, 1995b; Cleland *et al.*, 2006). Our findings suggest that gastropod preference may contribute to the differential success of seedlings and grass species composition commonly observed in California grassland communities. In California grasslands *Avena fatua* is extremely abundant, comprising almost 75% of above-ground biomass (Peters *et al.*, 2007), while *Bromus carinatus* is less abundant. The preference for *B. carinatus* and aversion to *A. fatua*, shown in our study, appears to reflect this composition; however, future studies are needed to fully assess whether gastropods are a contributing factor to this pattern. While our results showed no difference in preference for *Nassella pulchra* and *B. hordeaceus*, the impact of herbivory on these two species nonetheless may have different consequences. For example, whereas *N. pulchra* is highly seed limited (Hamilton *et al.*, 1999; Seabloom *et al.*, 2003; Orrock *et al.*, 2008) the widespread distribution of *B. hordeaceus* suggests that it is not or that it may have relatively fewer predators. Therefore, the same amount of absolute herbivory by *Helix aspersa* may have a greater relative effect on the recruitment and future abundance of *N. pulchra* than *B. hordeaceus*.

Other herbivores may have additional effects on the recruitment of these grasses in the field. For example, Orrock *et al.* (2009) have demonstrated that recruitment of seed limited *Nassella pulchra* is further constrained by mammalian consumers; thus, gastropod herbivory may have a significant cumulative effect on the successful establishment of *N. pulchra*. Meanwhile, a study by Borchert and Jain (1978) found that mice showed a strong preference for *Avena fatua* seed. As such, rodents may have a greater effect on the recruitment of *A. fatua* than *Helix aspersa*. Interestingly, *A. fatua* and *Bromus hordeaceus* are of European origin as is *H. aspersa*. Other studies have showed no correlation between plant origin and their vulnerability to introduced generalist herbivores (Buschmann *et al.*, 2005; Strauss *et al.*, 2009); however, in their introduced ranges, exotic plants may be less constrained by herbivores than native plants which are subject to consumption by both their native specialist predators and introduced generalists (Strauss *et al.*, 2009).

This study shows that *Helix aspersa* exhibits species-specific preferences for grass seedlings and these differences in preference may arise due to species-specific differences in nutritional quality and/or anti-herbivore defenses rather than differences in seedling biomass. Gastropod herbivores can consume nearly half of aboveground production in California grasslands (Peters *et al.*, 2006) and have the ability to reduce the abundance of preferred grasses (Peters *et al.*, 2006). Our work suggests that snail preference for particular grass species, coupled with the heavy mortality imposed by snail herbivory, may make snails important agents of recruitment limitation often observed for native grasses (Hamilton *et al.*, 1999; Seabloom *et al.*, 2003; Orrock *et al.*, 2008) that are thought to have been much more abundant prior to the arrival of exotic grasses (Heady, 1977).

Acknowledgments.—We thank Theresa Rusca for her help with growing plants and feeding the snails, and Eric Hochberg at the Santa Barbara Museum of Natural History for helping to identify the snails. We are grateful to Elsa Cleland, Jonathan Levine, Sharon Motheral, O.J. Reichman and Theresa Rusca for their helpful comments and advice. This work was supported by the National Science Foundation (Grant DEB-0444217), an NSF Research Experience for Undergraduates Supplement (Grant DEB-0619375), and the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant DEB-0072909), the University of California and the Santa Barbara Campus.

LITERATURE CITED

- BORCHERT, M. I. AND S. K. JAIN. 1978. Effect of rodent seed predation on four species of California annual grasses. *Oecologia*, **33**:101–113.
- BUSCHMANN, H., P. J. EDWARDS AND H. DIETZ. 2006. Responses of native and invasive Brassicaceae species to slug herbivory. *Acta Oecol.*, **30**:126–135.
- , M. KELLER, N. PORRET, H. DIETZ AND P. J. EDWARDS. 2005. The effect of slug grazing on vegetation development and plant species diversity in an experimental grassland. *Funct. Ecol.*, **19**:291–298.
- CATES, R. G. AND G. H. ORLIANS. 1975. Successional status and the palatability of plants to generalized herbivores. *Ecology*, **56**:410–418.
- CLELAND, E. E., H. A. PETERS, H. A. MOONEY AND C. B. FIELD. 2006. Gastropod herbivory in response to elevated CO₂ and N addition impacts plant community composition. *Ecology*, **87**:686–694.
- COTTAM, D. A. 1985. Frequency-dependent grazing by slugs and grasshoppers. *J. Ecol.*, **73**:925–933.
- D'ANTONIO, C. M. AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Ann. Rev. Ecol. Syst.*, **23**:63–87.
- DIRZO, R. 1980. Experimental studies on slug-plant interactions I. The acceptability of thirty plant species to the slug *Agriolimax caruanae*. *J. Ecol.*, **68**:981–998.
- FENNER, M., M. E. HANLEY AND R. LAWRENCE. 1999. Comparison of seedling and adult palatability in annual and perennial plants. *Funct. Ecol.*, **13**:546–551.
- GRIME, J. P., S. F. MACPHERSON-STEWART AND R. S. DEARMAN. 1968. An investigation of leaf palatability using the snail *Cepaea nemoralis* L. *J. Ecol.*, **56**:405–420.

- HAMILTON, J. G., C. HOLZAPFEL AND B. E. MAHALL. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia*, **121**:518–526.
- HANLEY, M. E. 2004. Seedling herbivory and the influence of plant species richness in seedling neighbourhoods. *Plant Ecol.*, **170**:35–41.
- , M. T. BULLING AND M. FENNER. 2003. Quantifying individual feeding variability: implications for mollusc feeding experiments. *Funct. Ecol.*, **17**:673–679.
- AND E. L. FEGAN. 2007. Timing of cotyledon damage affects growth and flowering in mature plants. *Plant Cell and Environment*, **30**:812–819.
- , M. FENNER AND P. J. EDWARDS. 1995a. The effect of seedling age on the likelihood of herbivory by the slug *Deroceras reticulatum*. *Funct. Ecol.*, **9**:754–759.
- , ——— AND ———. 1995b. An experimental field study of the effects of mollusk grazing on seedling recruitment and survival in grassland. *J. Ecol.*, **83**:621–627.
- AND B. B. LAMONT. 2001. Herbivory, serotiny and seedling defence in Western Australian Proteaceae. *Oecologia*, **126**:409–417.
- HEADY, H. F. 1977. Valley grassland, p. 491–514. In: M. G. Barbour and J. Major (eds.). Terrestrial Vegetation of California. John Wiley, New York.
- HULME, P. E. 1994. Seedling herbivory in grassland - relative impact of vertebrate and invertebrate herbivores. *J. Ecol.*, **82**:873–880.
- . 1996. Herbivores and the performance of grassland plants: A comparison of arthropod, mollusc and rodent herbivory. *J. Ecol.*, **84**:43–51.
- LOCKWOOD, J. R. 1998. On the statistical analysis of multiple-choice feeding preference experiments. *Oecologia*, **116**:475–481.
- MANLY, B. F. J. 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. *Oecologia*, **93**:149–152.
- . 1995. Measuring selectivity from multiple-choice feeding-preference experiments. *Biometrics*, **51**:709–715.
- ORROCK, J. L., M. S. WITTER AND O. J. REICHMAN. 2008. Apparent competition with an exotic plant reduces native plant establishment. *Ecology*, **89**:1168–1174.
- , ——— AND ———. 2009. Native consumers and seed limitation constrain the restoration of a native perennial grass in exotic habitats. *Rest. Eco.*, **17**:148–157.
- PEREA, J., A. GARCIA, G. GOMEZ, R. ACERO, F. PENA AND S. GOMEZ. 2007. Effect of light and substratum structural complexity on microhabitat selection by the snail *Helix aspersa* Muller. *J. Mollusc. Stud.*, **73**:39–43.
- PETERS, H. A. 2007. The significance of small herbivores in structuring annual grassland. *J. Veg. Sci.*, **18**:175–182.
- , E. E. CLELAND, H. A. MOONEY AND C. B. FIELD. 2006. Herbivore control of annual grassland composition in current and future environments. *Ecol. Lett.*, **9**:86–94.
- , G. HSU, E. E. CLELAND, N. R. CHIARIELLO, H. A. MOONEY AND C. B. FIELD. 2007. Responses of temporal distribution of gastropods to individual and combined effects of elevated CO₂ and N deposition in annual grassland. *Acta Oecol.*, **31**:343–352.
- POTTS, D. C. 1975. Persistence and extinction of local populations of the garden snail *Helix aspersa* in unfavorable environments. *Oecologia*, **21**:313–334.
- ROA, R. 1992. Design and analysis of multiple-choice feeding-preference experiments. *Oecologia*, **89**:509–515.
- SEABLOOM, E. W., W. S. HARPOLE, O. J. REICHMAN AND D. TILMAN. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci. USA*, **100**:13384–13389.
- STRAUSS, S. Y., M. L. STANTON, N. C. EMERY, C. A. BRADLEY, A. CARLETON, D. R. DITTRICH-REED, O. W. EVERVIN, L. N. GRAY, A. M. HAMILTON, J. H. ROGGE, S. D. HARPER, K. C. LAW, V. Q. PHAM, M. E. PUTNAM, T. M. ROTH, J. H. THEIL, L. M. WELLS AND E. M. YOSHIZUKA. 2009. Cryptic seedling herbivory by nocturnal introduced generalists impacts survival, performance of native and exotic plants. *Ecology*, **90**:419–429.
- YAO, Y. 1965. An approximate degrees of freedom solution to the multivariate Behrens-Fisher problem. *Biometrika*, **52**:139–147.