

Impact of *Lygus* spp. (Hemiptera: Miridae) on Damage, Yield and Quality of Lesquerella (*Physaria fendleri*), a Potential New Oil-Seed Crop

STEVEN E. NARANJO,^{1,2} PETER C. ELLSWORTH,³ AND DAVID A. DIERIG^{1,4}

J. Econ. Entomol. 104(5): 1575–1583 (2011); DOI: <http://dx.doi.org/10.1603/EC11089>

ABSTRACT Lesquerella, *Physaria fendleri* (A. Gray) S. Watson, is a mustard native to the western United States and is currently being developed as a commercial source of valuable hydroxy fatty acids that can be used in a number of industrial applications, including biolubricants, biofuel additives, motor oils, resins, waxes, nylons, plastics, corrosion inhibitors, cosmetics, and coatings. The plant is cultivated as a winter–spring annual and in the desert southwest it harbors large populations of arthropods, several of which could be significant pests once production expands. *Lygus* spp. (Hemiptera: Miridae) are common in lesquerella and are known pests of a number of agronomic and horticultural crops where they feed primarily on reproductive tissues. A 4-yr replicated plot study was undertaken to evaluate the probable impact of *Lygus* spp. on production of this potential new crop. Plant damage and subsequent seed yield and quality were examined relative to variable and representative densities of *Lygus* spp. (0.3–4.9 insects per sweep net) resulting from variable frequency and timing of insecticide applications. Increasing damage to various fruiting structures (flowers [0.9–13.9%], buds [1.2–7.1%], and seed pods [19.4–42.5%]) was significantly associated with increasing pest abundance, particularly the abundance of nymphs, in all years. This damage, however, did not consistently translate into reductions in seed yield (481–1,336 kg/ha), individual seed weight (0.5–0.7 g per 1,000 seed), or seed oil content (21.8–30.4%), and pest abundance generally explained relatively little of the variation in crop yield and quality. Negative effects on yield were not sensitive to the timing of pest damage (early versus late season) but were more pronounced during years when potential yields were lower due to weed competition and other agronomic factors. Results suggest that if the crop is established and managed in a more optimal fashion, *Lygus* spp. may not significantly limit yield. Nonetheless, additional work will be needed once more uniform cultivars become available and yield effects can be more precisely measured. Densities of *Lygus* spp. in unsprayed lesquerella are on par with those in other known agroecosystem level sources of this pest (e.g., forage and seed alfalfa, *Medicago sativa* L.). Thus, lesquerella production may introduce new challenges to pest management in crops such as cotton.

KEY WORDS *Lygus hesperus*, *Lygus elisus*, *Lygus lineolaris*, *Physaria fendleri*, crop damage

Urbanization, cost, and availability of water, and changing world markets are influencing agricultural production patterns in the western United States. One response has been an increasing interest in new alternative crops that can either replace existing crops or augment crop rotational schemes (Dierig et al. 2011). *Physaria* spp. (Brassicaceae), commonly called lesquerella, are native to the New World with the greatest concentration of species occurring in the southwestern United States and northern Mexico (Rollins and Shaw 1973). *Physaria* spp. contain high

levels of hydroxy fatty acids in their seed oil (Jones and Wolf 1960, Smith et al. 1961). Currently, imported castor oil is the only commercial source of these valuable fatty acids, which are used in many industrial applications, including the production of biolubricants, biofuel additives, motor oils, resins, waxes, nylons, plastics, corrosion inhibitors, cosmetics, and coatings (Roetheli et al. 1991, Goodrum and Geller 2005). In the mid-1980s, collaborative research was initiated to develop lesquerella as a potential alternative crop for the arid southwestern United States (Roetheli et al. 1991). Through extensive breeding efforts, agronomically improved cultivars of lesquerella have been selected for seed yield and seed oil quality characteristics. Optimal methods for planting, irrigating, and harvesting are being developed, largely adapted from the production of wheat, *Triticum aestivum* L., and other small grain crops. The primary species cultivated in the west is *Physaria fendleri* (A. Gray) S. Watson; it contains >25% oil in its seeds and

This article presents the results of research only. Mention of a proprietary product does not constitute endorsement or recommendation for its use by USDA.

¹ USDA–ARS, Arid-Land Agricultural Research Center, 21881 N. Cardon Ln., Maricopa, AZ 85138.

² Corresponding author, e-mail: steve.naranjo@ars.usda.gov.

³ Maricopa Agricultural Center, Department of Entomology, University of Arizona, 37860 West Smith-Enke Rd., Maricopa, AZ 85138.

⁴ USDA–ARS, National Center for Genetic Resource Preservation, 1111 S. Mason St., Fort Collins, CO 80521.

Table 1. Summary of experimental designs for examining the effect of *Lygus* spp. on lesquerella production, 2005–2009, Maricopa, AZ

Yr	Experimental design ^a	Replicates	Plot size (m)	Insecticide application trigger	Treatment ^b	No. insecticide applications ^c
2005	CRD	4	12.2 by 12.2	Threshold	1, 3, 5, or 10 adults + nymphs/sweep, UTC	6, 2, 1, 1
2006	RCBD	4	12.2 by 24.4	Threshold	0.5, 2, 4, or 8 adults + nymphs/sweep, UTC	8, 4, 2, 1
2007	RCBD	5	12.2 by 24.4	Calendar	Weekly, biweekly, or triweekly, UTC	6, 3, 2
2009 exp 1	RCBD	5	12.2 by 24.4	Calendar	Weekly, biweekly, or triweekly, UTC	10, 5, 3
2009 exp 2	RCBD	5	12.2 by 24.4	Calendar	Weekly, weekly starting 2, 5, or 8 wk post-initiation, UTC	10, 8, 5, 2
2009 exp 3	RCBD	5	12.2 by 24.4	Calendar	Weekly, weekly ceasing 2, 5, or 8 wk pretermination, UTC	10, 8, 5, 2

^a CRD, completely randomized design; RCBD, randomized complete block design.

^b UTC, untreated control; the weekly and UTC treatments in 2009 were shared among all three experiments.

^c Presented in order of the treatments listed in the preceding column and excluding the untreated control plots.

has many desirable agronomic traits. The crop is not currently grown commercially, but adoption and expansion of the crop are promising (Dierig et al. 2011).

As a new crop in the desert agroecosystem, almost nothing is known about the arthropods inhabiting lesquerella, and what impacts they might have on crop production. In Arizona, lesquerella is planted in the fall and harvested in late spring to early summer. The plant flowers indeterminately and produces a profusion of bright yellow flowers over an extended portion of the late winter and spring that are highly attractive to some insects including *Lygus* spp. (Hemiptera: Miridae) (Naranjo et al. 2008, Blackmer and Byers 2009). These flowers give rise to pods (siliques) containing up to 30 small seeds that contain the valuable oil. Surveys indicate that lesquerella harbors a huge diversity of arthropod taxa, including many beneficial organisms, such as predators, parasitoids, bees, and other pollinating insects (Naranjo et al. 2008; S.E.N., unpublished data). Lesquerella also serves as a host of several potential pest species, including *Lygus* spp. At least three species of *Lygus* are found in the crop, *Lygus hesperus* Knight, *Lygus lineolaris* (Palisot de Beauvois), and *Lygus elisus* Van Duzee. *L. hesperus* and *L. lineolaris* are major pests of a wide range of agronomic and horticultural crops throughout the United States and Canada (Scott 1977, Young 1986, Wheeler 2001). Several of these species and others are pests of another brassica crop with similar growth characteristics, canola (*Brassica napus* L.), where they can cause significant yield losses through feeding on reproductive structures (Butts and Lamb 1990, 1991; Turnock et al. 1995; Cárcamo et al. 2002). In Arizona, *L. hesperus* has been considered the most significant pest of cotton, *Gossypium hirsutum* L., for more than a decade based on its relative contribution to damage and control costs (Ellsworth and Jones 2001). The objectives of this study were to quantify plant damage by the *Lygus* spp. complex and to evaluate the potential of these insect species to negatively affect lesquerella seed yield and quality.

Materials and Methods

Study Site. All experiments were conducted at the Maricopa Agricultural Center, University of Arizona,

Maricopa, AZ, from 2005 to 2009. Lesquerella seed were broadcast planted with a Brillion seeder (Brillion Farm Equipment, Brillion, WI) at a rate of ≈ 11 kg/ha followed by shallow incorporation into benches that were set up for level basin flood irrigation. Lesquerella is a perennial plant but is cultivated as a winter–spring annual. Seeds were sown in mid-October of each year and plots were set up the following March once plants had established and began to flower. In total, 135 kg/ha of nitrogen was applied, half at planting and half at the onset of flowering. Total irrigation was 63–76 cm with three irrigations in the fall for seed germination and establishment, and the remaining water applied every 10–14 d during the spring. Pre- and postemergence herbicides were applied to enhance plant stand. Lesquerella has indeterminate growth and continues to flower until late spring when high temperatures and cessation of irrigation diminish plant growth and initiate seed maturity. Plots were harvested in early June (see Experimental Design).

Experimental Design. The same general design was used over the 4 yr of study, although plot size, replication and design structure varied over time depending on total crop availability (Table 1). Methods used to affect changes in *Lygus* spp. abundance also varied over time based on the experience gained as the study progressed. In all years, experimental units (plots) were established within solid planted fields ranging from 0.3 to 1.1 ha. In all years, the distance between plots and blocks was 4 m. Three related studies were conducted in 2009. The first was similar to the 2007 study, and the second and third studies were designed to examine the relative importance of early and late season damage to the crop. The weekly application and untreated control plots were shared among the three studies in this final year.

All insecticide applications consisted of a tank mix of acephate (1.12 kg (AI)/ha) for control of *Lygus* spp., plus a low dose of permethrin (44.8 g (AI)/ha) to act as a temporary bee repellent (lesquerella is pollinated by honey bees [*Apis mellifera* L.] and other native bees). All applications were applied by ground using a Hi-Cycle tractor (John Deere, Moline, IL) fitted with a custom spray boom delivering a total volume of 187 liters/ha with Teejet Twinjet 8003 nozzles spaced every 50.8 cm. Applications were made in

the early morning to minimize drift and disruption of bee foraging.

Insect and Plant Sampling. A standard 38.1-cm sweep net was used to sample *Lygus* spp. in the lesquerella plots. The sweeps motion was standardized to capture a linear area of ≈ 100 cm in width in front of the sweeper's walking path and just above ground level. Due to the seasonally increasing stature of the plant, earlier season sweeps samples capture proportionally less canopy volume than later in the season. The crop never exceeded 40 cm in height. In total, 10 sweeps were taken from randomly selected starting points through the central area of each plot. The act of driving the tractor through the field for insecticide application automatically created four tire-width alleys in each plot. Sampling was alternated among the three central most subplots created by these alleys making sure to begin sweeps at least 1 m in from the plot edge. Samples were collected weekly beginning in early to mid-March and continued until mid- to late May each year. In 2005 and 2006, these samples were processed immediately. The mean number of total *Lygus* spp. (adults and nymphs combined) per sweep over all replicate plots of a given treatment were used to trigger insecticide applications. In 2007 and 2009, samples were stored in a -20°C freezer and processed during the summer and fall. A subsample of insects from the untreated control plots was used to determine species composition throughout the season in each year using the key of Mueller et al. (2003).

Damage to the fruiting structures of the plant was assessed four to five times per season (approximately biweekly) in each plot in all years. Ten stems were randomly collected from each plot on each sampling date and returned to the laboratory for evaluation. Four parameters were assessed: flower damage, bud damage, seed pod damage, and missing seed pods. Fruiting structures are arranged in an alternate pattern on the stems making it easy to count the number of each structure and assessing their presence or absence. Preliminary observations in the laboratory showed that *Lygus* spp. damage to the flowers, buds, and pods were characterized by obvious tissue distortion, lesions, or both. Because the numbers of fruiting structures and potential fruiting sites varied among stems, damage was quantified as the proportion of damage to each structure out of the total present or the proportion of missing pods over all 10 stems in a sample.

Harvest samples were taken from each plot with a small plot grain combine (Hege, Germany) in early June of each year. A 2.44-m-wide swath was taken down the entire length of the center of each plot. The harvest bags were stored in a greenhouse with the coolers shut off for 2 wk to allow thorough drying. A thrasher was then used to separate seeds from the pods and chaff, and total seed weight was then determined. Total seed oil content was determined from a subsample of the bulk harvest using nuclear magnetic resonance (Oxford-MQ5094, Concord, MA). In addition, 1,000-seed weight was determined from a subsample of the bulk harvest to assess average seed size.

Statistical Analyses. Mixed model analysis of variance ([ANOVA] SAS version 9.1, SAS Institute, Cary, NC) was used to test for treatment differences in seed yield, seed weight and seed oil content. Mixed model, repeated measures ANOVA was used to test for differences in plant damage parameters over multiple dates in each year of study. In years using a randomized block design, block and block \times treatment interactions were entered as random factors. The first order heterogeneous autoregressive option (ARH1) was used to estimate the repeated measure covariance structure and Satterthwaite's correction was used to estimate degrees of freedom. Tukey's tests were used to perform mean separation if a significant ($P < 0.05$) ANOVA was indicated. Proportional parameters from plant damage assessments were arcsine-square root transformed as needed for normality and to achieve homogeneity of variances. No other parameters needed transformation before analysis. All data are presented as untransformed means.

Stepwise regression analyses (SAS version 9.1) were performed to further characterize the relationship between seed yield, individual seed weight, seed oil content, and plant damage as a function of *Lygus* spp. density. Preliminary analyses indicated no consistent patterns of correlation (Spearman's rank correlation) between plant responses and *Lygus* spp. density (adults, nymphs, or both combined) from individual dates or pooled over early, middle, and late portion of the season. Thus, final regression analyses were based on the individual seasonal average plant parameters and seasonal average insect densities from each plot in each year. Both adults and nymphs were entered as independent variables. Standardized coefficients were estimated to better gauge the relative importance of each group independent of the magnitude of their densities.

Results

Insect Composition and Abundance. A combination of *L. hesperus*, *L. lineolaris*, and *L. elisus* were found in lesquerella plots all 4 yr of the study comprising, on average, 52, 14, and 34%, respectively, of the total *Lygus* spp. sampled. In 2005, 2006, and 2009, all three species were similar in abundance in the early portion of the season and then *L. hesperus* became dominant by mid-April. The pattern was different in 2007 during which *L. lineolaris* was dominant in the early season, species composition was evenly distributed in mid- to late March, and *L. elisus* became dominant by mid-April.

Lygus spp. abundance was successfully manipulated by varying the frequency and timing of insecticide application (Fig. 1; Table 1). As expected, abundance increased progressively as the frequency and total number of insecticide applications declined. Nymph abundance seemed to be more responsive than adult abundance to insecticide sprays in 2005, but both nymphs and adults were affected by sprays in the remaining years. General *Lygus* spp. pressure declined over the course of the study with the densities ob-

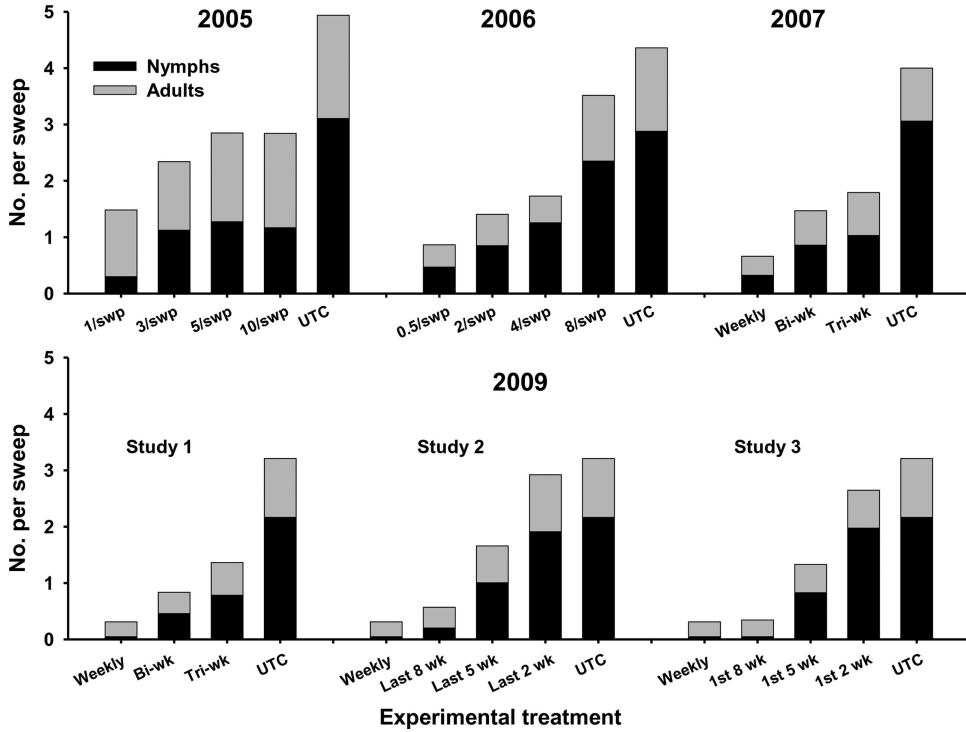


Fig. 1. Seasonal mean abundance of *Lygus* spp. adults and nymphs in the treatment plots 2005–2009, Maricopa, AZ. Abundance was manipulated by variable numbers of insecticide applications based on differential thresholds (2005–2006) or frequency and timing of sprays (2007, 2009).

served in the untreated control plots highest in 2005 (average of 4.9 per sweep) and lowest in 2009 (average of 3.2 per sweep). This is consistent with the overall decline in regional abundance of *L. hesperus* observed over the past several years in Arizona (P.C.E., personal observation).

Plant Damage. Studies from 2005 to 2007 revealed significant differences ($P < 0.05$) in damage to various plant reproductive structures relative to *Lygus* spp. abundance treatments (Table 2). Plants sustained relatively low levels (<5.4%) of damage to flowers in 2006 and 2007, and treatment differences were signif-

Table 2. Mean \pm SE proportional plant damage for *P. fendleri* relative to treatments in which *Lygus* spp. abundance was manipulated with variable insecticide applications, 2005–2007, Maricopa, AZ

	Flower damage	Bud damage	Missing pods	Pod damage
2005				
1/sweep		0.021 (0.009)a	0.128 (0.019)a	0.288 (0.034)a
3/sweep		0.033 (0.007)ab	0.164 (0.028)ab	0.302 (0.026)a
5/sweep		0.041 (0.011)ab	0.154 (0.007)a	0.332 (0.017)a
10/sweep		0.031 (0.009)ab	0.173 (0.009)ab	0.332 (0.019)a
Untreated control		0.067 (0.016)b	0.228 (0.022)b	0.425 (0.031)b
F, df; P		2.7; 4, 60; 0.04	3.3; 4, 60; 0.02	6.7; 4, 60; <0.01
2006				
0.5/sweep	0.009 (0.006)	0.027 (0.008)a	0.039 (0.006)a	0.258 (0.024)a
2/sweep	0.010 (0.007)	0.039 (0.018)ab	0.055 (0.009)ab	0.264 (0.010)a
4/sweep	0.034 (0.006)	0.057 (0.014)ab	0.062 (0.005)b	0.279 (0.007)ab
8/sweep	0.028 (0.008)	0.066 (0.022)ab	0.062 (0.008)b	0.318 (0.020)b
Untreated control	0.030 (0.010)	0.071 (0.013)b	0.059 (0.003)b	0.320 (0.008)b
F, df; P	2.5; 4, 15; 0.09	3.5; 4, 12; 0.04	4.3; 4, 7.3; 0.05	5.0; 4, 13.2; 0.01
2007				
Weekly	0.018 (0.009)a	0.024 (0.004)	0.012 (0.002)a	0.194 (0.009)a
Biweekly	0.018 (0.009)a	0.022 (0.007)	0.012 (0.002)a	0.230 (0.015)ab
Triweekly	0.054 (0.011)b	0.025 (0.009)	0.014 (0.002)ab	0.228 (0.024)ab
Untreated control	0.046 (0.012)b	0.028 (0.006)	0.018 (0.002)b	0.252 (0.011)b
F, df; P	3.2; 3, 16.5; 0.05	1.7; 3, 12.8; 0.21	3.9; 3, 21; 0.02	4.9; 3, 12.3; 0.02

Means followed by different letters within a column for a given year indicate a significant difference ($P < 0.05$; Tukey's test); 2005 and 2006, $n = 4$; 2007, $n = 5$.

Table 3. Stepwise linear regression of various *P. fendleri* damage components on the abundance of *Lygus* spp. nymphs and adults, Maricopa, AZ, 2005–2009

	Regression coefficient ^a			Standardized coefficient ^b		F	P	r ²	n
	Intercept	Nymphs	Adults	Nymphs	Adults				
2005									
Bud damage	0.077	0.020	0.052	0.377	0.352	6.1	0.01	0.42	20
Missing pods	0.126	0.031	NS	0.756	0.0	24.0	<0.01	0.57	20
Pod damage	0.276	0.043	NS	0.743	0.0	22.2	<0.01	0.55	20
2006									
Flower damage	0.053	0.046	NS	0.597	0.0	9.9	0.005	0.35	20
Bud damage	0.009	0.061	NS	0.580	0.0	9.1	<0.01	0.34	20
Missing pods	0.046	0.006	NS	0.441	0.0	4.4	0.05	0.19	20
Pod damage	0.267	0.013	NS	0.370	0.0	4.5	0.05	0.20	20
2007									
Flower damage	0.163	NS	NS	0.0	0.0				20
Bud damage	0.076	0.017	NS	0.476	0.0	5.3	0.03	0.23	20
Missing pods	0.106	0.008	NS	0.442	0.0	4.4	0.05	0.20	20
Pod damage	0.467	0.021	NS	0.504	0.0	6.1	0.02	0.25	20
2009^c									
Flower damage	0.207	0.058	0.229	0.539	0.735	5.8	<0.01	0.20	50
Bud damage	0.080	NS	0.049	0.0	0.235	4.3	0.04	0.11	50
Missing pods	0.246	NS	0.028	0.0	0.297	4.7	0.04	0.09	50
Pod damage	0.527	0.033	0.141	0.347	0.517	4.1	0.05	0.10	50

^a Stepwise linear regression; NS indicates that the variable failed to meet the 0.15 significance level for entry into the model.

^b Standardized coefficients estimate the relative strength of the variables independent of their numerical scales; calculated as the quotient of the parameter estimate and the ratio of the sample SDs of the dependent and independent variables.

^c Based on pooled data from all three studies in 2009.

icant ($P < 0.05$) only for the latter year during which the two highest levels of insect suppression differed from the lowest level of suppression and the untreated check. Overall flower bud damage also was relatively small (<7.1%) in these years, with significant differences only being observed between the highest level of insect suppression and the untreated control in both 2005 and 2006. Damage to seed pods was considerably higher (upwards of 43%) and varied significantly by treatment in all 3 yr, with the lowest levels associated with the highest level of insect control (Table 2). The percentage of missing pods was highly variable, ranging from 1.8% in 2007 to 22.8% in 2005. Again, the lowest rates were associated with the highest levels of pest suppression. There were no significant interactions between time and damage ($P > 0.05$).

In 2009, overall levels of damage to the various reproductive structures were similar to prior years, with relatively low levels of damage to flowers (6.9–13.9%) and flower buds (0.9–2.4%), low levels of seed pod loss (4.4–6.3%), but relatively high levels of damage to these pods (27.5–33.8%). Although there was a general trend of higher damage with increasing pest abundance, no statistical differences ($P > 0.05$) were observed relative to experimental treatments for any parameter regardless of the relative timing of pest pressure during the season. Again, there were no significant interactions between time and damage ($P > 0.05$).

Regression analyses revealed relatively consistent positive relationships between *Lygus* spp. abundance and damage to plant reproductive structures (Table 3). In addition, analyses showed that these relationships were mainly significant only for nymph abundance with adult abundance failing to enter the stepwise regression model in most instances. Adult *Lygus*

spp. contributed to the model in a few cases, mainly in 2009. In 2005, both life stages contributed to flower bud damage and standardized coefficients showed that both contributed equally. In 2009, only adults were associated with bud damage and missing pods, whereas both life stages were associated with flower and pod damage. In these latter cases, adults were generally associated with higher levels of damage (Table 3). Although associations between *Lygus* spp. and plant damage were significant over all 4 yr of the study, pest abundance described relatively little of the variation in plant damage in most years. In 2005, between 42 and 55% of the variation in damage to reproductive structures was explained by *Lygus* spp. abundance. In the remaining years, only 9–35% of this variation was explained by pest density (Table 3). Additional analyses examined plant damage as a function of combined adult and nymph abundance but results were reflective of results from entering adults and nymphs as separate independent variables. When either stage led to a significant relationship then the combined stages did as well. There were no instances in which the combination of adults and nymphs led to a significant result when neither stage alone was significant. Furthermore, examination of *Lygus* spp. abundance and plant damage relationships for each sampling date in 2005–2007 showed no consistent pattern over years in terms of when insect feeding might be most important (data not shown). This is consistent with the lack of such a time-dependent relationship from the 2009 studies where insect abundance was explicitly manipulated during specific portion of the season.

Crop Yield and Quality. In general, lesquerella seemed resilient to the effects of *Lygus* spp. feeding in terms of seed yield, individual seed weight and seed oil

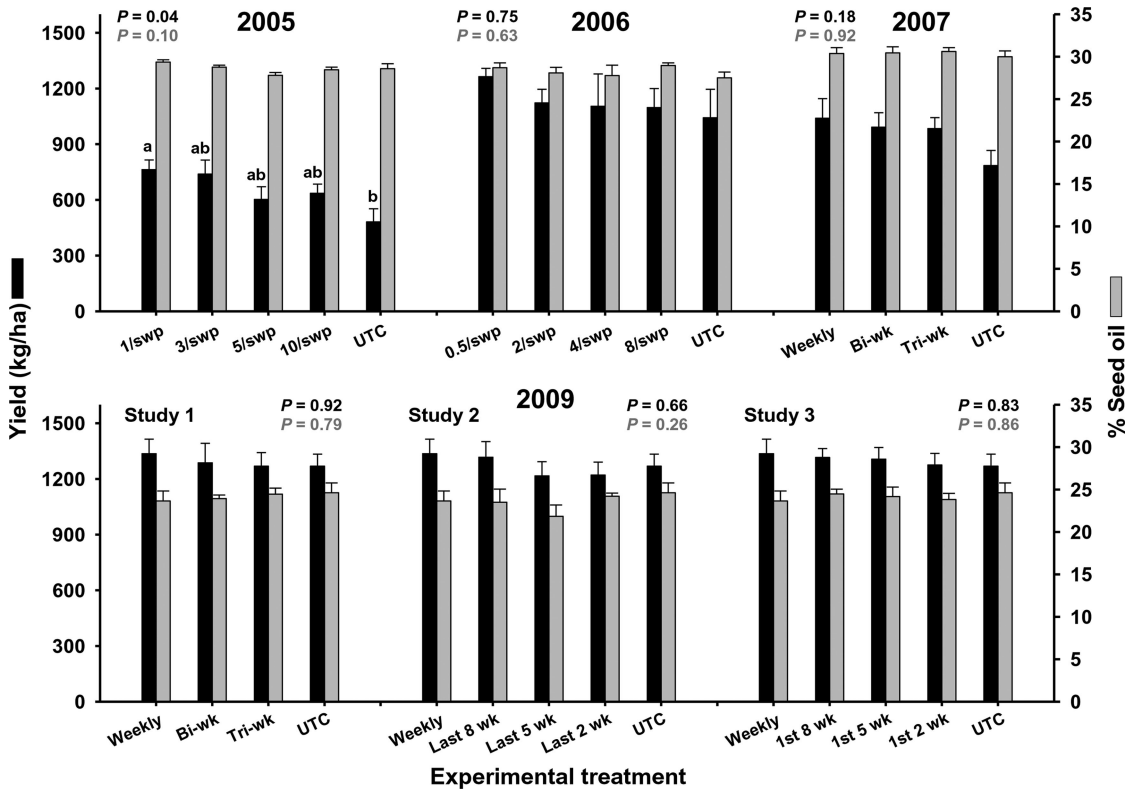


Fig. 2. Seed yield (black bars) and percentage seed oil content (gray bars) of *P. fendleri* in relation to treatments in which abundance of *Lygus* spp. were manipulated by variable numbers of insecticide applications based on differential thresholds (2005–2006) or frequency and timing of sprays (2007, 2009), Maricopa, AZ. *P* values indicate tests of significance for treatment effects (yield, black text; seed oil content, gray text) based on mixed model ANOVA. Bars denoted with different letters within a year were significantly different ($P < 0.05$; Tukey test).

content (Fig. 2). In 2005, yields declined significantly ($F = 3.1$; $df = 4, 15$; $P = 0.05$) as the level of insect suppression declined. Yields in the untreated control plots declined nearly 37% from the treatment plots receiving the highest levels of pest suppression. However, despite a general pattern of declining yield (albeit small) with increasing pest abundance, similar significant declines in yield were not observed relative to treatment in the remaining 3 yr of study. Likewise, seed oil content, a primary quality trait of consideration for the cultivation of this crop, was also unaffected ($P > 0.05$) by treatment (Fig. 2). Individual seed weight was significantly affected by treatment in only one of the 4 yr (2009 study 2: $F = 3.1$; $df = 4, 16$; $P = 0.05$) but marginally significant ($P < 0.07$) in 2005 and 2007. In all cases, higher seed weights were observed in treatments with lower levels of insect suppression.

Stepwise regression analyses based on seasonal plot by plot measures of yield parameters and insect abundance showed a slightly different pattern. Significant declines in yield were observed in two of the 4 yr of study (Table 4). In 2005, only nymphs were associated with this decline, but in 2007 both nymphs and adults entered the model, with abundance of both stages negatively related to yield. The standardized coefficients in this instance showed a stronger contribution

by nymphs. In these 2 yr, insect abundance explained 34–52% of the variation in seed yield. Likewise, seed oil content was significantly and negatively associated with nymph (but not adult) abundance in both 2005 and 2006, but insect abundance explained relatively little of the variation in oil content (18–26%). Seed weight was significantly ($P = 0.02$) and positively associated with adult abundance only in 2009 (Table 4). Again, insect abundance in general explained little of the variation in seed size (11–19%). Additional analyses examining plant damage as a function of combined adult and nymph abundance were consistent with results from entering adults and nymphs as separate independent variables. When either stage led to a significant relationship then the combined stages did as well, and there were no instances in which the combination of adults and nymphs led to a significant result when neither stage alone was significant. Finally, as with damage, correlations between *Lygus* spp. abundance on any given date and yield and quality measure damage showed no consistent pattern over years in terms of when insect damage might be most important (data not shown). This is again consistent with results from 2009 where insect abundance was explicitly manipulated during specific portion of the season.

Table 4. Stepwise linear regression of various *P. fendleri* yield and quality components on the abundance of *Lygus* spp. nymphs and adults, Maricopa, AZ, 2005–2009

	Regression coefficient ^a			Standardized coefficient ^b		F	P	r ²	n
	Intercept	Nymphs	Adults	Nymphs	Adults				
2005									
Yield	794.9	-108.1	NS	-0.72	0.0	19.9	<0.01	0.52	20
% Oil	29.07	-0.34	NS	-0.43	0.0	4.40	0.05	0.18	20
1,000 seed wt	0.650	0.019	NS	0.43	0.0	4.2	0.06	0.19	20
2006									
Yield	1126.0	NS	NS	0.0	0.0				20
% Oil	29.24	-0.66		-0.51	0.0	6.2	0.02	0.26	20
1,000 seed wt	0.609	NS	NS		0.0				20
2007									
Yield	846.1	-147.6	-450.1	-0.85	-0.65	4.32	0.03	0.34	20
% Oil	30.36	NS	NS	0.0	0.0				20
1,000 seed wt	0.522	0.032	NS	0.42	0.0	3.8	0.07	0.17	20
2009^c									
Yield	1291.1	NS	NS	0.0	0.0				50
% Oil	23.86	NS	NS	0.0	0.0				50
1,000 seed wt	0.468	NS	0.036	0.0	0.33	6.1	0.02	0.11	50

^a Stepwise linear regression; NS indicates that the variable failed to meet the 0.15 significance level for entry into the model.

^b Standardized coefficients estimate the relative strength of the variables independent of their numerical scales; calculated as the quotient of the parameter estimate and the ratio of the sample SDs of the dependent and independent variables.

^c Based on pooled data from all three studies in 2009.

Discussion

Plant damage was consistently and positively associated with *Lygus* spp. abundance, primarily the abundance of nymphal stages. However, this did not consistently lead to reduction in seed yield or seed oil content, the two critical harvest components important to commercial production of the crop. We found a pattern of lower numerical seed yields with increasing *Lygus* spp. abundance every year, but significant reductions in only two of four years. Similar to plant damage, yield effects were most often associated with the abundance of nymphs. Seed oil content varied little with insect abundance but was negatively related to nymphal abundance in two years. Seed size also varied little with *Lygus* spp. abundance, only being positively related to adult abundance in 1 yr. This positive relationship is probably related to loss of damaged seed during harvest and thrashing combined with the response of the plant to place more resources into the seeds of damaged pods. Even when significant relationships were found, insect abundance, which was effectively manipulated in our experiment, explained relatively little of the variance suggesting the influence of other variables. One factor is the genetic uniformity of the crop itself. The crop is not grown commercially and available seed arose from a single germplasm release. The crop is open pollinated, contributing even further to inter-plant variation. Thus, there is high interplant variation in yield potential and response to damage.

The differential effect of *Lygus* spp. nymphs and adults on crop damage and yield has been noted in various crops. Mostafa and Holliday (2008) suggested that the lack of late season *Lygus* spp. effects on seed alfalfa yields may result from adult dominated age-structure at this time of the season. Mostafa (2007, cited in Mostafa and Holliday 2008) further showed a

higher level of injury from *Lygus* spp. nymphs compared with adults on buckwheat. *L. hesperus* late-instar nymphs have been clearly linked with reductions in cotton lint yields (Ellsworth and Barkley 2003), and thresholds that incorporate pest age-structure resulted in fewer sprays and better yields (Ellsworth 2000). These results have been corroborated by Zink and Rosenheim (2005) who showed that cotton flower bud abscission was associated with late stage *L. hesperus* nymphs. Observational studies have shown that adults and nymphs of *L. hesperus* readily fed on flowers, buds, and seed pods of lesquerella (S.E.N., unpublished data), and there is little doubt that both stages cause plant damage. Nonetheless, even though insecticide manipulations altered nymphal and adult abundance, our results suggest that plant damage and yield were most responsive to nymphal abundance.

Lygus spp. are dominant herbivores in lesquerella, with *L. hesperus* generally being the most abundant, particularly in late spring, followed by *L. elisus* and a small percentage of *L. lineolaris*. The densities of *Lygus* spp. observed in lesquerella are on par with those in forage alfalfa, seed alfalfa, and canola (Butts and Lamb 1991; Mostafa and Holliday 2008; S.E.N., personal observation). The lack of any differences in damage or yield relative to time of infestation suggests that all three *Lygus* species function similarly and can be treated as a guild for pest management purposes. A variety of other herbivores inhabit lesquerella, including caterpillars, thrips, aphids, leafhoppers, and flea-hoppers (S.E.N., unpublished data), and these insects were undoubtedly affected by acephate sprays. Thus, these herbivores probably contributed to and potentially confounded some of the patterns we observed in plant damage and yield and may warrant further investigation as potential pests. The potential effect of insecticides on pollinators also cannot be discounted.

We used a low dose of a pyrethroid in an effort to temporarily repel bees from treated plots and our samples indicated that bees were equally abundant in both treated and untreated plots (S.E.N., unpublished data). However, there could have been more subtle effects from insecticides that reduced pollination and associated seed set, thereby contributing to further variation in seed yield.

There was a clear relationship between yearly yield levels and the demonstration of yield effects. For example, average yields in plots with the highest levels of pest control in 2005 were just over 750 kg/ha, and both ANOVA and regression analyses showed strong yield effects. Weeds were particularly problematic in this year due to poor pre- and postemergence weed management, and it is known that lesquerella production can be severely affected by weed competition (Dierig et al. 2011). Likewise, in 2007, where significant yield effects were once again observed, average yields in plots with the highest level of pest control were <1,040 kg/ha. In this year, irrigation frequency and amount were not adjusted to account for the higher clay content and large portions of the lesquerella field where our experiment was conducted were damaged by overwatering. In both these years crop stands were relatively sparse and individual plants did not seem to compensate by adding additional lateral growth, probably due to their poor competitive abilities with weeds (Dierig et al. 2011) in combination with root damage from poor soil conditions. When crop stands were robust, yields averaged >1,260 kg/ha and yield effects due to increasing *Lygus* spp. abundance were absent. This suggests that plants were able to compensate for insect damage through mechanisms other than lateral growth, perhaps through addition of stems and flowering sites in response to lost or damaged reproductive tissue. These patterns also suggest that if the crop is established and managed in a more optimal manner, pest insects such as *Lygus* spp. may not significantly limit yield. Nonetheless, additional work is needed once more uniform cultivars become available to more precisely measure yield effects. Overall, our yields in all years were similarly to adjacent fields that were being used to mimic commercial practice for seed production.

The effects of *Lygus* spp. on canola, a related plant with a similar growth form to lesquerella, have been well studied (Butts and Lamb 1990, 1991; Turnock et al. 1995; Wise and Lamb 1998a,b). Canola plants are able to compensate for bud and flower loss such that the total number of seed pods is unaffected even while seed yields may decline with increasing pest pressure (Butts and Lamb 1990, Jones et al. 2003, Cárcamo and Blackshaw 2007). Our results suggest that seed pod numbers declined slightly on individual stems (Tables 2 and 3) with increasing *Lygus* spp. abundance, but we did not measure total stems per plant or per unit area. As noted, we also observed a trend for increasing individual seed weight as insect abundance increased. This could be another form of compensation where additional plant resources are placed in seeds that survive damage. Regardless of how yield compensa-

tion is manifested in lesquerella, it seems that compensation requires plants to be produced under more optimal conditions relieved from weed competition and other agronomic stresses. Unlike lesquerella, the timing of damage is important in canola. Butts and Lamb (1991) found the best yield enhancements when insect controls were implemented during early pod development and Cárcamo and Blackshaw (2007) found that only *Lygus* spp. abundance during the early pod stage was negatively associated with canola seed yield. The lack of such a response in lesquerella may be largely due to its indeterminate flowering behavior and lack of varietal uniformity, leading to overlapping development of buds, flowers and seed pods throughout the season.

The future commercial production of lesquerella may pose new challenges for agroecosystems in the southwestern deserts of the United States. The crop provides breeding habitat for *Lygus* spp. that although perhaps not representing a concern for lesquerella production could have a negative impact on surrounding crops. One of the major weeds in lesquerella and other spring crops, the related London rocket (*Sisymbrium irio* L.) is difficult to control with available herbicides (Dierig et al. 2011) and is also a suitable host for *Lygus* spp. (Diehl et al. 1998, Carroll et al. 2005). Thus, the lesquerella system may be particularly problematic in generating *Lygus* spp. that may affect crops such as cotton. Although lesquerella production is generally terminated at a point when cotton would not be a suitable habitat for *L. hesperus*, insects dispersing from lesquerella could bridge this gap and continue to reproduce in crops such as alfalfa and on weeds in the landscape and then later move to cotton—although earlier than normal *Lygus* spp. damage in adjacent, early planted cotton has been observed (P.C.E., personal observation). Thus, depending on who is growing lesquerella (e.g., growers that produce cotton as well) and the level of community coordination there may be a need to suppress populations of insect pests such as *Lygus* spp. in lesquerella even if there is little direct benefit to the crop itself. Such an approach has been practiced many years for safflower, *Carthamus tinctorius* L., another major host of *Lygus* spp., in California (Sevacherian et al. 1977, University of California 1996). Carrière et al. (2006) showed that both alfalfa (a host unsprayed for *Lygus*) and seed alfalfa (a host sprayed for *Lygus*) created conditions of elevated *Lygus* densities in cotton grown within 375 and 1,500 m of these source crops, respectively. If and when lesquerella becomes commercialized, additional research will be needed to further define its role and impact within the agricultural landscape.

Acknowledgments

We thank Virginia Barkley, Kim Beimfohr, Rebecca Burke, Gail Dahlquist, Emilie Latxague, Letticia Rodarte, Anna Sonoqui, Melissa Stefanek, and Julianne Trejo for expert technical assistance. We thank Terry Coffelt, Guangyao (Sam) Wang, and James Barbour for comments on an earlier draft of this manuscript. This work was partially supported by

USDA-CSREES, RAMP, Developing and Implementing Field and Landscape Level Reduced-Risk Management Strategies for *Lygus* in Western Cropping Systems (Project 0207436).

References Cited

- Blackmer, J. L., and J. A. Byers. 2009. *Lygus* spp. (Heteroptera: Miridae) host-plant interactions with *Lesquerella fendleri* (Brassicaceae), a new crop in the arid southwest. *Environ. Entomol.* 38: 159–167.
- Butts, R. A., and R. J. Lamb. 1990. Injury to oilseed rape caused by mirid bugs (*Lygus*) (Heteroptera: Miridae) and its effect on seed production. *Ann. Appl. Biol.* 117: 253–266.
- Butts, R. A., and R. J. Lamb. 1991. Pest status of *Lygus* bugs (Hemiptera: Miridae) in oilseed *Brassica* crops. *J. Econ. Entomol.* 84: 1591–1596.
- Cárcamo, H. A., and R. E. Blackshaw. 2007. Insect pest incidence and injury to herbicide-tolerant canola in western Canada. *Agron. J.* 99: 842–846.
- Cárcamo, H., J. Otani, C. Herle, M. Dolinski, L. Dosdall, P. Mason, R. Butts, L. Kaminski, and O. Olfert. 2002. Variation of *Lygus* species assemblages in canola agroecosystems in relation to ecoregion and crop stage. *Can. Entomol.* 134: 97–111.
- Carrière, Y., P. C. Ellsworth, P. Dutilleul, C. EllersKirk, V. Barkley, and L. Antilla. 2006. A GIS-based approach for areawide pest management: the scales of *Lygus hesperus* movements to cotton from alfalfa, weeds, and cotton. *Entomol. Exp. Appl.* 118: 203–210.
- Carroll, S. C., M. N. Parajulee, and M. D. Arnold. 2005. *Lygus* survey in the Texas high plains: species composition and host-plant sequencing, pp. 1754–1761. In *Proceedings of the Beltwide Cotton Conferences*, 4–7 January 2005, New Orleans, LA. National Cotton Council of America, Memphis, TN.
- Diehl, J., P. Ellsworth, and L. Moore. 1998. *Lygus* in cotton: identification, biology and management. Cooperative Extension no. 1. College of Agriculture, University of Arizona, Tucson, AZ.
- Dierig, D. A., G. Wang, W. B. McCloskey, K. R. Thorp, T. A. Isbell, D. T. Ray, and M. A. Foster. 2011. Lesquerella: new crop development and commercialization in the U.S. *Ind. Crops Prod.* 34: 1381–1385.
- Ellsworth, P. C. 2000. Lygus control decision aids for Arizona cotton, pp. 269–280. In *Cotton*, a College of Agriculture Report, Series P-121. University of Arizona, Tucson, AZ.
- Ellsworth, P. C., and V. Barkley. 2003. Making late season decisions to terminate insecticide use against *Lygus*. Cotton, a College of Agriculture Report, Series P-134, University of Arizona, Tucson, AZ.
- Ellsworth, P. C., and J. S. Jones. 2001. Cotton IPM in Arizona: a decade of research, implementation & education, pp. 1088–1096. In P. Dugger and D. Richter (eds.), *Proceedings of the Beltwide Cotton Conferences*, 9–13 January 2001, Anaheim, CA. National Cotton Council of America, Memphis, TN.
- Goodrum, J. W., and D. P. Geller. 2005. Influence of fatty acid methyl esters from hydroxylated vegetable oils on diesel fuel lubricity. *Bioresour. Technol.* 96: 851–855.
- Jones, Q., and I. A. Wolf. 1960. The search for new industrial crops. *Econ. Bot.* 14: 56–68.
- Jones, J. W., H. A. Cárcamo, J. K. Otani, R. A. Butts, R. H. McKenzie, E. D. Solberg, and J. DeMulder. 2003. Does canola compensate for lygus bug damage? Final Report 1999M462. Canola Council of Canada and Alberta Agricultural Research Institute, Edmonton, AB, Canada.
- Mostafa, A. M. 2007. Plant bugs (Hemiptera: Miridae) on buckwheat and seed alfalfa crops in Manitoba: dynamics, yield implications and management. Ph.D. dissertation, University of Manitoba, Winnipeg, Canada.
- Mostafa, A. M., and N. J. Holliday. 2008. Insecticidal control of late-season plant bug (Hemiptera: Miridae) infestations in Manitoba has no effect on alfalfa seed quantity and quality. *Can. J. Plant Sci.* 88: 763–770.
- Mueller, S. C., C. G. Summers, and P. B. Goodell. 2003. A field key to the most common *Lygus* species found in agronomic crops of the central San Joaquin Valley of California. Agriculture and Natural Resources Publication 8104, University of California.
- Naranjo, S. E., D. Dierig, and P. C. Ellsworth. 2008. Survey and evaluation of *Lygus* bugs on lesquerella and guayule, two new desert crops in the western USA. *J. Insect Sci.* 8: 49. (www.insectscience.org/8.49/ref/abstract40.html).
- Roetheli, J. C., K. D. Carlson, R. Kleiman, A. E. Thompson, D. A. Dierig, L. K. Glaser, M. G. Blase, and J. Goodell. 1991. Lesquerella as a source of hydroxy fatty acids for industrial products. Growing Industrial Materials Series, October 1991. Cooperative Research Service, U.S. Department of Agriculture, Washington, DC.
- Rollins, R. C., and E. Shaw. 1973. The genus *Lesquerella* (Cruciferae) in North America. Harvard University Press, Cambridge, MA.
- Scott, D. R. 1977. An annotated listing of host plants of *Lygus hesperus* Knight. *Bull. Entomol. Soc. Am.* 23: 19–22.
- Sevacherian, V., V. M. Stern, and A. J. Mueller. 1977. Heat accumulation for timing *Lygus* control measures in a safflower-cotton complex. *J. Econ. Entomol.* 70: 399–402.
- Smith, C. R., Jr., T. L. Wilson, T. K. Miwa, H. Zobel, R. L. Lohmar, and I. A. Wolff. 1961. Lesquerolic acid. A new hydroxy acid from lesquerella seed oil. *J. Org. Chem.* 26: 2903–2905.
- Turnock, W. J., G. H. Gerber, B. H. Timlick, and R. J. Lamb. 1995. Losses of canola seeds from feeding by *Lygus* species (Heteroptera: Miridae) in Manitoba. *Can. J. Plant Sci.* 75: 731–736.
- University of California. 1996. Integrated pest management for cotton in the western region of the United States, 2nd ed. University of California, Division of Agriculture and Natural Resources Publication 3305, Communications Services-Publications, Oakland, CA.
- Wheeler, A. G., Jr. 2001. Biology of the plant bugs. Cornell University Press, Ithaca, NY.
- Wise, I. L., and R. J. Lamb. 1998a. Economic threshold for plant bugs, *Lygus* spp. (Heteroptera: Miridae), in canola. *Can. Entomol.* 130: 825–836.
- Wise, I. L., and R. J. Lamb. 1998b. Sampling plant bugs, *Lygus* spp. (Heteroptera: Miridae), in canola to make control decisions. *Can. Entomol.* 130: 837–851.
- Young, O. P. 1986. Host plants of the tarnished plant bug, *Lygus lineolaris* (Heteroptera: Miridae). *Ann. Entomol. Soc. Am.* 79: 747–762.
- Zink, A. G., and J. A. Rosenheim. 2005. Stage-dependent feeding behavior by western tarnished plant bugs influences flower bud abscission in cotton. *Entomol. Exp. Appl.* 117: 235–242.

Received 24 March 2011; accepted 20 July 2011.