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The effect of banker plant species on the fitness of *Aphidius colemani* Viereck and its aphid host (*Rhopalosiphum padi* L.)

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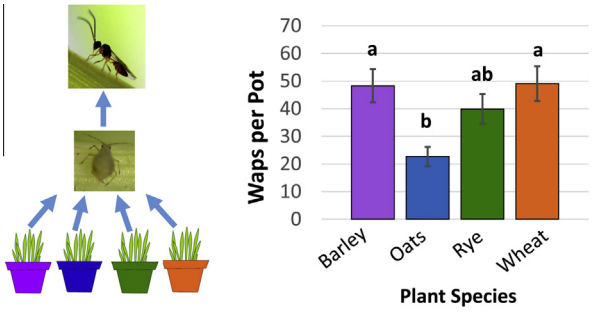
HIGHLIGHTS

- Plant effects were investigated for open rearing of *A. colemani* on *R. padi*.
- Cultivars within each grain species tested did not significantly affect outcomes.
- Wasp emergence was lowest from aphids reared on Oats; sex ratio was low on Rye.
- As plant species had varying effects on *A. colemani*, no optimal grain was identified.

GRAPHICAL ABSTRACT



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ABSTRACT

Banker plants, a type of open-rearing unit, are increasingly used in greenhouse crops to sustain natural enemy populations at times of low pest abundance. The most common banker plant system is a non-crop, cereal plant which supports *Rhopalosiphum padi* L. as an alternative host for *Aphidius colemani* Viereck. Although bottom-up effects of plants are known to affect natural enemies, this aspect has generally been ignored in previous investigations of banker plant efficacy. Here, we tested four cereal plant species with three varieties each to investigate host plant effects on *R. padi* and *A. colemani*. Though limited differences were observed in laboratory experiments spanning one aphid or parasitoid generation, longer greenhouse experiments spanning several generations revealed significant plant effects on both insects. *R. padi* performed poorly on oats (*Avena sativa* L.), resulting in wasps with the longest female development time, lowest emergence rates, and the lowest number of wasps produced per unit. Rye (*Secale cereal* L.) – intermediate in terms of aphid performance – produced a significantly male-biased wasp population with the smallest males. Conversely, *R. padi* placed onto either wheat (*Triticum aestivum* L.) or barley (*Hordeum vulgare* L.) performed consistently well in terms of aphid and parasitoid fitness and abundance, though neither species was obviously superior over the other. Overall, cultivars within each plant species did not significantly affect outcomes. As each plant species tested had different positive effects on aphid and parasitoid phenotypes, the potential benefits of mixing of cereal species is an area for future investigation.

1. Introduction

Open-rearing systems for natural enemies of greenhouse pests (a.k.a. "banker plants") are an increasingly-popular tool in integrated pest management (IPM) within greenhouse crops, to the point where some types are now available commercially (Huang et al., 2011). Banker plants provide resources, such as food, prey, or hosts, for biological control agents. Typically, banker plants consist of a non-crop plant that is infested with non-pestiferous herbivores to serve as alternative hosts or prey for parasites or predators (though see Stacey, 1977 and Wong and Frank, 2012 for

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other types of banker plants). Using this system, natural enemy survival and reproduction are decoupled from pest abundance, allowing natural enemies to remain in the habitat when pest abundance is low (e.g. Bennison, 1992). This can also reduce the density and frequency of natural enemy releases required to maintain pest suppression. Lastly, banker plants provide growers with "fresh" predators or parasitoids, which are likely more efficacious than insects that have spent several days in transit to the grower (Huang et al., 2011). Research on banker plant efficacy is limited, despite their potential benefits, and the reported success of banker plants have been mixed (e.g. Bennison and Corless, 1993; Jacobson and Croft, 1998; van Driesche et al., 2008; Wong and Frank, 2012; Prado and Frank, 2014). For banker plants to become a greater component of greenhouse IPM programs they must produce predictable results, and be effective and easy to use. Furthermore, many growers are interested in producing their own banker plants to further cut down on costs (Huang et al., 2011). We consider it a priority to provide information to growers and industry specialists regarding the best banker plant species to invest time, money and effort in.

Overall, the efficacy of banker plants relies on the prolonged ability of the alternative prey to support a larger natural enemy population than could be supported by the pest alone. Currently, the most widely-used banker plant system in greenhouse crops consists of a cereal plant (e.g. oats) that supports populations of bird-cherry oat aphids, *Rhopalosiphum padi* L. (Hemiptera: Aphididae). Because *R. padi* feeds only on grasses (Poaceae), it is not a threat to most greenhouse vegetable and ornamental crops, yet can serve as an alternative host for *Aphidius colemani* Viereck (Hymenoptera: Braconidae: Aphidiinae). This wasp is a primary parasitoid of two important greenhouse pest aphids: melon aphid, *Aphis gossypii* Glover, and green peach aphid, *Myzus persicae* (Sulzer), but can also parasitize > 40 different aphid species (Stary, 1975), including *R. padi* (Elliott et al., 1994). Although many different grass species (e.g. wheat, maize, millet, barley, oats, corn and wild grasses) have been used by researchers in investigations of the *R. padi–A. colemani* open-rearing system (Frank, 2010), no research has comprehensively compared these plants to determine which best supports *R. padi* and *A. colemani* populations.

There are many consequences for banker plant efficacy that could be incurred via the lowest trophic level. Herbivorous insects feeding on low quality plants – due to inadequate nutrition, defensive chemicals or lack of host adaptation – may grow and reproduce more slowly, may be smaller in size, less nutritious, or even toxic (Price et al., 1980). Were this to occur, it would likely reduce the number of available hosts for parasitoid reproduction, directly affecting parasitoid abundance (Turlings and Benrey, 1998). Perhaps just as importantly, such low quality herbivores can also have indirect effects on parasitoids. These include increased parasitoid development time, and reduced female sex ratio, size, fecundity, survival, and longevity (Fox et al., 1990; Idris and Grafius, 1996; Benrey and Denno, 1997; Eben et al., 2000; van Emden and Kifle, 2002; Cicero et al., 2012). Such effects have been shown to translate into reduced biological control by parasitoids in greenhouse crops (Bentz et al., 1996; Jansson, 2003).

To test our prediction that the species of cereal used as the banker plant can affect the quality of aphid parasitoids, we conducted a series of laboratory and greenhouse experiments to determine the development rates and reproductive output of the aphid host *R. padi* and the parasitoid *A. colemani* on several common cereal crops. We also investigate how these aphid-plant combinations interact to affect *R. padi* abundance and *A. colemani* quality and abundance over time. We use these results to suggest methods to optimize the open rearing of *A. colemani* in greenhouses.

2. Materials and methods

2.1. Plant material and maintenance

Seeds for all cultivars of barley, oat, rye and wheat were obtained from Wyatt-Quarles Seed Company (Garner, NC); see Table 1 for cultivars tested. For the experiment in Section 2.3.1, plants were grown a growth chamber set at 25 ± 1 °C and ca. 40–50% RH. For all other experiments, plants were grown in research greenhouses in Raleigh, NC under ambient light conditions (avg. temp = 28 °C). Plants were watered as needed (generally twice a week) and received a 14-14-14 (N-P_2O_5-K_2O) fertilizer mix through the additional of 250 mL of Osmocote® (The Scotts Company LLC, Marysville, OH) mixed throughout 79 L of potting mix (2B Mix; Fafard®, Anderson, SC).

2.2. Insects

A polyclonal colony of *R. padi* was started using approximately 35 aphids of mixed instar, obtained from winter cover crops from 4–5 sites in NC from January to March 2009. Aphids were reared on a mix of all cereal plant types listed in Table 1 for ca. 10 generations before experiments began. In all cases, aphids were randomly chosen from plants within the colony, thus aphids were of known instar, but unknown age. Aphids also had the potential to be either naïve or experienced with the host plant upon which they were being placed (being statistically more likely to be naïve). We acknowledge that aphid fitness has the potential to be affected by previous (natal) host. However, this situation more closely reflects conditions faced by a grower interested in starting their own banker plant system. Here, growers would likely obtain grain seeds from the easiest available source, which is unlikely to match the host plant species/cultivar of commercially-reared *R. padi* populations.

A. colemani were obtained as aphid mummies from Koppert Biological Systems Inc. (Howell, MI). The natal host of these *A. colemani* was a greenhouse pest aphid (likely *M. persicae*), reared on a non-grain plant (van Schelt, Koppert Biological Systems, personal communication). Mummies were placed in 60 × 60 × 60 cm cages made from PVC pipe wrapped in organza fabric until wasps emerged. Mummies and wasps were kept in a laboratory at ambient conditions (ca. 21 ± 2 °C and 30–40% RH) with a 5% honey-water solution using a moistened dental wick placed in a beaker as a food source for adult wasps until use in experiments. Females were used in all experiments within 24 h of emergence; the sex of the wasps used was confirmed using a dissecting scope.

2.3. Effect of banker plant species and cultivar on R. padi fitness and abundance

2.3.1. Aphid development and fecundity at constant temperatures

To study potential effects of banker plant species and cultivar on the fitness of *R. padi* at a constant temperature, three cultivars of each of barley, oat, rye and wheat were planted separately in 10 cm pots (n = 15 for each species/cultivar combination in

Table 1
Cereal species and cultivars tested.

Plant species	Cultivar		
	1	2	3
Barley, *Hordeum vulgare* L.	Nomini a	Price	Thoroughbred
Oats, *Avena sativa* L.	90–6590	Brooks	Rodgers
Rye, *Secale cereal* L.	AGS104 a	Wren 96	Wren Abrozzi
Wheat, *Triticum aestivum* L.	Neuse	Roane	USG 3209

Table 1), with two seeds per pot. Seedlings were thinned to 1 plant per pot after germination using scissors to cut the extra seedling at soil level. When plants reached 8 cm tall they were infested with two arbitrarily selected apterous aphids from grain plants within the aphid colony. Plants were individually covered with a cage made from a soda bottle and placed in a growth chamber at 25 ± 1 °C and 60% RH. Specifically, clean, 0.5 L soda bottles had their bottoms cut off 17 cm from the cap and the bottom edge was inserted into the soil of each pot (ca. 2 cm deep). Each bottle had two 2.5 cm diam. holes (cut in opposing sides) and a 2.5 cm diam. hole in the lid, all covered with thrips-proof screening, for ventilation. Aphids were allowed to reproduce freely for 24 h, at which time all but one aphid nymph was removed. The remaining nymph was observed at 4–8 h intervals (6:00, 10:00, 14:00, 18:00 and 22:00) for molting and survival until the first appearance of new nymphs. Nymphs that died were often difficult to detect if they fell on the soil surface; there was also the possibility that "missing" aphids actually abandoned the plant due to unsuitability. As the consequences of death or dispersal are likely the same in this case, all "missing" aphids were assumed to be dead. Larviposition was quantified daily and all nymphs laid within a 24 h interval were removed with a fine paintbrush. The daily quantification of new nymphs was stopped after the first 48 h period with no new nymphs. The adult aphids from every replicate were then preserved in 70% ethanol. To determine if there was a relationship between size and fecundity, hind tibial length of a subset of aphids was measured using a dissecting microscope with an ocular micrometer. Hind tibial length is positively correlated with dry mass in aphids, and thus is considered an appropriate proxy for size (see Nicol and Mackauer, 1999).

2.3.2. Aphid development and fecundity at fluctuating high temperatures

The experiment outlined in Section 2.3.1 was repeated during July 2009 to assess aphid life table parameters when reared on banker plants under higher (Summer) temperatures. Methodology was identical to that above, except that plants were kept within an environmentally controlled greenhouse compartment instead of growth chambers, and aphids were observed four times per day (instead of five times) for the onset of reproduction (i.e. 7:00, 11:00, 15:00 and 19:00). Temperature readings were taken at each observation point. Average daily temperature within the greenhouse compartment was 30.0 ± 0.5 °C (range: 26.0–34.4 °C). Aphid size was not recorded for this experiment.

2.3.3. Aphid abundance over time

Experiments were conducted in a research greenhouse to determine how host plant species and cultivar affected abundance of *R. padi* over several generations. The experiment was conducted in September 2009, with average daily temperatures of 28.0 ± 0.3 °C (min. temp. = 24 °C, max. temp. = 30 °C) within the greenhouse compartment. Plant types in Table 1 were grown in 25 cm pots (20 seeds per pot). There were 5 replicates of each cultivar, and the entire experiment was conducted 3 times (total $n = 15$). Individual pots were fit with a cylindrical plexi-glass cage (90 cm tall; 24.5 cm diam.) to contain aphids. The open top of the cylinder was covered with thrips-proof screening, as were two 10.5 cm^2 windows on opposing sides of the cylinder. When planting, seeds were deposited near the center of each pot so that leaves would not touch the side of the cage during growth. Plants were used in experiments when they reached ca. 15 cm tall. To standardize the number of plants per pot, the number of germinating seeds was counted; any pot producing more than 15 plants/pot had the extra seedlings removed. At this time, plants were infested with 20 *R. padi* nymphs of mixed ages (3rd and 4th instars), selected arbitrarily from the aphid colony. Each week, we counted 10 randomly-selected leaves per plant. After 4 weeks the experiment was terminated; this represented approximately 5 aphid generations (assuming a nymph-to-adult development time of 6.2 days at 28 °C; Auad et al., 2009).

2.4. Effect of banker plant species and cultivar on A. colemani fitness and abundance

2.4.1. A. colemani development at constant temperatures

Experiments were conducted to assess the effect of aphid host plant (species and cultivar) on *A. colemani* fitness. Plants were infested with adult aphids, caged as in Section 2.3.1., and kept in two separate growth chambers set at 25 ± 1 °C and 60% RH. All plant species/cultivar combinations were replicated across both chambers. Adult aphids were allowed to larviposit for 24 h, and were then removed. One to ten nymphs (12 ± 12 h old) were retained on the plant, with any excess removed with a fine paintbrush. After 2 days (when nymphs were 60 ± 12 h old), a single female *A. colemani* was released into each cage by allowing it to crawl or fly from an aspirator vial. Wasps were allowed to parasitize aphids for 3 h. The wasps were then removed using an aspirator. Aphids on plants were monitored daily for mummy development and mummies were removed daily with a fine paint brush and stored in Petri dishes (15 cm diam.; lined with moistened filter paper) within the same incubator. Mummies were checked 4 times each day (8:00, 13:00, 17:00, 22:00) for successful emergence and to determine development time. F1 adults were preserved in 70% ethanol and sexed. Their size was determined by measuring hind tibial length, which has been shown to be highly correlated with dry mass in Aphidiine wasps (see Chau and Mackauer, 2001). The experiment was conducted 5 times, with 1 to 5 replicates per plant cultivar, depending on the trial replicate (total $n = 27–33$ wasps/plant species).

2.4.2. A. colemani fecundity and abundance over time

Trials were conducted in a research greenhouse to investigate effects of banker plant species/cultivar on *A. colemani* populations over time. As banker plants are most often used in the Spring and Early Summer, when aphid pests start to become a problem, the experiment was conducted from March to May 2010. The average daily temperature over the course of the experiment was 22.0 ± 0.2 °C (range: 19.2–27.2 °C). Methodology was identical to that used in Section 2.3.3, except that 2 female wasps were added to each cage after 20 3rd-4th instar *R. padi* were allowed to mature and reproduce freely for 1 week. As it was not possible to sample insects over time without potentially losing flying wasps from cages, the abundance of aphid mummies was determined at the end of a 6 week period (approx. 3–4 wasp generations, assuming a 12 day development time at 22 °C; Zamani et al., 2007). All mummies collected were monitored daily for wasp emergence over 5 days; emergence rates and sex ratio for each pot was determined. Emerged wasps were preserved in 70% ethanol, and, for a subset of females ($n = 2–5$ per cultivar, depending on availability), we counted the number of eggs within their ovaries at a later date. Specifically, we placed wasps on a glass slide and pulled their ovipositor to reveal the ovaries; eggs were spread out on a slide, photographed using a microscope-mounted camera, and counted from the photograph using ImageJ software (National Institute of Health, Bethesda, Maryland). Hind tibial length of this subset was measured to determine the effect of banker plant species on parasitoids size and the relationship between fecundity and size.

2.5. Statistical analyses

Data from our 4–5× daily observations (Section 2.3.1) were used in our calculations of *R. padi* pre-reproductive development time to give a more precise estimate. Here, the midpoint of each observation interval was used, as in Jandricic et al. (2010). For other life table statistics, data were converted to a single daily observation point (*i.e.* 24 h from the start of the experiment) since reproduction was assessed once daily. The Euler equation was used to calculate intrinsic rate of increase (r_m) for *R. padi*; results were also generally confirmed using the less cumbersome estimation presented in Wyatt and White (1977). The Euler equation is given as $\sum e^{-rx} l_x m_x = 1$, where x is the time in days (including immature stages), l_x is the proportion of individuals in the original cohort alive at time x (including immature mortality), and m_x is defined as the mean number of female offspring produced per surviving aphid during time interval x (1 day). The intrinsic rate of increase was obtained by iterating 'rx' in the equation until $\sum e^{-rx} l_x m_x = 1$ (see Southwood, 1978). Net reproductive rate ($R_o = \Sigma l_x m_x$) was calculated as per Birch (1948), and is defined as the average offspring over a female's lifetime if she conformed to age-specific survival and fecundity rates. Total fecundity (here defined as the total number of offspring produced by an aphid reaching adulthood) and reproductive life (*Lr*; the period of time from the initiation of reproduction to the last day of reproduction for an aphid reaching adulthood; Asin and Pons, 2001) were also calculated.

For r_m and R_o values, we calculated 95% CIs using the jackknife procedure, as in Davis et al. (2006). To compare these inherently population-level values across plant species, jackknife pseudo values were compared using an ANOVA (although we acknowledge the caveats of this method for comparing r_ms, as discussed in Lawo and Lawo (2011)). To generate pseudo values, we first calculated the r_m including all females. We then omitted the ith female and calculated the ith jackknife value ($r_{m,-i}$) based on the remaining females. This was repeated until each female was systematically omitted. Finally, the following formula was applied to calculate the ith -pseudo value: $r_{m,i} = n \cdot r_m - (n-1) \cdot r_{m,-i}$. This process was repeated for R_o; however, as the jackknife procedure can overestimate variation for this life history parameter (see Jha et al., 2012), the ANOVA of these values should be considered highly conservative.

We used a mixed model ANOVA to determine the effect of plant species (fixed effect) on laboratory measured values such as development time, total fecundity, size, aphid *Lr*, wasp emergence, and wasp sex ratio. As our desire was to make generalizations about all possible varieties within a particular plant species, plant cultivar was treated as a random effect in all analyses. Growth chamber or greenhouse bench (block) were also treated as random effects, as was trial replicate if the experiment was repeated over time. Statistical analyses were conducted using SAS v. 9.3 (SAS Institute, 2011). Data were log(x + 1) transformed to better meet assumptions of the ANOVA if necessary (all cases indicated in the footnotes of tables).

In the case of wasp development under laboratory conditions (experiment 2.4.1), up to 9 offspring emerged from a single female parasitoid. As siblings are more likely to have similar development times and size, the identity of the mother wasp was included in the ANOVA as a random effect. Similarly, percent emergence data was weighted by the total number of offspring parasitized by a single mother, giving more weight to data produced from multiple offspring than from a single parasitized host. Wasps that did not parasitize any aphids (77 out of 193 wasps) in the allotted time were excluded from analysis; a logistic regression (using the PROC GLIMMIX procedure in SAS) was used to determine if plant species significantly predicted whether a parasitoid successfully attacked aphids. To analyze sex ratio (i.e. proportion of females produced), a logistic regression was used to determine if plant species significantly predicted the proportion of females. Wasp mother was again included as a random effect.

For our long-term greenhouse trials with aphids only (Section 2.3.3), a repeated measures mixed-model ANOVA, with plant as the repeated measure, was used to analyze aphid abundance. The Autoregressive (1) model was specified as the covariance structure. For our long-term greenhouse trial including parasitoids (Section 2.4.2) a simple ANOVA was used for all factors, as data were only taken at the end of a 6-wk period. However, a logistic regression was used to determine if plant species predicted the initial establishment of wasps on aphid-infested plants. A Poisson regression (PROC GLIMMIX, specifying a Poisson distribution) was also included to determine if the initial density of aphids on plants after 1 week of reproduction significantly predicted the number of mummies produced after 6 weeks.

For aphids and parasitoids in experiments 2.3.1 and 2.4.2, a linear correlation analysis was conducted to investigate the link between female size and fecundity. For aphids, numbers of actual offspring were used; for wasps, egg load of dissected females was used since *A. colemani* are pro-ovigenic and have their entire compliment of eggs upon emergence. All wasps were treated as individual data points, regardless of whether they were collected from the same plant pot (and thus potentially having the same mother). For all experiments described above, arithmetic means and standard errors are presented.

3. Results

3.1. Effect of banker plant species and cultivar on R. padi fitness and abundance

3.1.1. Aphid development and fecundity at various temperatures

At constant 25 °C (Table 2), there was no significant effect of plant species on *R. padi* development time ($F_{3,58} = 1.14$, $P = 0.34$), size ($F_{3,6.8} = 0.99$, $P = 0.45$), total fecundity ($F_{3,6.8} = 2.79$, $P = 0.12$) or intrinsic rate of increase ($F_{3,69} = 1.84$, $P = 0.15$). Aphid size was not significantly correlated with fecundity (Pearson's $r = 0.12$, $P = 0.46$, $n = 41$). However, reproductive life was significantly affected by plant species ($F_{3,57} = 4.14$, $P = 0.01$), as was net reproductive rate ($F_{3,69} = 5.93$, $P = 0.001$; Table 2). In both cases, aphids reared on wheat had the highest values, and were significantly different from oat, which had the lowest values. Although trends were similar under high, fluctuating temperatures – oat again having the lowest *Lr* and R_o while wheat had the highest – differences were not significant ($P \geqslant 0.09$ for plant species in all cases; Table 2). For all factors, plant cultivar contributed little to the variance component (<5% in all cases). Between experimental conditions, the intrinsic rate of increase for *R. padi* was higher when reared at high, fluctuating temperatures (Table 2).

3.1.2. Aphid abundance over time

Over the course of the 4-week greenhouse experiment, plant species was not significant as a main effect on the number of aphids per 10 leaves ($F_{3,7.9} = 3.42$, $P = 0.07$) (Fig. 1). However, sampling date and the interaction of plant species and date were significant factors ($F_{3,97.2} = 133.6$, $P < 0.0001$ and $F_{9,103} = 4.64$, $P < 0.0001$, respectively). Aphid numbers were significantly different across weeks at $P < 0.001$, except for the comparison between Week 1 (initial infestation) and Week 4 (when aphid populations on all plants declined due to reduced plant quality; see below) ($t_{119} = 17.13$, $P = 0.98$). When aphids reached their peak population at Week 2 (Fig. 1), wheat plants had the highest number of aphids per 10 leaves sampled and oats had the lowest. Numbers of aphids on wheat were statistically higher than both oats ($t_{28.2} = 5.96$,

Table 2
Fitness measures for *R. padi* reared on 4 different plant species for 1 generation at constant and fluctuating temperatures. Different letters indicate significant differences ($\alpha = 0.05$).

Plant species ($n = 12$)	Fitness measure						
	Mean (±SE) pre-reproductive time (h)[a]	Pre- reprod. mortality (%)	Mean (±SE) total fecundity[a]	R_o [Mean (95% CI) jackknife pseudo R_o values]	Mean *Lr* (d)[a]	Mean (± SE) hind tibial length (mm)[a]	r_m [Mean (95% CI) jackknife pseudo r_m values]
	Constant 25 °C						
Barley	137 ± 3.5 a	31.3	63.2 ± 5.73 a	42.9 [43.0 (25.1, 60.9)] a	13.1 ± 1.27 ab	0.549 ± 0.011 a	0.429 [0.415 (0.354, 0.476)] a
Oats	139 ± 4.5 a	38.1	49.0 ± 7.60 a	35.0 [33.1 (17.6, 48.5)] a	9.1 ± 1.22 a	0.570 ± 0.023 a	0.403 [0.386 (0.330, 0.442)] a
Rye	146 ± 3.8 a	5.6	61.2 ± 5.74 a	57.8 [57.8 (44.3, 71.3)] ab	13.6 ± 1.24 b	0.536 ± 0.007 a	0.425 [0.427 (0.396, 0.458)] a
Wheat	139 ± 2.9 a	5.6	74.0 ± 3.60 a	70.1 [70.2 (59.3, 81.1)] b	14.7 ± 1.08 b	0.557 ± 0.010 a	0.467 [0.457 (0.423, 0.490)] a
	Fluctuating high temperatures (26–34 °C)						
Barley	124 ± 3.0 a	21.4	63.1 ± 5.52 a	49.6 [49.6 (31.5, 67.6)] a	13.5 ± 1.89 a	–	0.498 [0.497 (0.434, 0.560)] a
Oats	129 ± 2.2 a	20.0	60.1 ± 5.37 a	48.1 [48.1 (31.6, 64.6)] a	11.5 ± 0.95 a	–	0.476 [0.477 (0.429, 0.525)] a
Rye	138 ± 3.8 a	26.7	63.1 ± 7.56 a	46.3 [46.3 (26.5, 66.2)] a	15.2 ± 1.62 a	–	0.442 [0.432 (0.366, 0.497)] a
Wheat	137 ± 2.7 a	0.0	67.3 ± 6.26 a	67.3 [67.3 (53.1, 81.5)] a	13.6 ± 1.54 a	–	0.511 [0.509 (0.481, 0.538)] a

[a] Only aphids successfully reaching adulthood were considered in calculations.

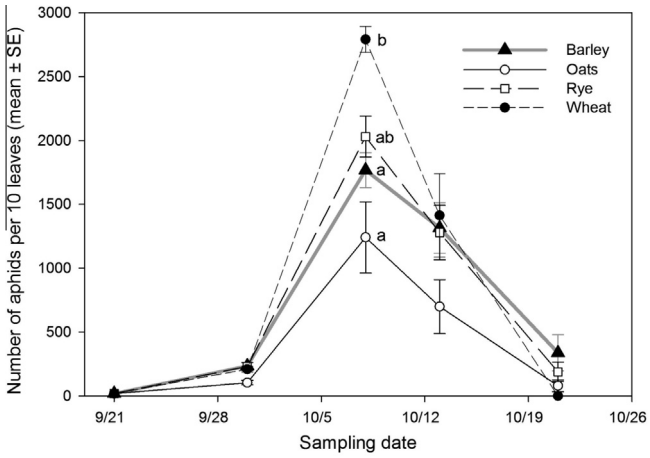

Fig. 1. Number of *R. padi* per 10 leaves of various grain species over 4 weeks under greenhouse conditions. Significant differences on 10/8 are indicated with different letters; all other comparisons within sampling dates were non-significant at $\alpha = 0.05$.

$P < 0.0001$) and barley ($t_{28.2} = 3.94$, $P = 0.0134$), accounting for the species × date interaction. Numbers of aphids on wheat were not significantly higher than rye ($t_{28.2} = 5.96$, $P = 0.22$). All other comparisons between plant species within a particular week were non-significant at $\alpha = 0.05$. Overall, plant cultivar only contributed to 15% of the variance component. A visual inspection of the plants indicated that all plants had started to decline in quality by Week 4, with many wilted and some dead.

3.2. Effect of banker plant species and cultivar on *A. colemani* fitness and abundance

3.2.1. *A. colemani* development at constant temperatures

In the laboratory trials, the particular growth chamber (block) insects were kept in contributed to 23–30% of the variance component. However, as trends were similar across growth chambers, data from the two blocks were combined. Across all tests, plant cultivar contributed to ⩽7% of the variance component. The individual P1 wasp from which F1 wasps were sourced had a stronger effect on variation (24–37%).

Host plant species did not significantly predict whether P1 wasps successfully parasitized aphids (Type III test of fixed effects in PROC GLIMMIX: $F_{3,7.7} = 0.9$, $P = 0.97$), or their attack rate (ANOVA: $F_{3,185} = 0.78$, $P = 0.51$). Though emergence was lowest on oats (Table 3), plant species did not significantly affect percent emergence of F1 wasps ($F_{3,111} = 2.16$, $P = 0.09$). However, plant species significantly contributed to development time of F1 females ($F_{3,64} = 9.10$, $P < 0.0001$). Development was shortest on barley-reared aphids, which was significantly different from wheat and rye ($t_{65.1} = 2.79$, $P < 0.03$ for both), but not oats ($t_{62.7} = 2.08$, $P = 0.17$; Table 3). Rye resulted in the longest development time for female wasps, though this was not significantly longer than wheat at $\alpha = 0.05$. Plant species did not have a significant effect on female size ($F_{3,52.5} = 2.33$, $P = 0.08$). For male wasps, outcomes were reversed; plant species did not have a significant effect on development time ($F_{3,6.2} = 2.49$, $P = 0.15$), but did have a significant effect on male size ($F_{3,108} = 4.37$, $P = 0.0061$). Male wasps produced on rye were significantly smaller than those from wheat and barley ($t_{112} \geqslant 3.04$, $P \leqslant 0.015$), and marginally smaller than those from oats ($t_{119} = 2.67$, $P \leqslant 0.043$).

Table 3
Fitness measures for *A. colemani* reared on *R. padi* from 4 different plant species over 1 generation under laboratory conditions (constant 25 °C). Different letters indicate significant differences ($\alpha = 0.05$).

Plant species (n)	Fitness measure (mean ± SE)							
	% P1 females successfully attacking	No. of successful attacks per female in 3 h	% Emerg.	Proportion female/pot[a]	Females		Males	
					Devel. time (h)	Hind tibial length (mm)[b]	Devel. time (h)	Hind tibial length (mm)[b]
Barley (131)	60.4% a	2.4 ± 0.37 a	85.3 ± 3.50 a	0.30 ± 0.06 a	227 ± 2.5 a	0.58 ± 0.01 a	228 ± 1.2 a	0.56 ± 0.01 a
Oats (121)	56.2% a	1.9 ± 0.34 a	70.6 ± 6.36 a	0.46 ± 0.07 a	232 ± 2.0 ab	0.58 ± 0.01 a	232 ± 1.9 a	0.57 ± 0.01 a
Rye (145)	62.3% a	1.8 ± 0.31 a	82.3 ± 5.08 a	0.34 ± 0.07 a	249 ± 3.4 c	0.57 ± 0.01 a	238 ± 2.2 a	0.54 ± 0.01 b
Wheat (135)	61.4% a	1.7 ± 0.29 a	78.2 ± 6.48 a	0.32 ± 0.07 a	235 ± 3.1 bc	0.59 ± 0.01 a	232 ± 2.3 a	0.57 ± 0.01 a

[a] Proportion of females.
[b] Data log $x + 1$ transformed prior to analysis.

Table 4
Fitness measures for *A. colemani* reared on *R. padi* on 4 different plant species at the end of 6 weeks under greenhouse conditions (fluctuating temperatures). Different letters indicate significant differences ($\alpha = 0.05$).

Plant species ($n = 36$)	Mean (±SE) number of aphids/10 leaves at time of wasp release	Fitness measure (mean ± SE)						
		No. of mummies/pot	Percent emerge./pot	No. of wasps produced/pot[a]	Proportion female/pot	No. of females/pot[a]	Female hind tibial length (mm)	Egg load/female[a]
Barley	102.5 ± 10.34 a	60.0 ± 6.66 a	78.6 ± 3.12 a	48.3 ± 5.97 a	0.39 ± 0.059 ab	20.4 ± 4.25 a	0.58 ± 0.01 a	161.6 ± 5.80 a
Oats	68.8 ± 8.09 b	44.5 ± 6.25 a	53.5 ± 3.42 b	22.7 ± 3.51 b	0.50 ± 0.052 a	12.0 ± 2.72 a	0.57 ± 0.01 a	163.2 ± 5.65 a
Rye	84.0 ± 6.72 ab	50.9 ± 6.04 a	77.1 ± 2.91 a	39.9 ± 5.37 ab	0.26 ± 0.051 b	13.8 ± 3.76 a	0.59 ± 0.01 a	175.7 ± 6.29 a
Wheat	109.6 ± 10.27 a	61.5 ± 7.26 a	76.8 ± 3.30 a	49.1 ± 6.26 a	0.42 ± 0.070 ab	23.0 ± 5.36 a	0.57 ± 0.01 a	154.1 ± 7.93 a

[a] Data log $x + 1$ transformed prior to analysis to better meet the assumptions of the ANOVA.

The sex ratio of F1 wasps was not significantly predicted by plant species (Type III test of fixed effects in PROC GLIMMIX: $F_{3,137.6} = 1.26$, $P = 0.29$).

3.2.2. A. colemani fecundity and abundance over time

In the longer-term greenhouse experiments (Table 4), plants were omitted if wasp colonies failed to establish at the start of the experiment (39 out of 149 plants total). Plant species did not significantly predict if wasps failed to establish (Type III test of fixed effects: $F_{1,3} = 0.13$, $P = 0.92$). Trial replicate accounted for 14–22% of the variance component for all tests; cultivar accounted for less than 2% of the variance component. Trends were similar across experiments, thus data were combined for all analyses. Similar to experiment 2.3.3, the ANOVA indicated that plant species affected initial numbers of aphids per plant ($F_{3,96.2} = 4.60$, $P = 0.004$) prior to the introduction of parasitoids. Aphid numbers were lower on oats compared with barley and wheat ($t_{96.2} \geqslant 2.86$, $P \leqslant 0.02$) but not Rye ($t_{96.2} \geqslant 1.28$, $P = 0.58$); all other comparisons were non-significant. Though plant species did not directly affect the number of mummies using an ANOVA ($F_{3,100} = 1.83$; $P = 0.14$), a Poisson regression revealed that the initial number of aphids per plant (affected by plant species; see above) significantly predicted the number of mummies produced after 6 weeks ($F_{1,69} = 113.28$, $P < 0.0001$). We also found that plant species on which the aphid host was reared affected wasp emergence rates ($F_{3,100} = 15.42$, $P < 0.0001$; Table 4). This resulted in an overall lower number of adults from oats compared to barley and wheat ($t_{100} \geqslant 2.89$, $P \leqslant 0.024$; main effect of species = $F_{3,100} = 3.94$, $P = 0.010$), but not Rye ($t_{100} = 2.14$, $P = 0.15$). The lowest number of females was produced from oats and rye, though these were not significantly different between plant types ($F_{3,100} = 0.47$, $P = 0.70$). Interestingly, a high proportion of females was produced from oats, though this was only significantly higher compared to rye ($t_{96.6} = 2.97$, $P = 0.020$; $F_{3,96.6} = 3.12$, $P = 0.0297$). Overall, size of *A. colemani* was correlated with egg load in our tests (Pearson's $r = 0.36$, $P < 0.001$, $n = 314$; Fig. 2). However, plant species did not have an effect on either size or fecundity ($P \geqslant 0.08$ for all tests).

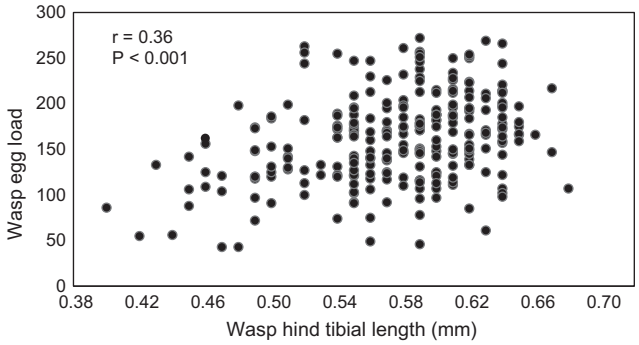

Fig. 2. Correlation between size of *A. colemani*, as determined using hind tibial length, and number of eggs, as determined through dissections. Aphid-plant species combinations on which *A. colemani* was reared did not have a significant effect on size or fecundity ($P \geqslant 0.05$).

4. Discussion

R. padi is considered an ideal host for *A. colemani* in a banker plant system because they produce "fresh" wasps, are non-pestiferous in greenhouse crops, and are less preferred than crop pest aphids (Frank, 2010). In some cases, use of these banker plants leads to target pest suppression (Bennison and Corless, 1993; Blümel and Hausdorf, 1996; Prado and Frank, 2014) but not others (Jacobson and Croft, 1998; van Driesche et al., 2008). Determining the optimal plant host for both organisms involved is a practical method of improving the efficacy of this biological control tool for growers, and has only been investigated superficially once before (see Jacobson and Croft, 1998). Our study is the first to examine plant species and cultivar effects on the *A. colemani*-banker plant system in depth. We found that effects of cultivar on aphid and parasitoid life history traits were consistent within each plant species. However, supporting our predictions, plant species had significant bottom-up effects on both aphid and *A. colemani* populations over time.

Plant species effects on *R. padi* life table characteristics were apparent in a single generation. Intrinsic rate of increase was consistent with previous studies (e.g. Leather and Dixon, 1984; Asin and Pons, 2001; Lumbierres et al., 2004), but was not affected by plant species. However, we observed reduced net reproduction and reproductive life on oats at constant 25 °C. Together, these effects were likely responsible for the 60% reduction in abundance we observed on oat compared to wheat over several aphid generations. Lowered aphid abundance imparts a direct, negative effect on parasitoid populations. With fewer aphids on oat, as well as rye, banker plants in our long-term greenhouse experiment, wasps had fewer hosts to select from. Thus, *A. colemani* on oats and rye were likely forced to oviposit in lower-quality (i.e. smaller) hosts (see Jarosik et al., 2003), leading to 17–54% fewer wasps and 32–48% fewer females than barley or wheat over 6 weeks. Releasing parasitoids at an effective, continuous rate is considered key to minimizing the amplitude of aphid population fluctuations in crops under biological control (Yano, 2006). Thus, plant species that produce fewer female wasps could result in aphid population explosions, especially if plant effects on parasitoids are compounded over the entire growing season.

Our results with *R. padi* support those of Leather and Dixon (1981), who also observed lowered *R. padi* fecundity on oat seedlings compared to barley or wheat. A multitude of factors could

explain this effect; grain species quality for *R. padi* could differ due to the availability and composition of free amino acids (Weibull, 1987, 1988), plant defensive chemicals (Figueroa et al., 2004), synthesis of plant "pathogenesis-related" proteins in response to aphid feeding (Ni et al., 2001), and interactions with symbiont fauna (e.g. Chen et al., 2000). Whatever the mechanism, negative plant effects on *R. padi* seemed somewhat ameliorated at higher, fluctuating temperatures in our study. It has been suggested that endosymbionts may be favoured at higher temperatures, resulting in greater amino acid production in the aphid (Davis et al., 2006) – though this may not be true in all aphid species or at all temperature ranges (see Chiu et al., 2012). If true for *R. padi* at the temperatures tested in our study, endosymbiont increase could potentially make up for deficits in nutrition, leading to more similar performance across plant species under these conditions. If grain species suitability for *R. padi* and *A. colemani* changes with temperature, then optimal banker plant species may vary by season or geographic location. More research is needed to confirm this hypothesis.

Plant suitability for an herbivore host can also indirectly affect the next trophic level. Our results support a link between aphid fecundity and wasp emergence, since *R. padi* reproduction and *A. colemani* emergence were lowest on oats. Although the mechanism is unknown, increased pupal mortality of wasps could be the result of inability of the parasitoid to gain sufficient resources from less nutritious aphids (Sampaio et al., 2008). Similarly, the intermediate abundance of aphids reared on rye in both of our greenhouse experiments also suggests a nutritional deficit to the aphid, which increased development time in female *A. colemani*, and produced smaller *A. colemani* males and fewer females. Smaller males are not likely to impact biocontrol outcomes, given that Cloutier et al. (2000) found that small and large males of *Aphidius nigripes* perform similarly in terms of mate location and mating success. However, these other traits might. A long-held and widely accepted positive trait for natural enemies is an intrinsic rate of increase the same or greater than the target pest (Messenger, 1964; Sabelis, 1992). A longer development time of female *A. colemani* would reduce this species' r_m, which is reported to already be lower than its host's r_m under ideal lab conditions (e.g. at ca. 25 °C, r_m for *A. gossypii* = 0.45, Wyatt and Brown, 1977; r_m for *A. colemani* = 0.438, van Steenis, 1993). Moreover, the altered sex ratio on rye – whether due to differential sex allocation by mothers or differential mortality between the sexes from poor host resources (Jarosik et al., 2003) – ultimately means that fewer females are present in the greenhouse for parasitism, and thus, control.

One purpose of banker plants is to provide "fresher" and "better" wasps compared with commercial sources that have spent extended time in transit (Huang et al., 2011). Our results highlight that the latter may not be the case under certain plant species choices. Prado and Frank (2014) indicated that store-bought *A. colemani*, obtained directly from the supplier as mummies (produced on non-grain aphids) and allowed to parasitize *R. padi* upon emergence, produced FI offspring with an emergence rate of 70% and a M:F sex ratio of 0.43. If we compare to these values, our results over 3–4 wasp generations on *R. padi* indicate a reduction in emergence vs. store-bought wasps by 7–9% when reared on oats, and a reduction in the proportion of females produced by 16% on rye. That "fresher" but less fit wasps were potentially produced in our study highlights that plant effects should be considered and tested before species are arbitrarily chosen, as often seems to be the case with this biological control tool.

That cultivar had no significant effect on life table characteristics or abundance of *R. padi* or its parasitoid in our study concurs with Krauss et al. (2007). They demonstrated that plant cultivar only had a small effect on *R. padi* and parasitoid abundance, while nutritional conditions of plants (in the form of added fertilizer) strongly affected outcomes. However, our results are in opposition with other studies, especially those investigating commercial plant cultivars bred for herbivore resistance. For example, various plant genotypes have been shown to negatively affect aphid intrinsic rate of increase (Taheri et al., 2010) or survival and size of aphid parasitoids (Ashouri et al., 2001). Thus, aphid-resistant grain cultivars should obviously be avoided in the production of banker plant units. However, beyond such basic precautions, growers should feel free to choose whatever cultivar is most readily available.

Some practical recommendations and future research directions can be made based on our data. First, without significant numbers of parasitoids to use up *R. padi* populations on grain plants, plants will only remain healthy (and therefore effective) for ca. 3–4 weeks using any grain species. Longer trials with realistic parasitoid pressure and plant care are still needed to determine the maximum effective duration of *A. colemani* banker plants in the greenhouse, as current reports are both limited and varied (Bennison and Corless, 1993; Jacobson and Croft, 1998). Second, no effect of cultivar was seen in any of the plant species. Thus, any cultivar of barley or wheat (the best performing host plants with regards to wasp numbers) should theoretically be a safe choice for growers interested in producing their own banker plants, as long as plants are properly cared for. Lastly, despite the above discussed negative effects of some plant species, trends in our data suggest that each host plant can ultimately contribute some positive fitness characteristic to *R. padi* and its parasitoid. For example, oats resulted in the highest wasp sex ratio per pot and rye produced the largest wasps with the highest egg load. Thus, future research could investigate mixtures of grain species as a potential way to further refine this system.

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