

Research article

Relationships of landscape, prey and agronomic variables to the abundance of generalist predators in cotton (*Gossypium hirsutum*) fields

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Abstract

A two-year field study investigated the possible effects of grain sorghum (*Sorghum bicolor* [L.] Moench) and uncultivated areas on the abundance of generalist predators in commercially-managed cotton (*Gossypium hirsutum* L.) fields in Texas, USA. From 63 to 70 fields were sampled for pests and predators over nine consecutive weeks during early stages of cotton development. Additional data on agronomic practices and landscape composition at three spatial scales were also collected for each field. Stepwise regression analyses were used to determine the relationships of landscape, agronomic and prey variables to the abundance of generalist predators. Because the variables most closely linked to predator levels could vary over time, separate regressions were conducted for three time periods corresponding to stages of grain sorghum growth (half-bloom, hard-dough, maturity) in each year. Significant relationships between predator abundance and agricultural landscape composition appear in both years and in all three time periods, but the specific relationships of landscape variables to cotton predator levels differed between and within years. At maturity in 2001, predator levels rose as the amount of uncultivated land from 1.6 to 3.2 km distant and the perimeter shared with grain sorghum increased. During 2002, the area of grain sorghum (half-bloom) and uncultivated land (hard-dough) within 1.6 km of cotton fields were both positively related to predator numbers. Cotton planting dates and the abundance of cotton fleahoppers (*Pseudatomoscelis seriatus* [Reuter]) were also strongly linked to predator numbers during both years. Results suggest that the total amount of grain sorghum or uncultivated land in an area is more important than the presence of these habitats adjacent to cotton fields, and that landscape composition may sometimes be the most important factor in determining predator abundance.

Introduction

Changes in crop production over the last several decades have transformed modern agriculture from a mosaic of small family farms to relatively large tracts of monoculture, resulting in a greatly simplified agricultural landscape (Nickel 1973; Hietala-Koivu 2002). This trend towards large monocultures represents a loss in plant diversity and has altered the composition and stability of arthropod populations in agriculture. Problems arising from this trend include

an increased severity of pest outbreaks (Root 1973; Andow 1991a) as well as a decrease in the number and effectiveness of natural enemies, particularly indigenous generalist predators (Rabb et al. 1976; Altieri and Letourneau 1982).

One way to address these problems is to increase plant diversity within agricultural fields. The use of polycultures (i.e., planting two or more crops on the same parcel of land) and the planting or growth of non-crop vegetation (e.g., weeds, flowering plants, and hedgerows) are tactics aimed at attracting, retain-

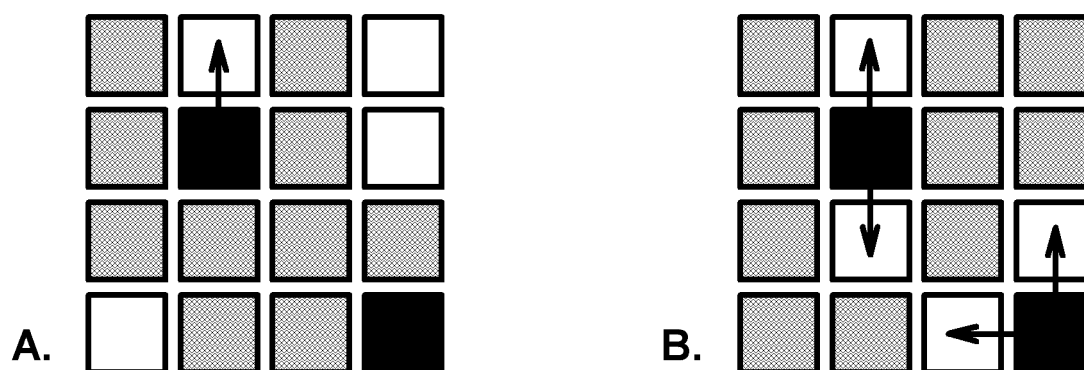


Figure 1. Representation of arbitrary (A.) and strategic (B.) placement of high value crops (white plots) relative to natural enemy sources (black plots). Arrows indicate movement of natural enemies into the crop of interest. A strategic placement of high value crops near sources of natural enemies should promote earlier or greater colonization by predators and parasitoids.

ing, or otherwise improving the performance of predators and parasitoids. Though frequently successful in research trials, creating functional, economically feasible programs of diversification in modern agriculture is challenging; polycultures can reduce yields via plant competition (Andow 1991b), while planting non-crop vegetation requires removing agricultural land from production (Landis et al. 2000). Required changes to agronomic practices including irrigation, planting, and weed or pest control may also reduce the feasibility of both strategies (Beets 1982). As a result, a recent review of habitat management in agriculture (Landis et al. 2000) notes that worldwide, only six such programs are widely adopted by growers in commercial agricultural systems.

Varied vegetation across a landscape may be more important to predators and parasitoids than diversity within agricultural fields (Elliot et al. 1998; Thies and Tschamntke 1999; Elliot et al. 2002). Therefore a more practical strategy may be working with the diversity already present in agricultural landscapes to optimize pest control by existing natural enemies. The arrangement of crops across a landscape may be largely arbitrary, but crops of higher value or pest vulnerability could be planted nearer to sources of natural enemy colonization or refugia (Figure 1). Such an arrangement reduces the distance natural enemies must move to arrive at higher value crops in an agricultural system, likely resulting in earlier or greater overall colonization by predators and parasitoids. Though perhaps more complex logistically, this strategy requires no modification of within-field management and no loss of available agricultural land. To implement such a strategy requires, at minimum, knowing

(1) the habitat or plant types that are beneficial to the crop of interest, and (2) the scale at which benefits may be realized.

Cotton production in the Southern Rolling Plains region of Texas provides a relatively simple model system for exploring the effects of existing habitat diversity on natural enemies at the landscape scale. In this area, land used for crop production is divided among winter wheat, cotton and grain sorghum. Remaining agricultural land is devoted to rangeland and forage production, but uncultivated areas with natural vegetation are also a large component of the landscape. Previous research in Texas and elsewhere suggests that grain sorghum is a source for predatory arthropods in adjacent cotton plots (Fye and Carranza 1972; Lopez and Teetes 1976) and is supported by research in the Southern Rolling Plains (Prasifka et al. 1999; Prasifka et al. 2003). Preliminary evidence also indicates uncultivated areas may increase predator numbers in nearby cotton fields (Heinz, unpublished data). Though grain sorghum and uncultivated areas appear to contribute to the predator fauna in cotton, the scale of any beneficial effects is currently unknown. Field studies conducted during 2001 and 2002 were designed to determine (1) if grain sorghum and uncultivated areas influence predator abundance in cotton on a landscape scale, and (2) how these effects, if detected, compare to biological and agronomic variables in determining predator abundance.

Materials and methods

Manipulation of landscape, biological and agronomic variables on a large scale was not technically feasible, so a large number of cotton fields were selected and used in what is sometimes referred to as a “natural experiment” (Pianka 1994); the variation among fields was used as a substitute for experimentally manipulated treatments. Totals of 70 (2001) and 63 (2002) commercial cotton fields over a three-county area were used with the permission of cooperating growers. These locations encompassed wide ranges of field areas, planting dates, cultivars grown, and crop management practices.

Predator and pest sampling

Approximately three weeks after planting, each field was sampled to determine pest and predator levels. Cotton plants at 13 arbitrarily selected locations were visually inspected within fields, though all sampling was conducted at least 60 m from the nearest field border. A total of 100 plants per field was searched in the earliest stages of cotton growth, but sampling was reduced to 40 plants per field after six unfurled leaves were present on each cotton plant. Pest numbers on each plant were counted, including bollworms (*Helicoverpa zea* [Boddie]), tobacco budworms (*Heliothis virescens* [Fabricius]), cotton aphids (*Aphis gossypii* Glover), cotton fleahoppers, (*Pseudatomoscelis seriatus* [Reuter]), and thrips (*Thrips* spp. and *Frankliniella* spp.). Because of their similar appearance, bollworms and tobacco budworms were pooled into one pest category referred to as heliothines. Further, numbers of eggs and larvae (heliothines) or nymphs and adults (cotton fleahoppers) were distinguished as separate pest categories. The same plants were inspected for predators including ladybeetles, (*Hippodamia convergens* Guérin-Méneville and *Scymnus lowei* Mulsant), minute pirate bugs (*Orius insidiosus* [Say] and *Orius tristicolor* [White]), damsel bugs (*Nabis* spp.), big-eyed bugs (*Geocoris punctipes* [Say] and *Geocoris pallens* Stål) and spiders (Araneae). Ladybeetles, spiders and minute pirate bugs are the most abundant predators in the Southern Rolling Plains (Prasifka et al. 1999) and considered key predators in Texas cotton against cotton aphids, fleahoppers, and heliothines, respectively (Breene et al. 1989; Slosser et al. 1998; Sansone and Smith 2001). All predators sampled were only counted as adults except spiders, which were counted at all life stages.

Sampling was conducted once weekly for nine weeks, unless inclement weather or recent pesticide use prohibited entry into fields.

Landscape and agronomic variables

In addition to predator and pest sampling, data on agronomic and landscape variables also were collected. Agronomic variables were classified as those factors potentially under control of a single grower and included the planting date and field shape (perimeter-to-area ratio) of selected cotton fields. The planting date of the nearest grain sorghum field also was included because sorghum maturity has been implicated as a cause of predator movement from grain sorghum to cotton (Fye 1972). Although pesticide use is certainly another important agronomic factor, reliable pesticide application data for all of the selected fields could not be obtained, so the inclusion of this parameter as an agronomic variable was prevented.

Area maps provided by the Texas Boll Weevil Eradication Foundation were used as a framework for obtaining landscape data. These maps indicated which agricultural fields in the area were used for cotton production each year. The information on these maps was verified and the location of grain sorghum and uncultivated areas was added (MapInfo Corporation 2000). Image analysis software (Jandel Scientific 1995) was then used to measure the following variables for each field: total lengths of field perimeter shared with grain sorghum and uncultivated land; total areas of grain sorghum and uncultivated land area within 1.6 km; the total areas of grain sorghum and uncultivated land between 1.6 and 3.2 km distant (Figure 2). These parameters were chosen to represent plant diversity at local (field perimeter), intermediate (0 – 1.6 km) and area (1.6 – 3.2 km) scales. Because the cotton fields selected varied widely in size (12 – 206 ha), landscape variables were scaled relative to cotton field size. For example, the amount of cotton perimeter shared with grain sorghum was expressed as a percentage of total cotton field perimeter. Accordingly, estimates of uncultivated land between 0 – 1.6 km from a specific cotton field were calculated as the total area of uncultivated land within 1.6 km divided by the cotton field’s area.

Analytical methodology and statistical analyses

Stepwise regression analysis was used to determine the relationships of biological, agronomic and land-



Figure 2. Sample image for analysis of landscape variables. Grain sorghum fields are shown in black and uncultivated land in white. Cotton, harvested wheat and fields recently left fallow are indicated in gray, with studied cotton fields indicated by numbers. Dashed-line circles indicate radii 1.6 and 3.2 km from centroid of cotton field number 32.

scape variables to predator abundance. This approach differs from analyses focused on constructing the best model as judged by the amount of variation explained (i.e., maximum R^2 , minimum SSE). The intent was to obtain regression models whose interpretation was as simple and straightforward as possible, thus increasing confidence that all model components represented meaningful effects. Given the additional complexity or 'noise' introduced by uncontrolled variables not used as potential predictors (e.g., local weather, pesticide use, cotton variety) and the high number of fields sampled, the inclusion of a given predictor in a regression is unlikely to be a spurious result.

Preliminary data analysis was conducted on independent variables to determine if landscape and agronomic conditions differed between years; if the ranges of conditions differed from one year to the next, the relationships of predator levels to independent variables might also be expected to vary. Most independent variables were not normally distributed, so the non-parametric Mann-Whitney test was used to compare independent variables between years. Suspected correlations between landscape variables were also examined. Extremely high correlations among these variables could cause a variable with no direct relationship to predator abundance to be accidentally included as a model predictor or hinder overall interpretation of results. Spearman's rank correlation

procedure was used to test for bivariate correlations among landscape variables. These and all other analyses were conducted using SPSS software (SPSS Inc. 2000).

In the stepwise regression analysis the dependent variable, predator density, consisted of the sum of all five predator categories sampled for each field on a given sampling date, giving an estimate of the number of predators per 100 cotton plants. Data from pest densities, landscape variables and agronomic practices were all used as independent variables. Scatter plots of predator abundance versus all independent variables were used to search for outliers before regressions were performed. Data were censored to remove (1) extreme values of independent variables, (2) instances of apparent sampling error, and (3) cases where pesticide applications were suspected (decreases $\geq 50\%$ in predator numbers for at least two weeks). In no case were more than two observations censored in a regression. Stepwise regressions (entry $\alpha = 0.05$, removal $\alpha = 0.10$) were then conducted for three sample dates per year at times corresponding to the half-bloom, hard dough and maturity stages of grain sorghum phenology (Vanderlip 1993). Only first order linear relationships between prey levels and candidate variables were included; at each step in the regressions, visual inspection of residuals plotted against possible predictors showed no evidence for

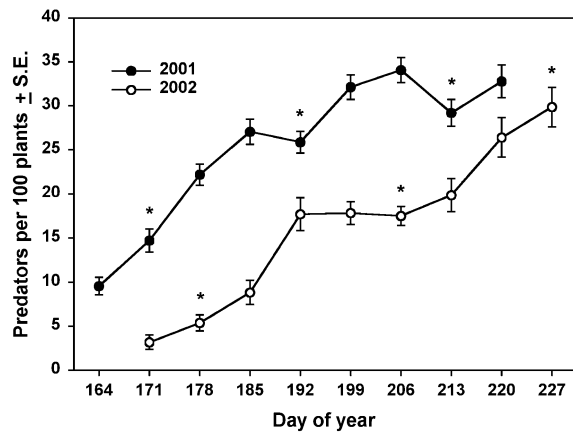


Figure 3. Number of generalist predators per 100 plants in sampled cotton fields during 2001 (filled circles) and 2002 (empty circles). Asterisks indicate dates for which stepwise regressions on predator levels were conducted.

non-linear or higher order relationships. Multiple sample dates were analyzed separately because factors influencing arthropod populations in agriculture may vary during the growing season (Brazzle et al. 1997), while the specific periods selected were timed to closely coincide with previous mark-recapture studies of predator movement in the Southern Rolling Plains.

Results

Trends in predator and pest populations

Mean predator levels increased steadily throughout the period of observation in both 2001 and 2002 (Figure 3). Among the five predator groups included in the analysis, ladybeetles and spiders were most common (38% each), with minute pirate bugs (13%), damsel bugs (9%), and big-eyed bugs (2%) found in lower numbers. Both the occurrence and peak abundances of various pest groups were segregated temporally (Figure 4-5). Thrips were found only in early sampling periods, whereas fleahoppers and heliothines reached their maximum densities around the middle and late sampling dates. Peak mean abundance of cotton aphids also increased 30-fold between 2001 and 2002.

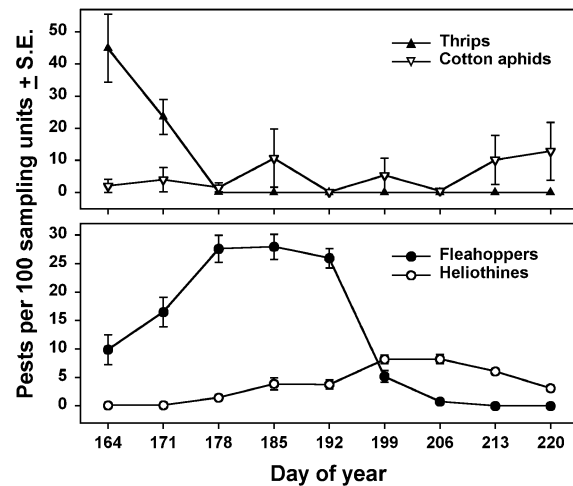


Figure 4. Mean number (\pm standard error) of pests per sampling unit versus time, 2001. Pest levels expressed as number per 100 plants, except for aphids (per 100 leaves) and thrips (per 100 terminals). Data for distinct life stages of heliothines and fleahoppers are pooled for presentation.

Comparisons and correlations of landscape and agronomic variables

Wide ranges of values for agronomic and landscape variables were apparent over both years (Table 1). Mann-Whitney test results showed differences in two agronomic variables between 2001 and 2002. First, the median cotton planting date was delayed 13 days in 2002, a result of unseasonable May rains over much of the study area. Also, cotton fields sampled in 2002 also tended to have greater perimeter-to-area ratios than in 2001. Among the landscape variables, greater relative areas of grain sorghum and uncultivated land were found within 1.6 km of selected cotton fields during 2002. Several significant Spearman's rank correlations ($\alpha = 0.05$) between landscape variables were found (Table 2). The strongest relationships were found between the relative amount of uncultivated areas at the intermediate (0 – 1.6 km) and area (1.6 – 3.2 km) scales in 2001 and 2002.

Regression analyses of predator abundance

Stepwise regressions explained up to 36% of the variation in predator levels among the study fields in 2001, though the strength of the regressions and the significant predictors of predator density differed among sampling periods (Table 3). Data collected in the early sampling period, which corresponded with

Table 1. Agronomic and landscape variables used in stepwise regressions of predator abundance, 2001-2002.

Variable	Median (range)		T	P
	2001	2002		
Cotton planting date (d)	143 (121 – 161)	156 (125% – 165)	3426.5	< 0.01
Cotton perimeter-to-area ratio ([km/ha ×] 100)	6.6 (3.2 – 12.6)	8.0 (4.0 – 14.0)	4092.5	< 0.01
Planting date of nearest grain sorghum field (d)	100 (87 – 109)	99 (71 – 118)	4666.0	0.91
Grain sorghum perimeter (%)	8.3 (0 – 79.6)	11.0 (0 – 62.0)	4676.5	0.95
Uncultivated perimeter (%)	8.2 (0 – 63.0)	10.2 (0 – 100.0)	4636.5	0.80
Grain sorghum area within 1.6 km	0.7 (0 – 15.2)	1.2 (0 – 15.8)	4191.5	0.02
Grain sorghum area between 1.6–3.2 km	2.8 (0 – 17.3)	3.6 (0 – 28.2)	4421.5	0.23
Uncultivated area within 1.6 km	2.0 (0 – 23.9)	3.4 (0 – 29.4)	4138.5	0.01
Uncultivated area between 1.6–3.2 km	12.8 (0.4 – 132.1)	17.1 (0.5 – 92.5)	4337.5	0.11

T = Test statistic for Mann-Whitney test ($n = 70$, $m = 63$). Area measures expressed as ratios relative to cotton field areas.

Table 2. Spearman's rank correlation coefficients (r_s) among landscape variables, 2001 and 2002.

Variable	Year	Uncultivated perimeter (%)	Grain sorghum % within 1.6 km	Grain sorghum % between 1.6–3.2 km	Uncultivated % within 1.6 km	Uncultivated % between 1.6–3.2 km
Grain sorghum perimeter (%)	2001	-0.310* ¹	0.629*	0.172	-0.039	-0.080
	2002	-0.242	0.617*	0.236	-0.127	-0.044
Uncultivated perimeter (%)	2001		-0.217	-0.299*	0.587*	0.413*
	2002		-0.308*	-0.369*	0.550*	0.480*
Grain sorghum area within 1.6 km	2001			0.574*	-0.048	-0.134
	2002			0.687*	-0.067	-0.127
Grain sorghum area between 1.6–3.2 km	2001				-0.164	-0.250*
	2002				-0.145	-0.156
Uncultivated area within 1.6 km	2001					0.890*
	2002					0.920*

Asterisks indicate significant ($\alpha < 0.05$) correlations between variables.

Table 3. Predictors of cotton predator abundance as indicated by stepwise regression analysis, 2001.

Sampling period	Variable	Partial correlation coefficient	t	P
Half-bloom	Cotton planting date	-0.441	-3.44	0.001
	Fleahopper adults	0.304	2.23	0.030
Hard-dough	Fleahopper adults	0.405	3.52	0.001
Maturity	Uncultivated area between 1.6–3.2 km	0.315	2.67	0.009
	Heliothine eggs	0.300	2.54	0.014
	Grain sorghum perimeter (%)	0.254	2.12	0.038

the half-bloom stage of grain sorghum maturity, best explained the abundance of predators during 2001 ($R^2 = 0.36$, $F(2,49) = 13.95$, $P < 0.001$). During this period, fields planted earlier tended to have greater numbers of predators, while those with greater numbers of fleahopper adults also showed higher predator abundance. At the hard-dough stage, only fleahopper adults entered the stepwise regression model, explaining little of the overall variation in predator abundance ($R^2 = 0.16$, $F(1,63) = 12.35$, $P < 0.001$). As

grain sorghum fields reached maturity, predator levels in cotton were positively related to the amount of uncultivated area from 1.6 to 3.2 km distant, the abundance of heliothine eggs, and the proportion of cotton field perimeter shared with grain sorghum ($R^2 = 0.30$, $F(3,65) = 9.46$, $P < 0.001$). This is the first period in which landscape variables were significant model components.

Results from 2002 data showed similarities to the previous year (Table 4). During the half-bloom

Table 4. Predictors of cotton predator abundance as indicated by stepwise regression analysis, 2002.

Sampling period	Variable	Partial correlation coefficient	t	P
Half-bloom	Cotton planting date	-0.470	-3.80	< 0.001
	Grain sorghum area within 1.6 km	0.349	2.66	0.011
Hard-dough	Uncultivated area within 1.6 km	0.271	2.11	0.040
Maturity	Cotton planting date	-0.414	-3.37	0.001
	Cotton aphids	-0.308	-2.40	0.020
	Fleahopper adults	0.284	2.19	0.032

period, cotton planting date was again negatively related to predator abundance, while cotton predator levels increased with the amount of grain sorghum between 1.6 and 3.2 km distant ($R^2 = 0.35$, $F(2,51) = 13.51$, $P < 0.001$). As in 2001, the model R^2 value was lowest during hard-dough, when only a positive effect of uncultivated land within 1.6 km entered the regression model ($R^2 = 0.07$, $F(1,56) = 4.43$, $P = 0.040$). At grain sorghum maturity, cotton planting date, fleahopper adult abundance, and cotton aphid levels were significant model components ($R^2 = 0.35$, $F(3,55) = 9.83$, $P < 0.001$). As in previous models, predator abundance was related negatively to cotton planting date and positively with fleahopper adult abundance, but a negative relationship between cotton aphids and predators was also indicated for this period.

Discussion

Effects of grain sorghum and uncultivated areas on predator abundance

The first goal of this study was to determine if landscape variables influenced cotton predator abundance. Although correlations cannot be used to define causality, the results convincingly suggest positive influences of the measured landscape variables on the abundance of predatory arthropods in cotton. Significant relationships between predator abundance and diversity across the agricultural landscape appear in both years and in all three sampling periods. At grain sorghum maturity during 2001, cotton fields with increasing uncultivated areas beyond 1.6 km or shared perimeters with grain sorghum had greater numbers of generalist predators than those without these landscape components. At grain sorghum's half-bloom period the following year, greater numbers of predators were associated with increasing amounts of grain

sorghum within 1.6 km of cotton fields; the same relationship was found in the hard-dough period with respect to the extent of uncultivated land.

Potential problems with the regression results include the inconsistent nature of results between years and the pair-wise correlations between landscape variables. The fact that the precise identity and timing of landscape variables in regression models differ between years is not a concern for at least three reasons. First, the distributions of four independent variables differed between years (Table 1), three of which entered at least one regression model.

Changes in the independent variables between years suggest that predators may have experienced slightly different conditions (or combinations of conditions) in 2001 and 2002.

Consequently, the expectation of consistent regression results between years is unrealistic. Second, landscape variables were always positively correlated with predator abundance. The fact that grain sorghum and uncultivated land always showed positive relationships with natural enemy abundance in cotton suggests that the general nature of any effects of landscape diversity was consistent. Finally, other variables in the regression models were also inconsistent between years (e.g., prey levels, Figure 9-10). As one exception, cotton planting date appeared as a model component in the half-bloom sampling period both years, though this is probably an artifact of experimental design; at this time, 10 to 50 days after planting of cotton fields, the most mature fields will almost certainly harbor greater predator numbers than plants at the cotyledon stage of growth.

Correlation among landscape variables was a concern for interpretation of results. Stepwise regression may prevent highly correlated variables from remaining in the same regression model, but does not ensure that the parameter entering the model is most appropriate. All pair-wise comparisons indicate several significant correlations (Table 2), but few are strong

enough to present serious problems ($|r_s| \leq 0.70$). However, strong correlations between the intermediate and area scales of uncultivated land ($r_s = 0.890$ [2001], $r_s = 0.920$ [2002]) indicate that the two variables are too similar to be effectively distinguished. An inspection of area maps shows that uncultivated land often occurs as a few large, continuous patches (Figure 2). Therefore, the rarity of discrete units prohibits distinction between these two scales of uncultivated land. Even with this limitation, the results suggest that the effects of landscape at intermediate and area scales are more important than adjacent habitats as predictors of predator abundance.

Magnitude of landscape effects

A second goal of the analysis was to estimate how the importance of the landscape composition compared with that of prey levels and crop management. Partial correlations represent the influence of one independent variable on predator abundance while taking into account the effects of other independent variables, and therefore represent the unique contribution of an independent variable to the overall R^2 . In the three regression models that used landscape variables in the final stepwise models, the influence of landscape variables appeared considerable. In two cases (maturity 2001; hard-dough, 2002) landscape variables were the most important model components based on partial correlations (Table 3-4). In the third instance (half-bloom 2002) the relationship between grain sorghum and predators was secondary only to cotton planting date. Because the selected fields differed phenologically by up to 40 days, cotton planting date was the single most important predictor over the duration of the study. To examine the importance of landscape variables in another way, squared partial correlations the contributions of each group of variables can be assessed as a fraction of the total R^2 from all models together. Using this comparison, agronomic variables and prey levels each accounted for 38% of the total predictive power of the regression models, and landscape variables accounted for the remaining 24%.

Landscapes and pest management

While the idea that agricultural fields are not isolated, non-interacting units is not new (Levins 1969), an increasing number of recent publications have examined the effects of diverse vegetation on predators or parasitoids at a landscape scale (Elliot et al. 1998;

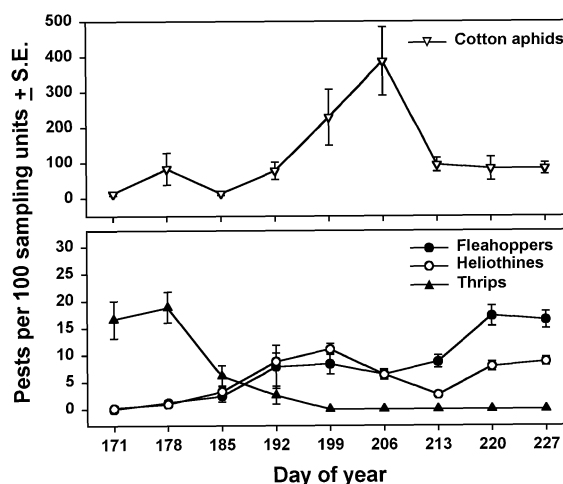


Figure 5. Mean number (\pm standard error) of pests per sampling unit versus time, 2002. Pest levels expressed as number per 100 plants, except for aphids (per 100 leaves) and thrips (per 100 terminals). Data for distinct life stages of heliothines and fleahoppers were pooled for presentation.

Menalled et al. 1999; Thies and Tscharrntke 1999; Östman et al. 2001a,b; Elliot et al. 2002a,b). Results of this study suggest that positive effects of grain sorghum and uncultivated land on cotton predator abundance may come from relatively distant areas, and that the influence of landscape composition can be of equal or greater importance than other types of variables. The corollary of such research is that increased natural enemy abundance and diversity will result in improved control of agricultural pests, though not all studies explicitly address the issue of pest management (Menalled et al. 1999; Thies and Tscharrntke 1999; Östman et al. 2001a). Further observational studies are planned to more explicitly examine the movement arthropods among cotton, grain sorghum and uncultivated areas, while manipulative studies will focus on establishing the direct impacts of grain sorghum and uncultivated areas on cotton pest management. These studies will be necessary in showing quantifiable benefits to agricultural production by managing agricultural systems on a landscape scale.

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