

1 **The importance of alternative host plants as reservoirs of the**
2 **cotton leaf hopper, *Amrasca devastans*, and its natural enemies**

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30

31 **Abstract**

32 Many agricultural pests can be harboured by alternative host plants but these can also harbour
33 the pests' natural enemies. We evaluated the capacity of non-cotton plant species (both
34 naturally growing and cultivated) to function as alternative hosts for the cotton leaf hopper
35 *Amrasca devastans* (Homoptera: Cicadellidae) and its natural enemies. Forty eight species
36 harboured *A. devastans*. Twenty four species were true breeding hosts, bearing both nymphal
37 and adult *A. devastans*, the rest were incidental hosts. The crop *Ricinus communis* and the
38 vegetables *Abelmoschus esculentus* and *Solanum melongena* had the highest potential for
39 harbouring *A. devastans* and carrying it over into the seedling cotton crop. Natural enemies found
40 on true alternative host plants were spiders, predatory insects (*Chrysoperla carnea*, Coccinellids,
41 *Orius* spp. and *Geocoris* spp.) and two species of egg parasitoids (*Arescon enocki* and *Anagrus*
42 sp.). Predators were found on 23 species of alternative host plants, especially *R. communis*.
43 Parasitoids emerged from one crop species (*R. communis*) and three vegetable species; with 39%
44 of *A. devastans* parasitized. We conclude that the presence of alternative host plants provides
45 both advantages and disadvantages to the cotton agro-ecosystem because they are a source of
46 both natural enemy and pest species. To reduce damage by *A. devastans* we recommend that
47 weeds that harbour the pest should be removed, that cotton cultivation with *R. communis*, *A.*
48 *esculentus* and *S. melongena* should be avoided, that pesticides should be applied sparingly to
49 cultivated alternative host plants and that cotton crops should be sown earlier.

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54 **Key words:** *Amrasca devastans*; survey; population density; plant characteristics; natural
55 enemies

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58 **Key message:**

- 59 • The relative advantages and disadvantages of alternative host plants (as sources of both
60 pests and their natural enemies) near crops are likely to vary across agro-ecosystems.
61 • In cotton, alternative host plants (both weeds and cultivated species) harbour
62 herbivorous pests, in particular during the inter-harvest period, but also harbour
63 beneficial predators and parasitoids.
64 • Pest damage would likely be reduced if weeds were removed and intercropping with
65 vegetables avoided. Adjusted sowing regimes could reduce vulnerability of seedling
66 crops to high pest densities.

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68 **Author contribution statement:** R. Saeed gathered the data, analysed the data and wrote the
69 manuscript. M. Razaq instigated the research and commented on the manuscript. I.C.W. Hardy
70 analysed the data and wrote the manuscript.

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74 **Introduction**

75 Agricultural production is commonly, and negatively, affected by insect pests (Kogan and
76 Jepson 2007; Gray et al. 2009) and the problem can be exacerbated by agro-intensification due
77 to rapidly growing human populations (Goodell 2009; Carriere et al. 2012). Some
78 phytophagous pests attack only a single cultivated plant species (monophagy) (Forare and
79 Solbreck 1997), while others have a wider range of host plants (polyphagy) including cultivated
80 plants and species which are not under agricultural production (Li et al. 2011). Ascertaining
81 the importance and extent of alternative host plants, both naturally growing and cultivated, can
82 be fundamental to preventing the development of polyphagous pest populations on a ‘main’ or
83 ‘focal’ agricultural species (Tabashnik et al. 1991). For instance, alternative host plants can
84 support reservoirs of pests during periods when main hosts are seasonally unavailable, with
85 pests subsequently migrating back onto the main host plants (Clementine et al. 2005).
86 Alternative hosts plants can also be agriculturally beneficial when they harbour populations of
87 natural enemies (Naveed et al. 2007). Thus, the availability, density and type of alternative host
88 plants (Power 1987; Atakan and Uygur 2005), and the prevalence of natural enemies (Koji et
89 al. 2012) can be important factors influencing the damage caused by insect pests. Due to the

90 great diversity of agricultural systems, and species involved, the relative advantages and
91 disadvantages of the presence of alternative host plants in the vicinity of crops is likely to vary
92 across agro-ecosystems.

93 The cotton leaf hopper, *Amrasca devastans* (Dist.) (= *Amrasca biguttula biguttula* (Ghauri
94 1983)) (Homoptera: Cicadellidae) sucks sap from plant leaves and also injects toxic saliva,
95 which can cause stunted plant growth, with leaves curling downwards and becoming yellow
96 and then brown and dry, and, in severe cases, the shedding of fruiting bodies (Rehman 1940;
97 Narayanan and Singh 1994). *Amrasca devastans* has been regarded in the Indian subcontinent
98 as the most common and most devastating major insect pest of cotton (*Gossypium hirsutum* L.)
99 since the first quarter of the 20th century: reported cotton yield losses range from 37-67%,
100 respectively (Ahmed 1982; Ahmad et al. 1985; Bhat et al. 1986) and crop failure can be
101 complete in given localities (Rao et al. 1968). Farmers in this area rely only on chemical
102 pesticides to manage *A. devastans* (Yousafi et al. 2013; Razaq et al. 2013), even though frequent
103 spraying is likely adversely affect the natural enemy fauna (Zidan 2012).

104 *Amrasca devastans* is not limited to feeding and breeding on cotton plants: it is regarded to be
105 a widely polyphagous herbivore that can remain active throughout the year due to the
106 continuous availability of alternative host plants. In many cotton growing areas in Asia, such
107 as Pakistan, agricultural practices have changed from mono-cropping to multi-cropping, due to
108 fragmentation of farms into small holdings of <5 hectares, and intercropping of fodder,
109 vegetables and oil seed crops with cotton is now common practice (Khan and Khaliq 2004;
110 Akram et al. 2011). These plants share many of the same pest and natural enemy species and
111 thus can act as reservoirs or carryover sources to the cotton crop (Godell 2009). Further, pest
112 management practices applied to one plant species can cause direct or indirect effects on pest
113 and natural enemy populations on others (Edwards, 1990). For instance, management of the
114 whitefly *Bemisia tabaci* (Genn.) on alternative hosts prior to the seasonal availability of cotton
115 plants can significantly reduce its carry over to cotton (Attique et al. 2003; Rafiq et al. 2008).

116 Despite the importance of *A. devastans*, there have been no quantitative reports on its
117 abundance on alternative host plant species that are found within cotton growing areas;
118 previous literature has only reported its occurrence (Huque 1994, Table 1). There is similarly
119 limited information on the occurrence and abundance of natural enemies on alternative host
120 plants (Rao et al. 1968). Here we report for the first time, temporal patterns of occurrence and
121 abundance of *A. devastans* and its natural enemies on a wide range of potential alternative (non-
122 cotton) host plants in cotton growing areas of Southern Punjab, Pakistan. This allows

123 evaluation of the role of non-cotton species in carrying over *A. devastans* populations between
124 cotton growing seasons, their importance in harbouring this pest during the growing season
125 and in maintaining populations of natural enemies.

126

127 **Materials and Methods**

128 We assessed *A. devastans* and its natural enemies in the cotton agro-ecosystem near Multan in
129 the Punjab province of Pakistan (between 30°11'52"N and 71°28'11"E). Multan is at an altitude
130 of 122m with land area dominated by silt loam soils. It has semi-arid climatic conditions
131 (average rainfall *circa* 186mm) marked by four distinct seasons: a very hot summer (April-
132 June), a wet season in which most of the precipitation occurs with south-western monsoon
133 (July-September) when temperature ranges from 19.5 to 43°C and a cooler or mild winter
134 (October-March), during which temperature ranges from 4.5 to 34.6°C (National Oceanic and
135 Atmospheric Administration data 1961-1990) (see also Fig. 1).

136 *Alternative host plant surveys*

137 Exploratory searches were conducted within 100km of Multan. There were a total of 50 visits
138 to each of 42 sites between 1 January and 31 December 2009, with 4 visits in each month
139 except for January in which there were 6 visits to each site. On each survey day, all the available
140 flora inside cotton farmland were examined visually and we also surveyed flora up to 500m
141 outside each cotton field. Plants hosting nymphal and/or adult *A. devastans* were usually
142 identified in the field according to Ali (1982), Ali and Nasir (1991) and Zafar (1996). Any
143 unidentified specimens were taken to the Botany Department of Bahauddin Zakariya
144 University, Multan, for identification by Dr Z.U. Zafar. If *A. devastans* was found on a plant
145 species on at least two survey dates at the same location, the species was considered to be an
146 alternative host. Alternative host plants were further categorized as 'true' host plants if they
147 harboured both nymphal and adult life stages of *A. devastans*, and as 'incidental' host plants if
148 they carried only a few adults for periods of approx. one week at a given location and on which
149 adults were found during at least two survey visits at each site (Mound and Marullo 1996;
150 Froudi et al. 2001). We also noted the availability of identified host plants on each visit
151 throughout the year. Host plants were further assorted for abundance ('abundant' [a large
152 number of the plant species present in all visited locations], 'fair' [found in small numbers in
153 all locations or in large number at few locations] and 'rare' [small numbers at few locations]),
154 plant growth habit or life form (herb, shrub, climber and tree), perenniality (annual, biennial

155 and perennial) and horticultural utility or host type (vegetable, crop, fruit, ornamental and
156 weed) according to a pre-existing system (Attique et al. 2003; Arif et al. 2009; Tiple et al. 2011;
157 Li et al. 2011).

158 *Pest population density estimates*

159 Eighteen of the field sites were selected, on the basis of high host plant availability, from those
160 surveyed in 2009, and were visited at 15 day intervals between January 2010 and December
161 2011. The prevalence of *A. devastans* on those alternative host plant species which had been
162 found to harbour both nymphal and adult life-history stages in 2009 (i.e. true alternative host
163 plants) was estimated by examining leaves according to the method of Horowitz (1993, see
164 also Leite et al. 2011). Specifically, three leaves were taken from each selected plant; one apical
165 leaf, one leaf from the middle of the plant and one leaf from the lower portion, and the numbers
166 of *A. devastans* nymphs and adults on them were counted. The number of alternative host plants
167 surveyed at each site depended on variation in their abundance (Attique et al. 2003): we
168 sampled from 3 to 33 plants per species per site per visit.

169 *Natural enemy populations*

170 To record predators, whole plant counts (Naveed 2006) were taken from the same true
171 alternative host plant species and from the same sites as selected for population density
172 estimates (see above). The number of plants per sample varied depending variation in
173 abundance (as above); we sampled from 3 to 5 plants per species per site per visit.

174 To assess the prevalence of parasitoid attack, a total of fifty leaves were removed from each
175 species of alternative host plant present at each site on each visit, taking leaves only from those
176 individual plants that harboured both nymphal and adult *A. devastans* and that could also bear
177 *A. devastans* eggs. These leaves were brought back to the laboratory and a 5cm² diameter leaf
178 discs was cut from the centre of each leaf and placed, on moist filter paper, in a 5cm²-diameter
179 petri dish and covered with a lid. Leaf discs were kept at 25±2°C and 65%±3% RH until nymphs
180 of *A. devastans* and adult parasitoids emerged. The proportion of parasitism of the *A. devastans*
181 on each leaf disc was calculated as the number of parasitoids emerged divided by the total
182 number of parasitoids plus *A. devastans* (following Naveed et al. 2011): we assumed that all
183 parasitoids belonged to solitary species, as all identified wasps belonged to egg-parasitoid
184 genera which are either exclusively or predominantly solitary (Jepsen et al. 2007; Segoli and
185 Rosenheim 2013).

186 *Statistical analysis*

187 Data analysis was carried out using the GenStat Statistical Package. As population density data
188 were non-normally distributed, non-parametric tests (Kruskal-Wallis, Spearman's rank
189 correlation) were employed to explore the influences of single recorded explanatory variables
190 (Siegel and Castellan 1988). We were constrained to treat all explanatory variables as random
191 effects. Within Kruskal-Wallis analyses, differences between group averages within treatment
192 categories were evaluated by multiple comparisons tests (Siegel and Castellan 1988). Across
193 similar analyses, significance thresholds were adjusted to control type I error rates using the
194 Bonferroni procedure (Quinn and Keough 2002). Proportion parasitism was analysed using
195 logistic ANOVA (Crawley 1993).

196

197 **Results**

198 *Alternative host plant surveys*

199 In 2009, *A. devastans* was recorded from 48 alternative host plant species belonging to 22
200 taxonomic families (Table 1). Thirty of these species have not previously been recorded as
201 hosts of *A. devastans*. Seven of the alternative host plant species were crops, 5 species were
202 fruit plants, 7 were ornamentals, 17 were vegetables and 12 were weeds. The alternative host
203 plants varied considerably in their growth habit; most were herbs (24 species) with the
204 remainder being climbers (8 species), shrubs (7 species) and trees (5 species). Most of the
205 alternative host plant species were classed as 'abundant' (28 species), followed by 13 'fair' and
206 seven 'rare' plant species in the surveyed area. The majority of the alternative plant species
207 were annuals (32), with only a few perennials (15) and one biennial species (Table 1).

208 Of the recorded alternative host plant species, 24 were categorized as 'true' host plants as these
209 plants harbour both nymphal and adult life stages of *A. devastans*. As the remaining 24 plant
210 species carried only a few adults for short periods, these were categorized as 'incidental' hosts
211 (Table 1): the remainder of this paper focuses on true alternative host plants.

212 The availability of true alternative host plants varied through the year. Weeds, fruit plants and
213 ornamentals were typically available throughout the year and crops were mainly available
214 between March and September (Fig. 2). Some vegetable species were present throughout the
215 year (*Abelmoschus esculentus* and *Solanum melongena*) while others were absent for 2 to 6
216 months: *Pisum sativum* and *S. tuberosum* were absent from April and May, respectively, until
217 October and members of the family Cucurbitaceae (*Citrullus lanatus*, *Cucumis melo* and *C.*

218 *sativus*) were typically absent from around October until around February (Fig. 2); these
219 patterns reflect the annual cycle of cultivation and harvest of each vegetable.

220 ***Pest population density estimates***

221 *Amrasca devastans* population density varied both in time and between true host plant species
222 (Fig. 3). The vegetable *A. esculentus* supported the highest densities of pests. On this species both
223 nymphs and adults were active from March to December, with densities of both peaking around
224 April to May during both 2010 and 2011. In January and February this host species was present
225 but the upper parts had been cut by farmers and *A. devastans* adults and nymphs were absent
226 (Fig. 3). The vegetable *S. melongena* harboured *A. devastans* adults throughout the season from
227 January to December with peak density in November. The presence of multiple nymphal instars
228 throughout the year indicated that breeding took place during all months, but nymphal densities
229 fluctuated greatly and peaked around April to May (Fig. 3). Populations of adult *A. devastans*
230 on *S. tuberosum* fluctuated in the same way as for *S. melongena* but the densities of nymphs were
231 very different, with nymphs present only when adults were present, and at very low density (Fig.
232 3). *Amrasca devastans* was only found on *P. sativum* during March in 2010, and March and
233 January in 2011, but densities were always very low (Fig. 3). The remaining species in the
234 vegetable host type category all showed the same pattern of *A. devastans* abundance, with both
235 adults and nymphs present around May to August and absent in the remaining months of the
236 year (Fig. 3).

237 The crop species *Ricinus communis* harboured adult and nymphal *A. devastans* throughout the
238 year with adult densities peaking in October and peak nymphal densities in May (Fig. 3). On
239 *Helianthus annuus*, adults and nymphal *A. devastans* were present from April to June with
240 maximum densities in April. The remaining crop plant species harboured *A. devastans* from
241 around May until around August (Fig. 3).

242 Among the weeds, *Xanthium strumarium* supported *A. devastans* adults and nymphal stages
243 throughout the period it was present in the field, with maximum adult densities in November
244 and nymphal densities in August. On *Abutilon indicum*, *A. devastans* adults were found for
245 most periods of the year except February, June and July 2010, and February 2011. Nymphs
246 were present throughout observation period except in June of both years. Both nymphal and
247 adult maximum densities were found in September during both the years. However, the weed
248 *Chenopodium murale* carried overwintering *A. devastans* in January and December. Of the
249 remaining weed species, *A. devastans* was present in low numbers from approximately April

250 to December. Plant species belonging to the fruit or ornamental host type categories carried
251 low densities of *A. devastans* adults and nymphs, with peaks occurring in May or June (Fig. 3).

252 Estimates of population densities (mean *A. devastans* per leaf) from true alternative hosts did
253 not differ significantly between 2010 and 2011 (Kruskal-Wallis test: $H=2.71$, $d.f.=1$, $P=0.07$)
254 so the data were pooled before further analysis of influence on the average number of *A.*
255 *devastans* per leaf. Densities of *A. devastans* (nymphs plus adults) were significantly affected
256 by all six of the plant characteristics explored (Table 2). Similarly, when data on nymphal and
257 adult *A. devastans* were analysed separately, there were significant differences in density
258 between plant families (Nymph: $H=408.8$, $d.f.=10$, $P<0.001$; Adults: $H=385.8$, $d.f.=10$,
259 $P<0.001$), with the highest densities on host plants in the family Malvaceae followed by the
260 Euphorbiaceae. Species effects were also found when nymphs and adults were analysed
261 separately (Nymph: $H=558.6$, $d.f.=23$, $P<0.001$; Adults: $H=548.9$, $d.f.=23$, $P<0.001$). Multiple
262 comparisons testing indicated that there were no significant differences in nymph or adult
263 numbers between *A. esculentus*, *R. communis* and *S. melongena*, which harboured the highest
264 densities of the pest.

265 In terms of host plant type, *A. devastans* was most prevalent on vegetables and least common
266 on fruit plants, with densities per plant type category ranging from approximately 0.1 to 1.0
267 individuals per leaf (Fig. 4). Multiple comparisons testing indicated that while numbers of *A.*
268 *devastans* differed across crop types overall (Table 2), differences were significant between
269 vegetables, crops and ornamentals, and not also between weeds and ornamentals. Similar
270 overall results were obtained when data on nymphal and adult *A. devastans* were analysed
271 separately (Nymphs: $H=44.31$, $d.f.=4$, $P<0.001$; Adults: $H=51.84$, $d.f.=4$, $P<0.001$).

272 *Amrasca devastans* prevalence varied significantly across host growth habits (Table 2) and
273 similar results were found for nymphs and adults when analysed separately (Nymphs: $H=59.43$,
274 $d.f.=3$, $P<0.001$; Adults: $H=98.21$, $d.f.=3$, $P<0.001$). Prevalence was greatest on herbs as
275 compared to shrubs, climbers and trees. Annual plants were found to harbour more adult *A.*
276 *devastans* than perennial or biennial plants ($H=11.38$, $d.f.=3$, $P<0.001$) while nymphs were
277 more abundant on perennial plants ($H=5.97$, $d.f.=3$, $P=0.024$). For both nymphs and adults,
278 population densities were greater on abundantly distributed plants than on plants with fair or
279 rare abundances (Nymphs: $H=95.90$, $d.f.=2$, $P<0.001$; Adults: $H=98.88$, $d.f.=2$, $P<0.001$).

280 Populations of *A. devastans* varied significantly between sampling months ($H=210.4$, $d.f.=11$,
281 $P<0.001$) with highest densities observed in May and June (Fig. 1, see also Fig. 3). *Amrasca*

282 *devastans* populations were positively correlated with mean monthly temperature (Spearman's
283 rank correlation test: $r_s=0.664$, $n=12$, $P=0.005$, Fig. 1) and inversely correlated with mean
284 monthly relative humidity ($r_s=-0.510$, $n=12$, $P=0.022$, Fig. 1). Temperature and relative
285 humidity were inversely correlated ($r_s=-0.462$, $n=12$, $P=0.032$, Fig. 1). There was also
286 significant variation across host species during each month (Table 3). *Amrasca devastans*
287 nymphs were most prevalent on *R. communis* from November to March but most prevalent on
288 *A. esculentus* from April to October. Adult *A. devastans* adults were most prevalent on *S.*
289 *tubersum* from November to January and *R. communis* in February and March. As found for
290 nymphs, adults were more prevalent on *A. esculentus* from April to October (Table 3).

291 *Natural enemy populations*

292 The natural enemies of *A. devastans* found on true alternative host plants comprised both
293 predators and parasitoids. Predatory arthropods were spiders (Order: Araneae) and insects: we
294 recorded *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) [green lacewing],
295 Coccinellid beetles (Coleoptera: Coccinellidae) and two genera of hemipterans: *Orius* spp.
296 (Hem.: Anthocoridae), *Geocoris* spp. (Hem.: Lygaeidae). Possible species within these genera
297 were *O. insidiosus* [minute pirate bug] and *G. punctipes* [big-eyed bug], as both have been
298 previously reported within Pakistani cotton agro-ecosystems (Mari et al. 2007). Among these
299 natural enemies, spiders and coccinellids were the most abundant predators, followed by *C.*
300 *carnea* (Table 4). Spiders were species in the families Lycosidae and Thomisidae and
301 coccinellid species included *Coccinella septempunctata* (L.), *C. undecimpunctata* (L.),
302 *Hyperaspis maindronii* Sicard, *Scymnus nubilus* Muslant, *Menochilus sexmaculatus* (F.) and
303 *Brumus suturalis* (F.). Dominant (numerically) coccinellids were *C. septempunctata*, *M.*
304 *sexmaculatus* and *B. suturalis*.

305 Densities of predators were significantly affected by all six of the plant characteristics explored
306 (Table 2). Plants in the family Euphorbiaceae harboured the highest densities of three predators,
307 due to large numbers of spiders, coccinellids and *C. carnea* present on the crop plant *R.*
308 *communis* (Table 4). Overall, predators were around three times more common on crop plants
309 than on vegetables, and least prevalent on weeds, fruiting plants and the one species of
310 ornamental (Table 4). All five groups of predators were found on most types of alternative host
311 plant, except for fruit plants where *Orius* spp. were the only predators found (Table 4, Fig. 5a).
312 Predators were most common on abundant perennial shrub plants (Tables 1, 4.) The only
313 predator found on rare plants was *C. carnea* (Tables 1 & 4).

314 All parasitoids found were hymenopterans in the family Mymaridae: *Arescon enocki* (Subba Rao
315 and Kaur) and *Anagrus* sp. These species oviposit in *A. devastans* eggs (Rao et al. 1968; Sahito
316 et al. 2010) that have been laid inside leaf veins (Agarwal and Krishnananda 1976). Overall,
317 *Anagrus* sp. was more common (58.8% of individual parasitoids) than *A. enocki*. The total
318 numbers of parasitoids that emerged were significantly affected by five of the six of the plant
319 characteristics explored but not by the plant's growth habit (Table 2). Parasitoids were most
320 common on perennial plants and emerged from leaves of abundant plant species only (Tables
321 1, 2, Fig. 6). Parasitoids did not emerge from leaves of weed, ornamental or fruit plant species,
322 but did emerge from three species of vegetables and one species of crop plant (Figs. 5b, 6). Across
323 these four plant species, the overall proportion of *A. devastans* eggs parasitized 0.386 (± 0.03
324 S.E.) and did not differ significantly between plant species (logistic ANOVA corrected for
325 overdispersion: $F_{3,42} = 2.47$, $P = 0.075$, Fig. 6). However, when parasitism by *A. enocki* and
326 *Anagrus* sp. were treated separately, there were significant differences in parasitism across
327 these plant species (*A. enocki*: $F_{3,42} = 21.64$, $P < 0.001$; *Anagrus*: $F_{3,42} = 9.82$, $P < 0.001$, Fig. 6) due
328 to specialism within vegetable species: *Anagrus* sp. was the only parasitoid to emerge from leaves
329 of *C. melo* var. *phutt* and 83.3% of the parasitoids that emerged from *L. aegyptica* were *Anagrus*
330 sp., while on *A. esculentus* only 13.8% of parasitoids that emerged were *Anagrus* sp.

331

332 Discussion

333 Of the 48 plant species that were found to harbour *A. devastans*, 30 were recorded as alternative
334 hosts for the first time. The other 18 species have been previously recorded by Bhatia (1932),
335 Cherian and Kylasam (1938), Rajani (1940), Husain and Lal (1940), Ghani (1946) and
336 Anonymous (1988). Twenty four of these species can be categorized as true alternative hosts
337 (Mound and Marullo 1996) for *A. devastans*, since they carried both adult and nymphal life-
338 history stages, and constitute the focus of this study (the other species are thus incidental hosts,
339 Froudi et al. 2001).

340 There was a clear ranking in terms of the importance of different true alternative host plants
341 for *A. devastans*. Species belonging to the families Malvaceae and Euphorbiaceae were the most
342 exploited by both nymphs and adults, as also found by Rao et al. (1968); in particular, *A.*
343 *esculentus* (okra), *S. melongena* (eggplant) and *R. communis* (castor oil plant) harboured the
344 highest densities of *A. devastans*. *Abelmoschus esculentus* is commonly grown near to cotton
345 fields (Baig et al. 2009) and sometimes intercropped with cotton (R.S. pers. obs.). The highest

346 densities of both nymphal and adult *A. devastans* that were observed on this plant in our study,
347 and also in laboratory evaluations (Ghani 1946), may be due to its chemical properties (crude
348 protein, lignin and nitrogen) being particularly favourable for *A. devastans* (Iqbal et al. 2011).
349 Although *A. esculentus* was present in fields throughout the year, it did not support *A. devastans*
350 populations in the months of January or February (see also Eijaz et al., 2012) possibly due to
351 adverse weather conditions (Chiykowski 1981), lower abundance (Power 1987) and plant
352 maturity (Anitha 2007). Despite regular spraying (farmers typically apply insecticides twice per
353 week once pest infestations have become apparent, R.S. pers. obs.), *A. devastans* populations
354 reached high density during April and May. Similar to *A. esculentus*, the vegetable *S. melongena*
355 is typically cultivated in close spatial association with cotton and *A. devastans* also breeds on this
356 alternative host throughout the year, with regular spraying (Yousafi et al. 2013) constituting a
357 possible cause of the observed fluctuations in adult and nymphal densities.

358 In contrast, *R. communis* is a perennial plant that is cultivated for oilseed on a commercial scale
359 in many countries (Parsons and Cuthbertson 1992); in Pakistan it is grown on a domestic scale on
360 marginal land or near field borders (Hattam and Abbassi 1994). These plants are exposed to
361 relatively little insecticide spray and hence *A. devastans* populations are able to exist on them
362 continuously, with observed fluctuation likely due to the growth stage of the plants and
363 meteorological conditions, as above. These three alternative host plants are thus the main reservoir
364 of *A. devastans* and the primary carry-over source to cotton (see also Huque 1994; Sirivansan
365 2009).

366 Although weed species, particularly *A. indicum* and *C. murale*, harbour comparatively low
367 populations of *A. devastans*, their availability throughout the year and potential to harbour refuge
368 populations when cotton is not present (inter-harvest period) suggests that weeds may play a
369 disproportionately important role in influencing pest dynamics.

370 Our population density studies showed that *A. devastans* persist in the cotton agro-ecosystem
371 throughout the year due to the continuous availability of at least some species of true alternative
372 host plants but the population density on each host plant varied according to its seasonal cycle.
373 These results accord with observations of Setamou et al. (2000) and Barman et al. (2010) who
374 found notable effects of season and growth stage of host plants on population density
375 fluctuation of *Mussidia nigrivenella* (Lepidoptera: Pyralidae) in the maize agro-ecosystem in
376 Benin and of *Lygus hesperus* (Hemiptera: Miridae) in the cotton agro-ecosystem in Texas
377 (USA) respectively.

378 In the cotton agro-ecosystem we observed, the usage of true alternative host plants by *A.*
379 *devastans* peaked in May and June, when temperatures were highest and humidity was lowest:
380 high pest densities on preferred alternative host plants are likely to promote local dispersal of
381 *A. devastans* individuals onto other available plant species. In a study of *A. devastans*
382 populations within cotton crops, Naveed (2006) concluded that both warm and humid weather
383 promoted pest population growth: the difference between this and our findings may be due to
384 the differing foci on cotton and non-cotton alternative hosts. In most areas of the Southern
385 Punjab, cotton sowing commonly starts in May (Ali et al. 2011), which coincides with the
386 greatest build-up of *A. devastans* populations. Hence, shortly after cotton seedling emergence,
387 *A. devastans* individuals are likely to migrate from nearby alternative vegetable, crop and weed
388 hosts into the cotton crop, leading to severe infestation and possibly the complete failure of the
389 crop (Ghani 1946). Chemical control is the only tactic being widely used by farmers to protect
390 the cotton crop from *A. devastans* infestation (Razaq et al. 2013). Harmful effects of pesticide
391 usage are well documented by many authors (Zhang et al. 2011; Zidan 2012). Due to excessive
392 and sole reliance on insecticides, *A. devastans* has now developed resistance against pyrethroid
393 insecticides (Ahmad et al. 1999).

394 In developed countries agriculturalists have reduced pesticide usage by employing biological pest
395 control (e.g. Bari and Sardar 1998; Tscharntke 2000; Thacker 2002; Gray et al. 2009). *Orius* sp.,
396 *G. punctipes*, *C. carnea*, Coccinellid spp. and spiders are all common predators of *A. devastans*
397 (Mallah et al. 2001; Vennila et al. 2007). We found the highest numbers of predators on crop
398 and vegetable alternative host plants, especially *R. communis*. *Ricinus communis* may provide a
399 favourable habitat for predatory arthropods due to relative low exposure to pesticides (see above)
400 or because its perennial bushy canopy provides both shelter during adverse environmental
401 conditions and harbours prey throughout the year. Further, *C. carnea* adults feed on *R. communis*
402 pollen (Sattar 2010).

403 In addition to the predators, two species of egg parasitoids commonly attacked *A. devastans* on
404 some vegetable and crop alternative host plants. Egg parasitoids may be particularly effective
405 in reducing damage by phytophagous species because hosts are parasitized prior to their
406 feeding on the plant (Wajnberg and Hassan 1994). However, our estimate of *A. devastans*
407 parasitism (38.6%) is only slightly greater than an empirically estimated minimum threshold
408 of 32-36% for biological control success (Tscharntke 2000), and we found no evidence for
409 parasitoid attack on other alternative plant species; this casts doubt on whether parasitoid action
410 alone could be sufficient to control *A. devastans* across the agro-ecosystem. *Arescon enocki* was

411 predominant on *A. esculentus* (see also Sahito et al. 2010) and *R. communis* and *Anagrus* sp. was
412 predominant on *C. melo* var. *phutt* and exclusive *L. aegyptica*. This variation is potentially due to
413 differing availability of nectar or differences in plant volatile profiles or plant morphology (e.g.
414 Micha et al. 2000; Kennedy 2003; Jervis and Heimpel 2005) or plant mediated outcomes to
415 competitive interactions between the parasitoid species (Hawkins 2000; Tschamntke 2000).

416 Given that there are at least seven species of natural enemies of *A. devastans* present on alternative
417 host pants, there is potential for these predators and parasitoids to suppress *A. devastans*
418 population outside of, and within, the cotton crop. The degree of any suppression will, however,
419 be dependent on many interrelated factors, which include the abundance of the natural enemy
420 populations, the extent and consequences of any competitive interactions between species (intra-
421 guild predation: Rosenheim et al. 1995; Hawkins 2000), the susceptibility of natural enemies to
422 pesticides (Tschamntke 2000) and the potential for the natural enemies to migrate from alternative
423 host plants into the cotton crop during the growing season, and out of the cotton crop at harvest
424 (Tschamntke 2000). Such factors will ultimately determine whether each species of alternative host
425 plant acts more as a source of natural enemies or as a source of *A. devastans*. It is also possible
426 that further plant species (that do not harbour *A. devastans* and are thus not among the ‘alternative
427 host plants’ we surveyed), could harbour different species of insect herbivores and serve as sources
428 of generalist natural enemies of *A. devastans*, thus additionally influencing the population biology
429 of this pest.

430 **Conclusions and recommendations**

431 In conclusion, our study has shown that alternative host plants can harbour *A. devastans*
432 populations and thus have high potential to act as reservoirs of pest individuals which can then
433 migrate into the cotton crop. These reservoirs will be particularly important during the inter-
434 harvest period, when cotton plants are not present. In this respect the presence of alternative
435 host plants is disadvantageous to the cotton agro-ecosystem but the disadvantage is mitigated
436 in two ways: first, alternative host plants harbour natural enemies of *A. devastans* and, second,
437 many alternative host plants are vegetables, crops and fruits and thus agriculturally beneficial
438 in their own right. The relative pros and cons of their presence in cotton growing areas are thus
439 not straightforward to evaluate, but our results indicate that the characteristics of given species
440 of alternative host plant species, such as type, growth habit, perenniality and abundance, will
441 influence this balance. This evaluation was based on a series of regular field surveys in which
442 the composition and numbers of plant species at each site and survey date, and thus the plant
443 characteristics examined, were not under experimental control. Further work may be required

444 to tease apart the influences of phylogenetically non-independent characters, such as type,
445 growth habit and perenniality.

446 Given current evidence, we recommend the following actions to reduce damage by *A.*
447 *devastans* via integrated pest management: (1) Remove alternative weeds host plants from
448 cotton fields and their vicinity. (2) Avoid intercropping and cultivation of the vegetables *A.*
449 *esculentus* and *S. melongena* in cotton fields, and also avoid growing the perennial *R. communis*
450 near cotton fields or in field margins. Despite harbouring natural enemies, these three species
451 harbour the highest densities of *A. devastans* throughout the year and thus appear to constitute
452 important carryover sources of the pest. (3) Avoid frequent use of pesticides on vegetables: when
453 applications are necessary, use selective insecticides which have minimal effects on natural enemy
454 species. (4) Modify the timing of sowing to desynchronize the period during which cotton plants
455 are in the early seedling stage, and especially vulnerable to *A. devastans* attack, from the peak
456 period of pest density.

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459

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466

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Table 1. Alternate host plants of the *Amrasca devastans* recorded during 2009-2010

Plant characteristics						Results		
Family	Host plant	Vernacular name	Host type ¹	Growth habit ²	Perenniality ³	New host record ⁴	Status ⁵	Abundance ⁶
Amaranthaceae	<i>Achyranthes aspera</i> L.	Phuttkanda	Weed	Shrub	Biennial	Yes	True	Abundant
	<i>Digera arvensis</i> Forsk	Diagra, Tandla	Weed	Herb	Annual	Yes	Incidental	Abundant
Apiaceae	<i>Corianderum sativum</i> L.	Dhania, coriander	Vegetable	Herb	Annual	Yes	Incidental	Fair
Asteraceae	<i>Helianthus annuus</i> Linn.	Sunflower	Crop	Herb	Annual	No	True	Abundant
	<i>Xanthium strumarium</i> L.	Cocklebur	Weed	Herb	Annual	Yes	True	Abundant
	<i>Gerbera jamesonii</i> Adlam	Gerbera	Ornamental	Herb	Perennial	Yes	Incidental	Rare
Bignoniaceae	<i>Tecoma stans</i> Juss.	Tecoma	Ornamental	Shrub	Perennial	Yes	Incidental	Rare
Boraginaceae	<i>Cordia dichotoma</i> G. Forst	Lasora	Fruit	Tree	Perennial	Yes	True	Rare
Brassicaceae	<i>Brassica rapa</i> L.	Turnip	Vegetable	Herb	Annual	Yes	Incidental	Abundant
	<i>B. campestris</i> var. <i>sarson</i>	Sarson	Vegetable	Herb	Annual	Yes	Incidental	Abundant
	<i>Raphanus sativus</i> L.	Radish	Vegetable	Herb	Annual	Yes	Incidental	Abundant
Chenopodiaceae	<i>Chenopodium murale</i> L.	Karund	Weed	Herb	Annual	Yes	True	Abundant
	<i>Chenopodium album</i> L.	White goosefoot, Bathoo	Weed	Herb	Annual	Yes	Incidental	Abundant
	<i>Spinacea oleraceae</i> L.	Spinach	Vegetable	Herb	Annual	Yes	Incidental	Abundant
Convolvulaceae	<i>Convolvulus arvensis</i> L.	Lehli	Weed	Climber	Perennial	Yes	Incidental	Abundant
Cucurbitaceae	<i>Cucumis melo</i> L. var. <i>phut</i>	Phutt	Vegetable	Climber	Annual	Yes	True	Abundant
	<i>C. melo</i> L. <i>sativus</i>	Muskmelon	Vegetable	Climber	Annual	Yes	True	Abundant
	<i>C. sativus</i> L.	Cucumber	Vegetable	Climber	Annual	Yes	True	Abundant
	<i>Citrullus lanatus</i> (Thumb) Mansf.	Watermelon	Vegetable	Climber	Annual	No	True	Fair
	<i>Lagenaria vulgaris</i> Ser.	Gourd, Kaddu	Vegetable	Climber	Annual	No	True	Abundant
	<i>Luffa aegyptica</i> Mill.	Sponge gourd, Tori	Vegetable	Climber	Annual	No	True	Abundant
	<i>Cucurbita pepo</i> L. var. <i>melopepo</i>	Squash	Vegetable	Climber	Annual	Yes	Incidental	Fair
Cyperaceae	<i>Cyperus rotundus</i> L.	Deela	Weed	Herb	Perennial	Yes	Incidental	Abundant
Euphorbiaceae	<i>Ricinus communis</i> L.	Castor oil plant	Crop	Shrub	Perennial	No	True	Abundant
Labiatae	<i>Ocimum basilicum</i> L.	Niazboo	Ornamental	Herb	Annual	Yes	Incidental	Rare
Leguminosae	<i>Trifolium alexandrinum</i> L.	Barseem	Crop	Herb	Annual	Yes	Incidental	Fair
Malvaceae	<i>Abelmoschus esculentus</i> L.	Okra, Bhindi, ladies' fingers, gumbo	Vegetable	Herb	Annual	No	True	Abundant
	<i>Abutilon indicum</i> Sweet	Mallow, Kanghi	Weed	Shrub	Annual	No	True	Abundant
	<i>Hibiscus rosa-sinensis</i> L.	China rose	Ornamental	Shrub	Perennial	No	Incidental	Rare
	<i>Malvaviscus arboreus</i> Cav. Diss	Cocks comb	Ornamental	Shrub	Perennial	Yes	Incidental	Rare
Moraceae	<i>Morus laevigata</i> L.	Shahtoot	Fruit	Tree	Perennial	Yes	Incidental	Fair
Myrtaceae	<i>Syzygium cumini</i> L. Skeels.	Jaman	Fruit	Tree	Perennial	Yes	Incidental	Fair
Pedaliaceae	<i>Sesamum indicum</i> L.	Sesame, Til	Crop	Herb	Annual	No	True	Rare
Papilionaceae	<i>Pisum sativum</i> L.	Peas	Vegetable	Shrub	Annual	No	True	Abundant
	<i>Cyamopsis tetragonoloba</i> L.	Guar	Crop	Shrub	Annual	Yes	True	Fair
	<i>Phaseolus mungo</i> L. Hepper	Rawan	Crop	Herb	Annual	No	True	Fair
Rhamnaceae	<i>Zizyphus mauritiana</i> Lamk	Ber	Fruit	Tree	Perennial	Yes	Incidental	Abundant
Rosaceae	<i>Rosa indica</i> L.	Rose	Ornamental	Shrub	Perennial	Yes	Incidental	Fair
Solanaceae	<i>Solanum melongena</i> L.	Brinjal (eggplant, aubergine)	Vegetable	Herb	Annual	No	True	Abundant
	<i>S. inacum</i> Dunal	Ester white egg plant	Ornamental	Herb	Annual	No	True	Fair
	<i>S. tuberosum</i> L.	Potato	Vegetable	Herb	Annual	No	True	Abundant
	<i>S. nigrum</i> L.	Mako	Weed	Herb	Annual	Yes	Incidental	Abundant
	<i>Nicotiana tabacum</i> L.	Common tobacco	Crop	Herb	Annual	No	True	Fair
	<i>Datura metel</i> L.	Thornapple, Datoora	Weed	Shrub	Annual	No	True	Abundant
	<i>Physalis alkakengi</i> L.	Mamola	Weed	Herb	Perennial	Yes	Incidental	Abundant
	<i>Capsicum frutescens</i> L.	Chillies	Vegetable	Herb	Annual	No	Incidental	Abundant
	<i>Withania somnifera</i> Dunal	Winter cherry, Aksen	Weed	Shrub	Perennial	Yes	Incidental	Fair
Tiliaceae	<i>Grewia asiatica</i> L.	Falsa	Fruit	Tree	Perennial	No	True	Fair

Notes:

^{1,2,3,5,6} Represent the categories of host plants scored according to Mound and Marullo (1996); Attique et al. (2003); Arif et al. (2009); Tiple et al. (2010); Li et al. (2011)

⁴ Yes = New alternative host plants in Pakistan with no previous world record; No= alternative host plants previously reported by Bhatia (1932), Cherian and Kylasam (1938), Rajani (1940), Husain and Lal (1940), Ghani (1946), Anonymous (1988)

Table 2. Effects of true alternative host plant variables on population density of *Amrasca devastans* and its natural enemies. Results are from Kruskal-Wallis one-way analyses of variance on pooled numbers of adult and nymphal *Amrasca devastans* and on predators (5 species pooled) and parasitoids (2 species) for 2010 and 2011. Host plant variables are as in Table 1.

Explanatory variable	d.f.	H value	P ^a
<i>Amrasca devastans</i>			
Family	10	426.5	< 0.001
Species	23	586.6	< 0.001
Type	4	50.36	< 0.001
Growth habit	3	89.91	< 0.001
Perenniality	2	9.62	0.003
Abundance	2	97.18	< 0.001
Predators			
Family	10	116.0	< 0.001
Species	23	166.7	< 0.001
Type	4	42.36	< 0.001
Growth habit	3	24.50	< 0.001
Perenniality	2	14.12	< 0.001
Abundance	2	22.98	< 0.001
Parasitoids			
Family	10	23.57	< 0.001
Species	23	37.02	< 0.001
Type	4	3.19	< 0.001
Growth habit	1	1.72	0.018 NS ^a
Perenniality	2	3.79	< 0.001
Abundance	2	3.19	< 0.001

^a Because 6 tests were carried out for each category of organisms we adjusted the significance criterion, according to the Bonferroni procedure, to be 0.05/6, i.e. <0.0083.

Table 3. Monthly variation in *Amrasca devastans* populations across true alternative host plant species

Data are pooled across 2010 and 2011.

Month	Preferred host plant	Difference across 24 host species		
		d.f.	H	P ^a
<i>Nymphs</i>				
January	<i>Ricinus communis</i>	23	71.3	< 0.001
February	"	23	59.9	< 0.001
March	"	23	72.1	< 0.001
April	<i>Abelmoscus esculentus</i>	23	114.0	< 0.001
May	"	23	133.6	< 0.001
June	"	23	113.3	< 0.001
July	"	23	114.8	< 0.001
August	"	23	114.3	< 0.001
September	"	23	136.1	< 0.001
October	"	23	90.8	< 0.001
November	<i>Ricinus communis</i>	23	83.8	< 0.001
December	"	23	83.6	< 0.001
<i>Adults</i>				
January	<i>Solanum tubersum</i>	23	85.9	< 0.001
February	<i>Ricinus communis</i>	23	49.9	< 0.001
March	"	23	71.3	< 0.001
April	<i>Abelmoscus esculentus</i>	23	134.9	< 0.001
May	"	23	124.0	< 0.001
June	"	23	112.3	< 0.001
July	"	23	123.5	< 0.001
August	"	23	143.3	< 0.001
September	"	23	141.1	< 0.001
October	"	23	84.3	< 0.001
November	<i>Solanum tubersum</i>	23	93.4	< 0.001
December	"	23	94.9	< 0.001

^a Because 12 tests were carried out for each *A. devastans* life history stage we adjusted the significance criterion, according to the Bonferroni procedure, to be 0.05/12, i.e. <0.0042: all results were significant at this more stringent level.

Table 4. Mean numbers of arthropod predators on true alternative host plants.
Numbers shown are means from up to 5 plants per species per site per visit, pooled across all sites and across two sampling years.

Host plant type and species	Predator					Overall Mean
	<i>Orius</i> spp. Minute pirate bug	<i>Geocoris</i> spp. Big eyed bug	<i>Chrysoperla</i> <i>carnea</i> Green lacewing	Coccinellid spp. Lady beetles	<i>Araneae</i> spp. Spiders	
Vegetable						
Mean	2.26	1.77	1.34	1.26	3.70	2.06
<i>Abelmoschus esculentus</i>	1.15	0.09	1.42	1.10	5.55	1.86
<i>Citrullus lanatus</i>	0.85	1.35	0.60	0.50	1.75	1.01
<i>Cucumis melo</i>	1.65	0.60	0.50	0.90	1.35	1.00
<i>Cucumis melo</i> var. <i>phutt</i>	5.35	4.25	0.60	1.10	7.50	3.76
<i>Cucumis sativus</i>	0.60	0.75	1.15	1.10	3.10	1.34
<i>Lagenaria vulgaris</i>	7.50	7.50	0	5.00	0	4.00
<i>Luffa aegyptica</i>	3.60	0	0.25	1.00	2.75	1.52
<i>Pisum sativum</i>	0	0	0	0.50	0.35	0.17
<i>Solanum melongena</i>	1.85	3.15	3.85	1.35	9.60	3.96
<i>Solanum tuberosum</i>	0	0	5.00	0	5.00	2.00
Crop						
Mean	2.13	0.23	4.86	7.93	15.31	6.09
<i>Cyamopsis</i> <i>tetragonoloba</i>	0	0	1.15	0	9.15	2.06
<i>Helianthus annuus</i>	0.25	1.35	2.85	2.60	5.10	2.43
<i>Phaseolus mungo</i>	5.00	0	3.75	0	2.50	2.25
<i>Nicotiana tabaccum</i>	0	0	0	0	1.35	0.27
<i>Ricinus communis</i>	7.50	0	11.40	45.00	73.75	27.53
<i>Sesamum indicum</i>	0	0	10	0	0	2.00
Weed						
Mean	0.50	0.67	0.75	2.48	1.00	1.08
<i>Abutilon indicum</i>	0	3.35	0	1.00	0	0.87
<i>Achyranthes aspera</i>	0	0	0	0.09	0	0.02
<i>Chenopodium murale</i>	0	0	0	10.00	0	2.00
<i>Datura metel</i>	0	0	0	0.08	0	0.02
<i>Xanthium strumarium</i>	2.50	0	3.75	1.25	5.00	2.50
Ornamental						
<i>Solanum incanum</i>	0.25	1.00	0.90	0.15	2.75	1.01
Fruit						
Mean	1.25	0	0	0	0	0.25
<i>Cordial dichotoma</i>	0	0	0	0	0	0
<i>Grewia asiatica</i>	2.50	0	0	0	0	0.50
Overall mean	1.69	0.97	1.97	3.03	5.69	2.67

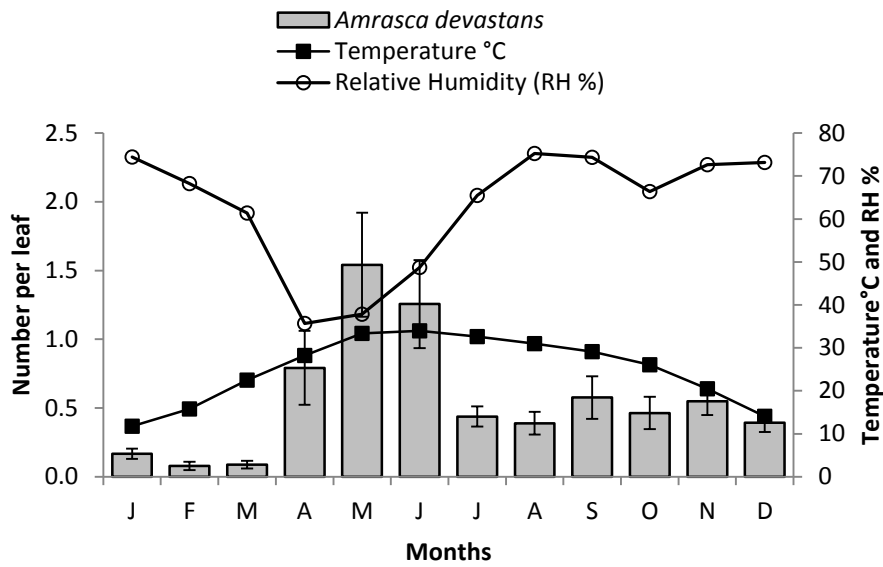


Fig. 1 Seasonal fluctuation (\pm S.E.) of *Amrasca devastans* on true alternative host plants. All data are pooled across 2010 and 2011. *A. devastans* bars represent nymphs plus adults. Meteorological data were obtained from the Central Cotton Research Institute, Multan

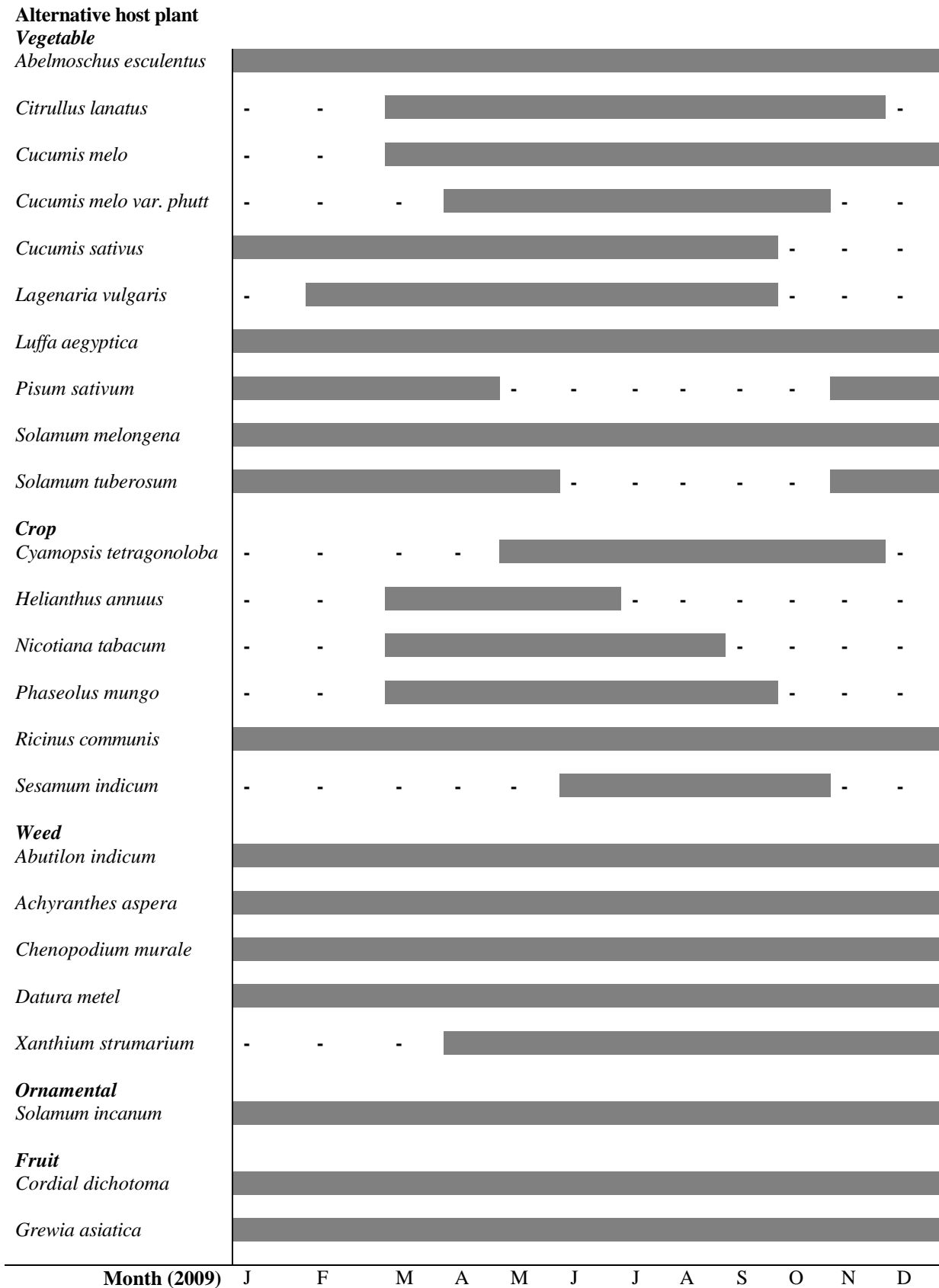


Fig. 2 Temporal availability of true alternative host plants of *Amrasca devastans*. Cotton is commonly sown from early May and remains in the field until harvest in October each year (indicated by line below months)

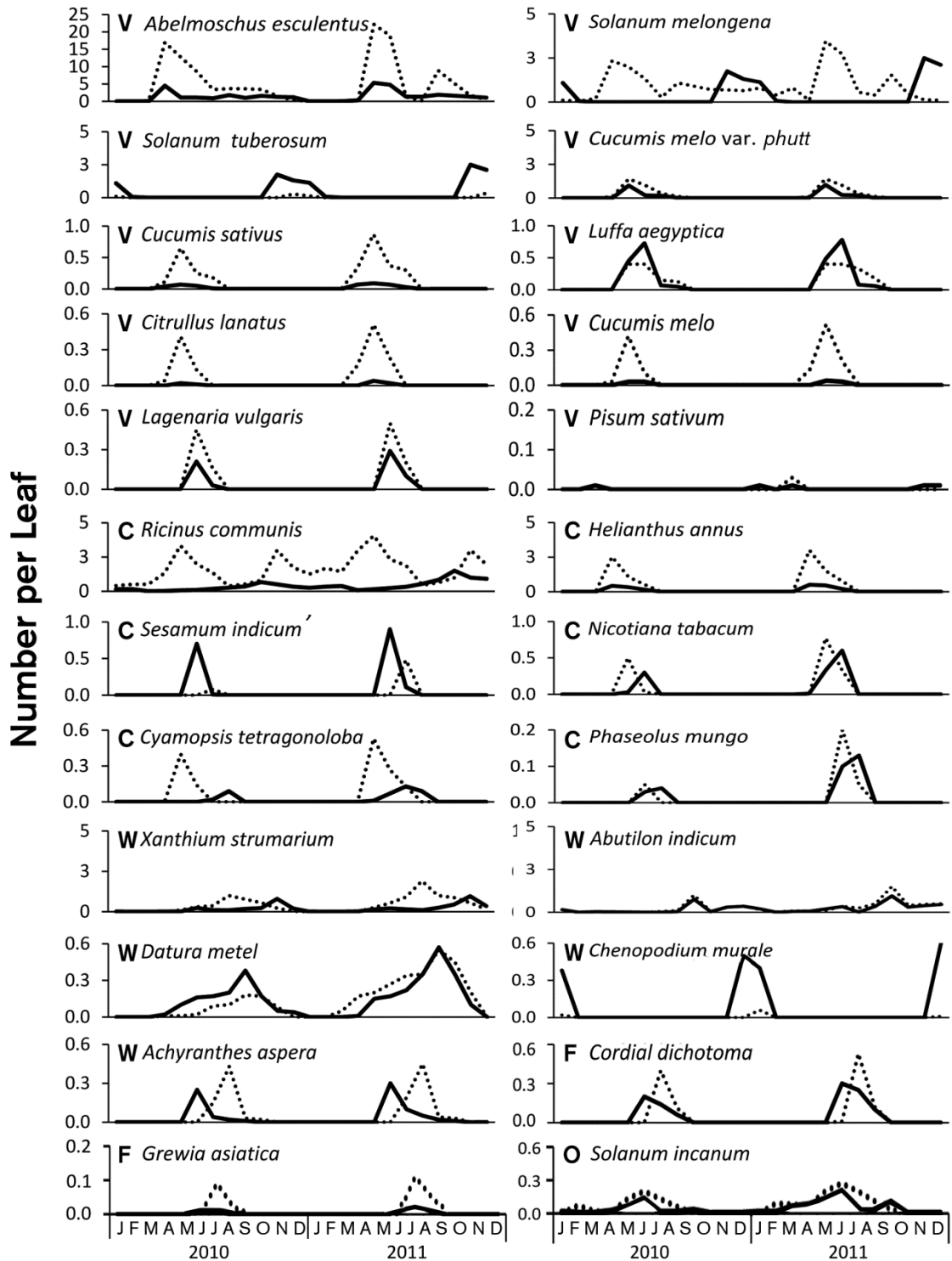


Fig. 3 Seasonal prevalence of *Amrasca devastans* on true alternative host plants.

Dotted lines indicate data on nymphs, solid bold lines indicate adults. F, O, C, W and V respectively indicate fruit, ornamental, crop, weed and vegetable plants. Note that different panels have different y-axis scales

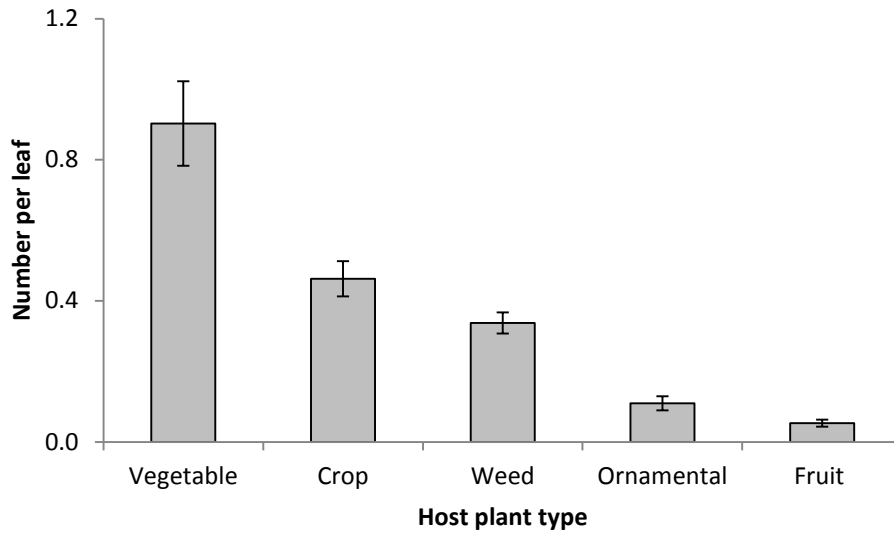


Fig. 4 Mean number (\pm S.E.) of *Amrasca devastans* on different true alternative host plant types (pooled data for 2010 and 2011, nymphs plus adults). The numbers of *A. devastans* differed significantly across host plant types overall but comparisons were not significantly different between vegetables, crops and ornamentals, and not also between weeds and ornamentals.

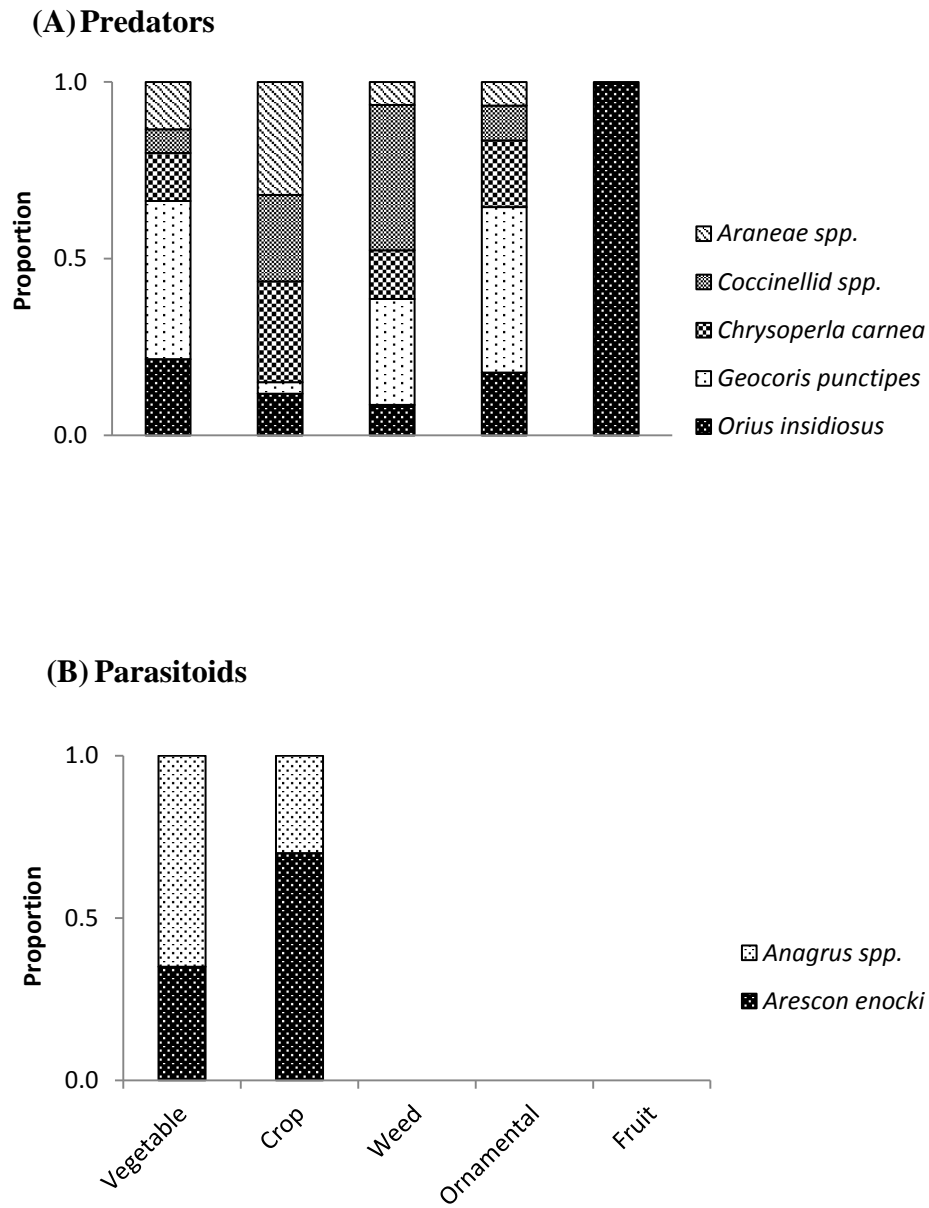


Fig. 5 Contribution of true alternative host plant types for carrying natural enemies of *Amrasca devastans* during the survey period. (A) predators, (B) parasitoids

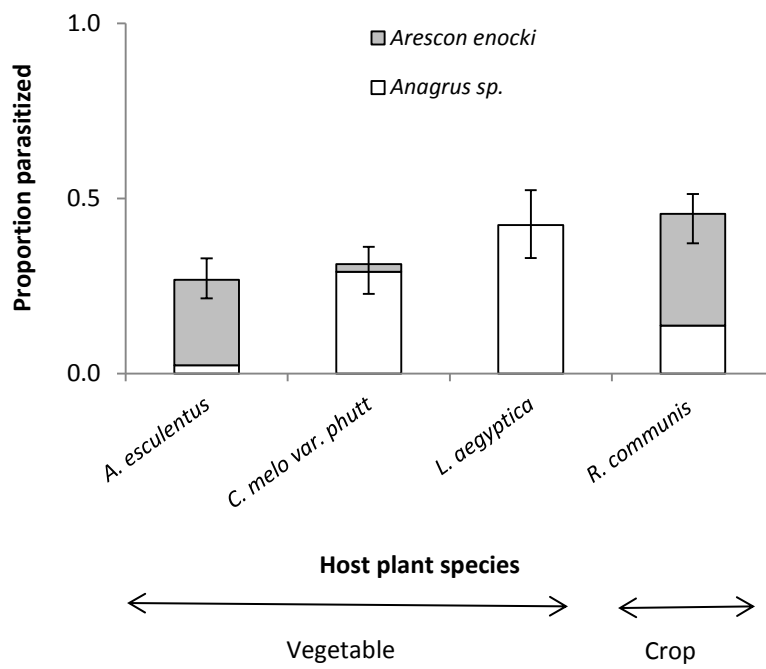


Fig. 6 Mean (\pm S.E.) parasitism of *Amrasca devastans* eggs laid on true alternative host plant species