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# Landscape context outweighs local habitat quality in its effects on herbivore dispersal and distribution

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**Abstract** Past studies with spatially structured herbivore populations have emphasized the primacy of intrinsic factors (e.g., patch quality), patch geometry (e.g., patch size and isolation), and more recently landscape context (e.g., matrix composition) in affecting local population abundance and dispersal rate. However, few studies have examined the relative importance of each factor, or how they might interact to affect herbivore abundance or dispersal. Here, we performed a factorial field experiment to examine the independent and interactive effects of patch quality (plant biomass, leaf protein, leaf phenolics) and matrix composition [mudflat or non-host grass (*Bromus inermis*)] on planthopper (*Prokelisia crocea*) emigration from host-plant patches (prairie cordgrass, *Spartina pectinata*). In addition, a field survey was conducted to examine the relative importance of patch quality, geography, and matrix composition on planthopper occupancy and density. In the experiment, we found that rates of emigration from low and intermediate quality patches were, on average, 21% percent higher for patches embedded in brome than mudflat. In contrast, the emigration rate was unaffected by matrix composition in nutrient-rich patches. Within matrix types, plant quality had little effect

on emigration. In the survey, planthopper density and the patch occupancy rate of planthoppers increased nonadditively with increasing patch size and the percentage of the surrounding matrix composed of mudflat. This study suggests that landscape-level factors, such as the matrix, may be more important than factors intrinsic to the patches.

**Keywords** *Prokelisia crocea* · *Spartina pectinata* · Metapopulation · Source–sink · Edge permeability

## Introduction

Populations inhabiting fragmented landscapes are generally envisioned as metapopulation or source–sink systems (Pulliam and Danielson 1991; Hanski 1999; Thomas and Kunin 1999). For such populations, dispersal is a critical factor influencing local abundances, patch occupancy, and regional population dynamics. Dispersal is required to establish populations on previously vacant patches and to sustain populations in sink habitats. Most studies of dispersal in subdivided populations have emphasized the importance of the intrinsic quality and geometry (e.g., size and isolation) of patches (Gilbert and Singer 1973; Thomas and Harrison 1992; Hanski 1994; Hill et al. 1996; Lurz et al. 1997; Brommer and Fred 1999; Doak 2000; Thomas et al. 2001; Fleishman et al. 2002; Matter and Roland 2002; Caudill 2003), though several recent examples demonstrate that dispersal rates are often strongly influenced extrinsically by landscape context (e.g., composition of the matrix; Roland et al. 2000; Ricketts 2001; Cronin 2003a; Haynes and Cronin 2003).

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Despite considerable focus on the effects of patch quality, patch geometry, and matrix composition on dispersal and population structure, few studies have assessed the relative importance of each of these factors on the movement or local abundances of a single species (but see Kuussaari et al. 1996; Bonte et al. 2003). In addition, researchers have often assumed that these factors (patch size, matrix types, patch quality) vary independently of one another and have additive rather than interactive effects on dispersal (e.g., Kuussaari et al. 1996; Moilanen and Hanski 1998; Ricketts 2001; Ries and Debinski 2001; but see Wiens et al. 1985; Summerville and Crist 2001). For herbivores distributed among discrete host-plant patches, there is evidence to suggest that the quality of patches often varies with the composition of the adjacent matrix, in part because matrix composition may affect patch quality by altering competitive interactions between plants in the matrix and patch or by altering nutrient subsidies across patch–matrix edges (reviewed in Haynes and Cronin 2004). Matrix composition and patch quality may also have synergistic or antagonistic effects on dispersal (Lawrence and Bach 1989; Haynes and Cronin 2004). Therefore, studies of dispersal are needed in which patch and matrix characteristics are manipulated independently using experimentally created patches.

Source–sink population structure is most often attributed to spatial variation in patch quality (Caudill 2003; Thomas and Kunin 1999). For the planthopper *Prokelisia crocea* (Van Duzee) (Hemiptera, Delphacidae), the composition of the matrix has also been shown to affect source–sink structure (J. T. Cronin and J. Reeve, unpublished manuscript). In a previous field experiment, Cronin and Reeve (in review) found that all host-plant patches (prairie cordgrass, *Spartina pectinata*) are absolute sources for the planthopper [i.e., birth rate ( $B$ ) > death rate ( $D$ )]. Patches in a matrix composed of the exotic grass smooth brome (*Bromus inermis* Leyss), however, are net exporters (relative sources) of planthoppers compared to patches in a mudflat matrix (relative sinks). For relatively small patches (<2 m<sup>2</sup>), emigration rates ( $E$ ) far exceed immigration rates ( $I$ ) when the matrix is composed of brome (Haynes and Cronin 2003; Cronin and Haynes 2004; J. T. Cronin and J. Reeve, unpublished manuscript). Patches in brome function as sieves, i.e., source populations that nonetheless require  $I$  to rescue them from extinction because  $E > B - D$  (Thomas and Kunin 1999).

In this study, we examined the effects of patch quality and matrix composition on the dispersal and spatial distribution of the planthopper. We performed

a factorial field experiment to examine the effects of patch quality (plant biomass, leaf protein, leaf phenolics) and matrix composition (mudflat, or the introduced grass *B. inermis*) on planthopper emigration from cordgrass patches. We also conducted a survey of 142 cordgrass patches to examine the influences of patch quality, patch geometry (patch size and isolation), and matrix composition on the distribution of planthoppers among patches. Given our previous findings (Haynes and Cronin 2003, 2006), we expected emigration rates to be higher in brome than mudflat. In addition, we predicted that emigration would decrease with increasing leaf protein levels as has been demonstrated often in other planthopper species in response to nitrogen levels (reviewed in Cook and Denno 1994). We also tested whether patch quality and matrix composition interact to affect planthopper dispersal, as predicted by Haynes and Cronin (2004). Previous surveys have indicated a strong effect of patch size and the percentage of mudflat in the matrix on patch occupancy and density (Cronin 2003a, 2004; Haynes and Cronin 2003), but patch quality has not been considered. This study provides compelling evidence that matrix composition and patch size are the dominant landscape attributes influencing the planthopper's spatial ecology, and that patch quality plays only a minor role.

## Materials and methods

### Study system

The planthopper's host plant, prairie cordgrass, is common throughout the American Great Plains, primarily in association with hydric grasslands and marshes (Mobberly 1956; Hitchcock 1963). Cordgrass reproduction occurs mostly through rhizomatous spread which results in the formation of clonal patches of highly variable size (Davelos et al 1996). In North Dakota tall-grass prairie, cordgrass patches vary in size from a few stems to 4-ha, and nearest neighbor patches are isolated from one another by <50 m (Cronin 2003b). Cordgrass patches are embedded within one of three matrix types: (1) mudflats sometimes dominated by saltwort (*Salicornia rubra* Nels.), (2) mixtures of predominantly native grass species (primarily foxtail barley *Hordeum jubatum* L., western wheatgrass *Agropyron smithii* Rydb., and little bluestem *Schizachyrium scoparium* Michx.), and (3) stands of exotic smooth brome (*B. inermis*) (see Haynes and Cronin 2003). Within our study sites, the matrix habitat consists of approximately equal proportions of mudflat,

native non-host grasses, and brome (Haynes and Cronin 2003).

The planthopper is a phloem-feeding specialist and is the dominant herbivore of prairie cordgrass (Holder and Wilson 1992; Cronin 2003a, 2003b, 2003c). In North Dakota, the planthopper is bivoltine with adult densities peaking in mid-June and early August. Adults survive up to two weeks in the field, and during this period females deposit eggs on cordgrass leaves near the midrib of the adaxial leaf surface. This species is wing-dimorphic, but >90% of individuals are macrotentous.

### Dispersal experiment

This experiment was designed to examine the effects of patch quality and matrix composition on planthopper emigration. The study was conducted within the Kelly's Slough National Wildlife Refuge (16 km west of Grand Forks, ND, USA) in an area of tall-grass prairie dominated by smooth brome. We established experimental patches of cordgrass in either unmanipulated smooth brome or in the center of small (4-m-diameter), experimentally created mudflats (one patch per mudflat). Each mudflat was created by applying Glyphomax Plus herbicide (Dow AgroSciences LLC, Indianapolis, IN, USA) and mowing and removing the dead vegetation. This procedure creates a surface of bare soil that, as with a natural mudflat matrix, reduces planthopper emigration relative to brome matrix (Cronin and Haynes 2004). Matrix effects on planthopper emigration are known to operate at small spatial scales of <1 m (Haynes and Cronin 2006).

Cordgrass used in the experiment was excavated as small ramets from a single source patch at the field site and then propagated in a common outdoor garden. The ramets were planted in 12 × 12 cm nursery pots filled with nutrient-free sand. The pots were kept in 35 × 47 cm plastic trays filled with 12 cm of water. We created three plant-quality levels by adding 0.15, 0.75, or 2.4 g of fertilizer [20:20:20 (N:P:K)] to each tray at two-week intervals for three months prior to the field experiment (modified from Olmstead et al. 1997). Leaf protein levels of the experimental plants encompassed the range observed in plants in the field (~1–3.2% dry mass).

In August 2003, when planthopper adults were at peak abundance, we returned the potted plants to the field site and arranged them into patches. Each patch consisted of nine pots placed together in a 3 × 3 arrangement that was sunk flush with the ground. Stem density was held constant at six stems per pot by pruning excess stems. Despite the small size of the

experimental patches, patches of equal or lesser size (0.13 m<sup>2</sup>) make up ~4.5% of all patches found in a nearby prairie, and are sufficient to detect matrix effects on planthopper dispersal (Haynes and Cronin 2003). Additionally, greenhouse experiments (K. J. Haynes, unpublished data) and modeling studies (Cronin and Reeve 2005) indicate that patches of this size can support viable source populations of planthoppers. Because the planthopper exhibits high emigration rates from small patches (Cronin 2003b), we expected high rates of emigration in this study.

We employed a randomized block design, with patch quality and matrix type as crossed, fixed factors. Each block consisted of six patches arranged along a linear transect, with patches separated by 6 m. The blocks were separated from one another by 8 m. Each combination of patch quality (low, medium, high) and matrix composition (brome, mudflat) was replicated once in each of ten blocks.

Immediately after establishing the cordgrass in patches, we released planthoppers into the experimental patches. Planthoppers for the experiment were collected with sweep nets from nearby cordgrass habitat and chilled during transport. Individuals were then marked with Dayglo fluorescent powder (Dayglo Corporation, Cleveland, OH, USA). The marker has no observable effects on planthopper survivorship or dispersal (Cronin 2003b). We released 50 adult female planthoppers in each experimental patch. This release density of ~1 per stem falls well within the range of densities commonly observed in natural cordgrass habitats (Cronin 2003b). It was not known whether the females had mated prior to their capture or were virgin. Males were not included in this study because the spatial spread of the species is mainly attributed to the dispersal of females (Cronin 2003b; Haynes and Cronin 2003).

We quantified the rate of planthopper emigration by revisiting patches daily for three days following the release. Planthopper loss from patches over these short time scales is mainly due to emigration rather than mortality (Haynes and Cronin 2003; Cronin et al. 2004). The effects of matrix composition and patch quality on planthopper emigration were evaluated with a randomized block ANOVA. Multiple comparisons between the six treatments were performed using Tukey's HSD test (Day and Quinn 1989). Because the daily rate of planthopper loss was high in the first 24 h post release and much lower thereafter, only the data from the first day were used in the analysis of planthopper emigration loss. The sharp decline in emigration from the first to second day after release may be explained by the existence of distinct classes of mobile

and sessile individuals (J. Reeve, K. J. Haynes, and J. T. Cronin, unpublished manuscript). Nonetheless, few planthoppers (<1%) left the patch immediately after being released (K. J. Haynes, unpublished data).

Following the completion of the dispersal experiment, we assessed the effects of patch treatments on three patch quality indices: plant-above-ground biomass and leaf-tissue levels of protein and phenolics. Plant biomass (measured as mean dry weight per stem) in each patch was estimated using measurements of basal stem diameter and stem height based on an allometric regression model (Cassidy et al. 2004). Independently derived data from measurements of the basal stem diameter (cm), stem height (cm), and dry weight (g) of cordgrass plants in a nearby prairie were used to generate the regression model [dry weight =  $0.01 \times (\text{diameter} \times \text{height}) - 0.5$ ,  $n = 29$ ,  $r^2 = 0.91$ ]. To assess leaf chemistry, we randomly selected one cordgrass stem per pot in each patch and collected the topmost unfurled leaf (samples taken from 4–10 transects, randomly selected). The leaves were immediately placed on dry ice, and then stored in an ultracold freezer at  $-70^\circ\text{C}$ . Samples consisting of five leaves per patch were later lyophilized (72 h) and ground in a Wiley mill. Spectrophotometric analysis using the Bradford method (modified for plant tissue by Jones et al. 1989) was performed to determine percent protein (percent dry mass) of the leaves. Leaf nitrogen content is considered a strong indication of plant quality (reviewed in Cook and Denno 1994), and nitrogen in plant tissue often occurs primarily within proteins (Ellis 1977). In addition, we determined the concentration of total phenolics (micromoles per gram dry weight) in leaf samples using Folin–Ciocalteu spectrophotometry (Waterman and Mole 1994). For the congeneric cordgrass *S. alterniflora*, simple phenolics are thought to be the principal secondary metabolites affecting nutritional quality (Valeila et al. 1979; Buchsbaum et al. 1984; Rietsma et al. 1988; Newell and Porter 2000). We assessed the effects of fertilization and manipulation of the matrix on patch quality indices (biomass, protein, and phenolics) using a randomized block MANOVA. Differences in these plant quality indices between fertilization levels were evaluated using Tukey's HSD tests. Finally, we tested for associations between the indices of plant quality—plant biomass, leaf protein, and leaf phenolics—using Pearson correlations.

#### Fertilization treatments and planthopper performance

Laboratory trials were conducted to determine the effect of the fertilization treatments on planthopper

survival. Concurrent with the field experiment, a subset of the potted cordgrass plants were transferred to a greenhouse at The University of North Dakota, Grand Forks, ND, USA. We determined the effects of the fertilization treatments on planthopper survival using the protocol described by Denno et al. (2000). A clear plastic cage (12 cm diameter  $\times$  40 cm height) was placed over the cordgrass stems in a pot and pressed into the sand. A lid made of fine-mesh (0.25 mm) polyester screen was placed over the top of the cage. Six field-caught adult female planthoppers were placed into each cage. We established ten replicate cages per fertilization level and arranged the cages at random in plastic trays. Visual counts of planthoppers were conducted daily for a total of 13 days. We evaluated the effect of fertilization level on the proportion of individuals surviving to day 13 using ANOVA. Prior to the analysis, an arcsine square-root transformation was used to normalize the data and homogenize variances.

We also quantified the oviposition rate of female planthoppers on cordgrass plants reared under the three fertilizer treatments. A 50-mm long by 26-mm diameter clip cage constructed from acetate tubing was placed at the base of a single leaf of a potted cordgrass stem (Cronin and Strong 1990). One female and one male planthopper were released into each clip cage. There were 12 replicate cages per fertilizer treatment. Field-caught females were allowed to lay eggs until they died. Egg crowding and reductions in leaf quality were minimized by transferring planthoppers to new leaves on the same stem on a weekly basis. After a five-day incubation period, the infested leaves were dissected to determine the number of eggs laid. We tested whether oviposition rate, measured as the mean number of eggs laid per female per day, was influenced by fertilization level with ANOVA. Eggs laid per day were ln-transformed for the analysis.

#### Field surveys

We assessed the influences of patch quality, patch geometry, and matrix composition on the distribution and abundance of planthoppers using a survey of 142 patches in a 65-ha remnant prairie, 20 km west of Grand Forks, North Dakota. For each patch, we estimated the mean number of planthopper eggs per cordgrass stem as well as the presence or absence of planthopper eggs per patch (Cronin 2003a, 2003b; Haynes and Cronin 2003; Cronin 2004). The survey was carried out in mid-July to correspond with the end of a planthopper generation. A 25  $\times$  25 cm sampling frame was haphazardly placed at three locations within each patch. Within the sampling frame, we counted the total

number of cordgrass stems and the number that were infested, and collected up to ten infested leaves from each patch. When we found no infested leaves in the sampling frames within a patch, the entire patch was searched intensively to ascertain the presence or absence of planthopper eggs. The geometry of each patch was assessed by measuring its size ( $m^2$ ) and isolation from other patches. Patch isolation, which is dependent upon the linear distance to, and size of, surrounding patches (Hanski 1994; Hanski and Kuussaari 1995), was determined from the nearest-neighbor patch in each of four quadrats (NE, NW, SE, and SW). Our index of isolation, ISOL, was computed as

$$\text{ISOL} = \frac{1}{\sum_i^4 S_i e^{-\text{DIST}_i}},$$

where  $S_i$  and  $\text{DIST}_i$  are the size of ( $m^2$ ) and distance to the nearest patch in the  $i$ th quadrat, respectively. We have found that ISOL is strongly correlated with a more comprehensive isolation measure that is based on all cordgrass patches within 40 m of a focal patch ( $r = 0.80$ ,  $n = 25$ ,  $P < 0.001$ ; Cronin 2003a, 2003b). Matrix composition was measured as the proportion of a 3-m buffer surrounding each patch that was composed of mudflat (Haynes and Cronin 2003). Matrix effects on planthopper dispersal and local abundance have been shown to occur over small spatial scales of  $<3$  m (Cronin 2003a; Haynes and Cronin 2003; Cronin 2004; Haynes and Cronin 2006). Patch quality was assessed using the leaf chemistry variables described above (leaf protein and phenolics). In this study, samples for chemical assays were obtained by randomly selecting five cordgrass stems per patch and collecting the topmost unfurled leaf (leaves within each patch pooled).

We examined the effects of patch quality, patch geometry (patch size and isolation), and matrix composition on planthopper egg densities and whether a patch was occupied by planthoppers using an information theoretic approach, whereby a set of candidate models is developed a priori and then the models are ranked according to fit balanced by a penalty for increasing numbers of parameters (Burnham and Anderson 2002). The development of a set of candidate models is started by forming a global model which includes all of the predictor variables considered to be potentially important. The remaining models are then created by reducing the global model.

Because the potential number of candidate models increases rapidly with the number of predictor variables, predictor variables should be chosen with care, on the basis of theory and prior knowledge of the

system (Burnham and Anderson 2002). For planthopper density, we assessed the relative fits of 17 models formed from six predictor variables. The global model included the effects of matrix, patch size, leaf protein, matrix  $\times$  patch size, matrix  $\times$  leaf protein, and patch size  $\times$  leaf protein. Interaction terms were not included within any model that did not also contain the component main effects. Leaf phenolics were not included in the analysis because the protein content of leaves alone represents a strong index of plant quality (reviewed in Cook and Denno 1994), and the levels of phenolics and nutrients in leaves are often negatively correlated (Siska et al. 2002). Patch isolation was excluded as a predictor variable because it is known to have very little effect on planthopper densities (Cronin 2003b, Haynes and Cronin 2003). Planthopper densities may be unaffected by the isolation of cordgrass patches because rates of emigration often far exceed immigration rates (Haynes and Cronin 2003, J. T. Cronin and J. Reeve, unpublished manuscript).

A set of 70 candidate models was developed to examine the factors influencing whether a patch was occupied by planthoppers. We included all of the predictor variables above with the addition of patch isolation, patch isolation  $\times$  matrix, and patch isolation  $\times$  patch size. Although patch isolation has little effect on planthopper density, the effects on rates of patch occupancy are substantial (Cronin 2003b, Haynes and Cronin 2003).

Planthopper density and patch occupancy were modeled using generalized linear models. For the analysis of planthopper density, we assumed that the observations came from a normal distribution and assigned an identity link function (McCullagh and Nelder 1989). We modeled patch occupancy using a binomial distribution and a logit link function. Prior to these analyses, four variables were ln-transformed to normalize their distributions (planthopper density, patch area, percentage mudflat, and patch isolation). Collinearity among predictor variables was ruled out by examining tolerance values (Quinn and Keough 2002). We also ruled out the possibility of overdispersion in the models using a binomial distribution by computing the variance inflation factor from the global patch occupancy model (Burnham and Anderson 2002).

The candidate models were ranked using the second-order Akaike information criterion ( $\text{AIC}_c$ ):

$$\text{AIC}_c = -2 \log L + 2K + \frac{2K(K+1)}{n-K-1},$$

(Burnham and Anderson 2002), where  $L$  is the maximum likelihood value,  $K$  is the number of fitted parameters, and  $n$  is the sample size. This approach

identifies a subset of candidate models that provide the most parsimonious fit to the observed data.  $AIC_c$  is a bias-corrected version of AIC recommended for analyses in which the sample size is small relative to the number of fitted parameters (i.e., when  $n/K < 40$ ) (Burnham and Anderson 2002). The relative support for each model was evaluated with  $AIC_c$  differences ( $\Delta_i$ ),  $\Delta_i = (AIC_c)_i - \min AIC_c$ , where  $\min AIC_c$  is the  $AIC_c$  of the best-fitting model. For a given model, the plausibility that it is the best model decreases with increasing  $\Delta_i$ . Models with  $\Delta_i$  values  $< 2$  were considered to have substantial support (Burnham and Anderson 2002). The approximate probability that a model within each set of  $R$  models was the best model was evaluated by computing its Akaike weight ( $w_i$ ):

$$w_i = \frac{\exp\left(-\frac{\Delta_i}{2}\right)}{\sum_{r=1}^R \exp\left(-\frac{\Delta_r}{2}\right)}$$

Finally, the fits of top-ranking models were assessed using  $r^2$  values for planthopper density models and Nagelkerke's  $r^2$  for patch occupancy models.

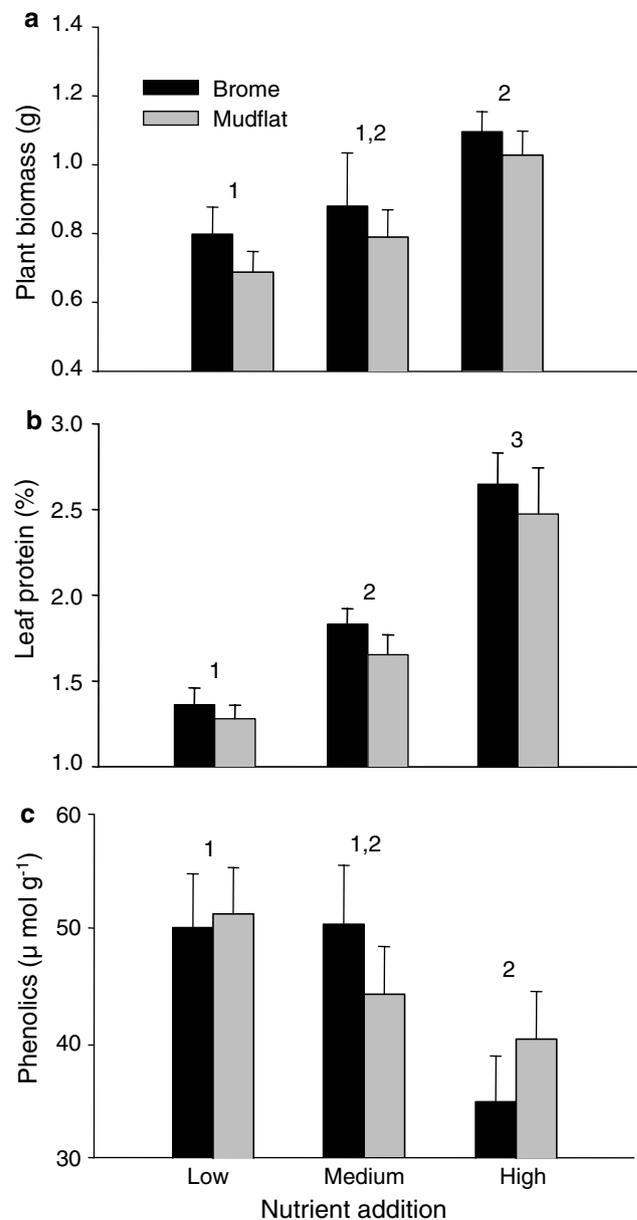
## Results

### Dispersal experiment

The quality of the experimental cordgrass patches, as measured by their biomass, and leaf-tissue concentrations of proteins and phenolics, was significantly affected by the level of fertilization (Wilks'  $\lambda = 0.110$ ,  $F_{(6,26)} = 25.58$ ,  $P < 0.001$ ). In general, biomass and protein concentration increased with increasing levels of fertilizer, whereas phenolic levels declined (Fig. 1). Patch quality was not significantly affected by matrix composition (Wilks'  $\lambda = 0.812$ ,  $F_{(3,13)} = 1.00$ ,  $P = 0.424$ ) or a matrix  $\times$  fertilizer interaction (Wilks'  $\lambda = 0.705$ ,  $F_{(6,26)} = 0.83$ ,  $P = 0.560$ ). Finally, leaf tissue protein and phenolics were negatively correlated (Pearson correlation,  $n = 24$ ,  $R = -0.547$ ,  $P = 0.006$ ). Plant biomass was positively correlated with protein ( $n = 24$ ,  $R = 0.614$ ,  $P = 0.001$ ) and negatively correlated with phenolics ( $n = 24$ ,  $R = -0.600$ ,  $P = 0.002$ ).

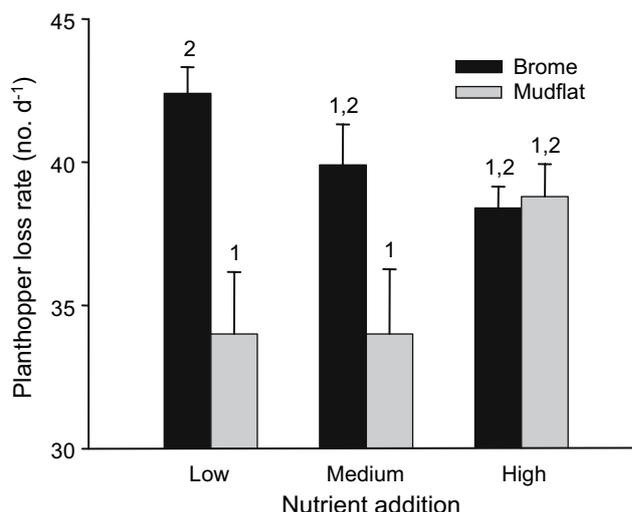
The loss rate of planthoppers from experimental patches was significantly influenced by matrix type ( $F_{(1,45)} = 12.784$ ,  $P = 0.001$ ) and an interactive effect of fertilizer level and matrix type ( $F_{(2,45)} = 4.082$ ,  $P = 0.023$ ). In patches receiving low and intermediate levels of fertilizer, the loss rates were 25 and 17% higher, respectively, for patches in the brome than mudflat matrix [ $P = 0.006$  and  $0.110$ , respectively

(Tukey's HSD tests); Fig. 2]. In contrast, planthopper emigration rate was unaffected by matrix composition in nutrient-rich patches ( $P = 0.999$ ). Overall, planthopper emigration rates were quite similar across the different fertilization levels ( $F_{(2,45)} = 0.588$ ,  $P = 0.560$ ). Finally, the loss rate of planthoppers was indistinguishable among blocks ( $F_{(9,45)} = 1.049$ ,  $P = 0.418$ ).



**Fig. 1a–c** Effects of fertilization (low, medium and high nutrient addition) and matrix treatments (brome or mudflat) on indices of prairie cordgrass (*Spartina pectinata*) patch quality. **a** Plant biomass, **b** leaf protein, **c** leaf phenolics (means  $\pm$  1 SE). Means labeled by different numbers are significantly different at the  $\alpha = 0.05$  level (Tukey's HSD tests only evaluated the effects of the three fertilization levels)

**Fig. 2** Effects of fertilization and matrix treatments on rate of planthopper (*Prokelisia crocea*) loss from an experimental patch (means + 1 SE). Fifty planthoppers were released initially in each patch. Rates of loss were determined from 24-h recapture data because most planthopper emigration events occurred during this period. Means labeled by different numbers signify significant differences at the 0.05 level (Tukey’s HSD tests evaluated the effects of all matrix and fertilization level combinations)



Effects of fertilization treatments on planthopper performance

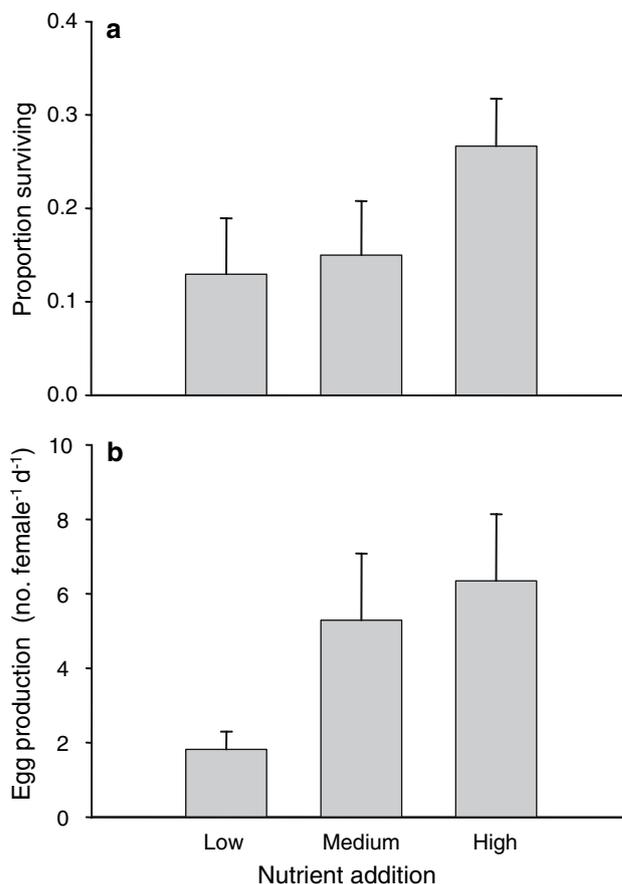
We found that neither planthopper survival nor oviposition rate was significantly influenced by the cordgrass fertilization treatments (survival:  $F_{(2,26)} = 2.31$ ,  $P = 0.119$ ; oviposition:  $F_{(2,31)} = 1.56$ ,  $P = 0.226$ ). In general, however, survival and oviposition rate increased with increasing levels of fertilization (Fig. 3), suggesting that the effects of fertilization on nutritional quality were positive.

Survey data

Based on AIC<sub>c</sub> differences, three models received substantial support as being the best model for predicting planthopper densities among cordgrass patches (Table 1). Four predictor variables—matrix, patch size, leaf protein, and matrix × patch size—were common to all three of these models. The highest-ranking model predicted planthopper density based upon matrix, patch size, leaf protein, and matrix × patch size (explaining 21.7% of the variation in planthopper densities). The approximate probability that the highest-ranking model truly was the best model was 0.339, as compared to 0.224 for the second-highest-ranking model (based on  $w_i$ ). Planthopper densities increased with increasing patch size, and the percentage of the nearby matrix that was mudflat (Table 2). However, the effects of patch size and matrix composition were multiplicative instead of purely additive. Finally, the variables leaf protein, leaf protein × patch size, and leaf protein × matrix occurred 1–3 times in the top three models; however, each of these variables had

comparatively weak effects on planthopper densities (Table 2).

Of the 142 cordgrass patches surveyed, 79% were occupied by the planthopper. Five models out of 70



**Fig. 3** Effects of fertilization treatments on aspects of planthopper performance. **a** Survival to 13 days, **b** egg production (means + 1 SE)

**Table 1** The top-ranking models for predicting the density and patch occupancy of planthoppers on the basis of landscape and patch attributes

Dependent variable <sup>a</sup>	Model rank	Model	AIC <sub>c</sub>	$\Delta_i^b$	$w_i$	$r^2$
Density	1	M, S, P, M × S	440.209	0	0.339	0.217
	2	M, S, P, M × S, S × P	440.728	0.520	0.261	0.224
	3	M, S, P, M × S, M × P	442.17	1.961	0.127	0.218
Occupancy	1	M, S, P, M × S	116.829	0	0.156	0.362
	2	M, S, M × S	117.418	0.589	0.116	0.348
	3	M, S, P, M × S, M × P, S × P	117.478	0.649	0.112	0.395
	4	M, S, P, M × S, S × P	117.992	1.163	0.087	0.371
	5	M, S, I, P, M × S	118.748	1.919	0.060	0.364

*M* Percentage of nearby matrix that is mudflat, *S* patch size, *P* leaf protein, *I* patch isolation

<sup>a</sup> We report Nagelkerke's  $r^2$  instead of  $r^2$  for the analyses of patch occupancy rates

<sup>b</sup> Only the models with  $\Delta_i < 2$  are shown

**Table 2** The effects of ln(percentage of nearby matrix that is mudflat), ln(patch size), leaf protein, and ln(patch isolation) on ln(planthopper density) and whether a patch was occupied by the planthopper

Dependent variable	Predictor variable <sup>a</sup>	$\beta_j \pm SE$
Density	%Mud	0.580 ± 0.171
	Size	0.369 ± 0.070
	Protein	-0.071 ± 0.202
	%Mud × Size	0.226 ± 0.121
	%Mud × Protein	0.174 ± 0.409
	Size × Protein	0.147 ± 0.135
Occupancy	%Mud	2.787 ± 1.306
	Size	1.413 ± 0.409
	Isolation	0.037 ± 0.068
	Protein	-0.579 ± 0.449
	%Mud × Size	1.963 ± 0.791
	%Mud × Isolation	0.127 ± 0.151
	%Mud × Protein	1.773 ± 1.103
	Size × Isolation	0.004 ± 0.044
Size × Protein	0.576 ± 0.405	

<sup>a</sup> For each variable  $x_j$ , we show its maximum likelihood estimate,  $\beta_j$ , from the highest-ranking model that includes  $x_j$

candidate models received substantial support. The variables matrix, patch size, and matrix × patch size occurred in each of these models, and leaf protein occurred in four of the five best models. The highest ranking model, including the variables matrix, patch size, leaf protein, and matrix × patch size, explained 36.2% of the variation in the presence or absence of planthoppers (based on Nagelkerke's  $r^2$ ). The selection certainty for this model, however, was low ( $w = 0.157$ ). The frequency of patch occupancy was strongly influenced by a positive, nonadditive effect of increasing patch size and the percentage of matrix habitat occupied by mudflat (Table 2). Patch occupancy was also influenced by patch size × leaf protein and matrix × leaf protein interactions (Table 2), but these variables were absent from most of the top-ranking models.

## Discussion

Matrix composition appeared to surpass patch quality in its effects on planthopper dispersal. In cordgrass patches of low and intermediate plant quality, emigration rates were 25 and 17% higher in the brome than mudflat matrix, respectively. These results provide further supporting evidence for our previous findings from field mark-recapture experiments (Haynes and Cronin 2003; Cronin and Haynes 2004) that the brome matrix promotes higher rates of emigration than the mudflat matrix. In high-quality patches, however, emigration rates were similar in the brome and mudflat matrix types. Compared to matrix effects on emigration, patch quality effects were much weaker. Within the matrix types, emigration rates differed by 10–14% between the low- and high-fertilizer treatments, and these differences were not significant.

Based on a series of field experiments, we know that the planthopper exhibits high rates of emigration from patches embedded in non-host grasses, and that this pattern is consistent for patches ranging in size from 0.1 to 2 m<sup>2</sup> (Haynes and Cronin 2003, Cronin 2003b, Cronin and Haynes 2004). Empirical and theoretical studies suggest that when patches are small or have high perimeter:area ratios, as in our system (29% of patches are smaller than 2 m<sup>2</sup>), individuals have frequent encounters with patch edges and rates of emigration are therefore strongly dependent on the permeability of the patch–matrix edge (Stamps et al. 1987; Schooley and Wiens 2004; Ries and Debinski 2001; Schtickzelle and Baguette 2003). Emigration rates are also strongly influenced by patch size; emigration rates in 0.2 m<sup>2</sup> patches exceeded rates in patches an order of magnitude larger by ~60% (Cronin 2003b). In light of the relationship between patch size and emigration, it remains a possibility that the overriding factor influencing dispersal might shift from

matrix composition for patches  $\leq 2 \text{ m}^2$  to patch quality in larger patches. An important avenue of future research would be to assess potential interactive effects of patch size and patch quality on herbivore dispersal, and to examine their interactive effects on source–sink population structure.

The interactive effect of patch quality and matrix composition on planthopper emigration might be explained by the behavioral response of arthropod predators to plant size and structural complexity. Studies with the conspecific cordgrass *S. alterniflora* have demonstrated that spiders quickly aggregate on fertilized plants, possibly in response to the greater biomass or structural complexity of these plants (Gratton and Denno 2003). Predator aggregation on heavily fertilized plants may have contributed to high rates of emigration from nutrient-rich patches in mudflat. Planthopper emigration is known to increase substantially with increasing density of generalist predators (Cronin et al. 2004), but we do not yet know how predators in our system respond to bottom-up factors. Studies providing experimental evidence of an interactive effect of matrix composition and patch quality on herbivore dispersal are scarce (but see Lawrence and Bach 1989). Movement behavior experiments with the chrysomelid beetle *Diabrotica undecimpunctata howardi* indicated that this herbivore was more likely to emigrate from unfertilized patches of the curcubit *Curcubita maxima* surrounded by tomato plants than from patches of any other combination of patch quality (unfertilized, fertilized) or matrix type (tomato, mowed grass; Lawrence and Bach 1989). However, host-plant quality (leaves per plant) was lower in patches bordered by tomato. Thus, it was not clear if matrix and patch quality had an interactive effect on dispersal in Lawrence and Bach's (1989) experiment, or whether the effect was confounded by the correlation between these two variables.

Our analysis of the survey data supports the view that matrix composition (and patch size) outweighs patch quality in influencing the distribution of planthoppers among cordgrass patches. Planthopper densities and patch occupancy increased with increasing patch size and proportion of the matrix composed of mudflat. These results are consistent with an earlier study spanning five generations, in which these two variables alone accounted for 34% of the variation in patch occupancy rates (Haynes and Cronin 2003). The matrix effect on planthopper densities can be explained by the behavior of planthoppers near patch–matrix boundaries. The cordgrass–mudflat edge represents a strong barrier to movement. For a planthopper advancing towards the patch–mudflat edge, the

probability of crossing the edge and entering the matrix is 14.7%. In contrast, cordgrass–brome edges are highly permeable (probability of edge-crossing = 44%; Haynes and Cronin 2006). Planthopper boundary behaviors and habitat-specific movement rates have been incorporated into a spatially realistic reaction–diffusion model (Cronin and Reeve 2005; J. Reeve, J. T. Cronin, and K. J. Haynes, unpublished manuscript). Equilibrium densities are invariably higher in cordgrass patches surrounded by mudflat, as compared to patches in brome.

The survey data also reveal that the effects of matrix composition and patch size on the planthopper were not purely additive. Planthopper density and patch occupancy increased with the percentage of the matrix that was mudflat and patch area in a positive, nonadditive fashion. Given that the importance of edge permeability and matrix composition for rates of emigration are likely to increase as patch size decreases (Stamps et al. 1987; Schooley and Wiens 2004; Ries and Debinski 2001; Schtickzelle and Baguette 2003), we discount the possibility that matrix effects on planthopper density become stronger as patch size increases. Instead, it is possible that emigration rates from patches bordered by non-host grasses are so high that increases in patch area have limited effects on planthopper density. Dispersal experiments are needed to fully resolve the mechanisms underlying the interactive effect of patch area and matrix composition on planthopper abundance.

In addition to the loss and fragmentation of habitats, anthropogenic effects that alter the structure of the surrounding landscape (e.g., through the introduction of exotic plants, urbanization) may threaten the persistence of native species (Noss 1991; Debinski and Holt 2000; Cronin and Haynes 2004). In our system, the consequences of the introduction of brome are likely to be varied and severe. Over a four-year period of time (2000–2004), brome has spread rapidly through the prairie landscape (F. P. Dilleuth and J. T. Cronin, unpublished manuscript). During this time, cordgrass patches have decreased in size by an average of 61% and patches surrounded by brome were more likely to disappear. Furthermore, by increasing emigration rates from cordgrass patches, the brome matrix has likely caused an increase in the number of sieve patches and elevated the risks of local and regional extinction (Cronin and Haynes 2004; J. T. Cronin and J. Reeve, unpublished manuscript). This study highlights the value of dispersal studies for improving our understanding of how looming changes to landscapes may affect the abundance and distribution of species.

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