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Estimating parasitoid impact on aphid populations in the field

Alexandre Leblanc, Jacques Brodeur*

Institut de Recherche en Biologie Végétale, Département de sciences biologiques, Université de Montréal, 4101 rue Sherbrooke est, Montréal, Québec H1X 2B2 Canada

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ABSTRACT

We developed a quantitative method to assess the capacity of parasitoids to reduce aphid populations in open fields. The method, designated as the propagated mortality analysis (PMA), estimates the impact of early parasitoid-induced mortality on forthcoming aphid populations and was built upon an existing model describing the bell-shaped population dynamics observed in many aphid species. The PMA was next used to assess the impact of the naturalized and most abundant parasitoid *Aphelinus* sp. on populations of the soybean aphid *Aphis glycines* under field conditions in north-eastern North America. Results from the PMA showed that *Aphelinus* sp. reduced both peak soybean aphid densities and cumulative aphid-days at the end of the pest management threshold period by only 1–7%, probably because of low levels of parasitism early in the season. The method we propose is simple to use, could apply to most aphid-parasitoid systems and would gain to be extended to other natural enemies.

1. Introduction

In biological control programs, the effectiveness of a natural enemy is often evaluated by the mortality it inflicts on a target pest, but less commonly by its future impact on the pest population (Kidd and Jervis, 2005). Assessing the future impact of a natural enemy is of particular importance when one wants to predict if their contribution at low pest densities can prevent pest populations from reaching either the economic injury level (i.e. the pest density at which damage compensate the cost of control) or the economic threshold (i.e. the pest density that allows enough time to intervene and prevent reaching the economic injury level) (Zadoks, 1985). Such a prediction is mainly relevant for multivoltine pest species, such as aphids, for which reproductive capacities often overcome natural control and may lead to pest outbreaks. It is also of primary interest for aphid parasitoids which tend to spread their attacks among aphid colonies (Mackauer and Völkl, 1993), therefore displaying a potential to regulate pest populations when host densities are low.

The impact of parasitoids on host populations is typically quantified through percent parasitism or, alternatively, through generational mortality using life tables (Kidd and Jervis, 2005; Van Driesche, 1983; Van Driesche et al., 1990; Waage and Cherry, 1992). These two methods emphasize instantaneous parasitoid-induced mortality and do not consider repercussions on subsequent aphid generations. Therefore, these methods are not suitable for directly assessing the capacity of a parasitoid species to hold its host's population below thresholds in biological control programs. Exclusion methods are currently the main experimental approach to quantify the impact of a parasitoid on its host, as parasitoid abundance can be linked to changes in host populations at a subsequent time (Kidd and Jervis, 2005). An alternative approach could be developed for open field situations if one has (i) the capacity to measure parasitoid-induced mortality and (ii) a good understanding of the host population dynamics.

Parasitoid-induced mortality can be easily quantified experimentally in aphid systems. The vast majority of aphid parasitoids belong to the families Braconidae and Aphelinidae (Hymenoptera) and develop as koinobiont endoparasitoids, meaning that their larval growth occurs within the aphid that continues to develop following parasitism (Boivin et al., 2012; Starý, 1970). The parasitoid larva kills its host just prior to pupation; the resulting hardened and swollen aphid cuticle, called a mummy, protects the parasitoid until adult emergence. Aphid mummies are conspicuous, they can often be identified to genus, and their sampling has become a common practice to estimate aphid mortality induced by parasitoids (Powell, 1982; Starý, 1970). Mummy counts, however, produce a biased estimate of parasitoid-induced mortality at any given time because mummy persistence in the field depends on the duration of parasitoid's development following mummification (Van Driesche, 1983). As an alternative, the rate of mummification directly represents how fast aphid mortality occurs upon mummification and thus is unbiased with respect to parasitoid development time.

Several aphid species of economic importance have a single, nearly symmetric, annual peak of abundance (Catangui et al., 2009; Costamagna et al., 2007; Fernandes et al., 1998; Lamb et al., 2013; Matis et al., 2007, 2011). This seasonal dynamic has been previously

* Corresponding author.
E-mail address: jacques.brodeur@umontreal.ca (J. Brodeur).

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described by a model of exponential population growth with linearly decreasing intrinsic growth rate over time, considering a predominant bottom-up regulation through plant phenology (Costamagna et al., 2007; Williams et al., 1999). This model has been validated for the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), in cage experiments where all natural enemies were excluded (Catangui et al., 2009; Costamagna et al., 2007). A similar model used an aphid relative growth rate that decreased proportionally with the cumulative number of individuals throughout the season (Matis et al., 2007), on the basis of resource exhaustion by aphids. This model has been validated for four aphid species without excluding natural enemies (Matis et al., 2007, 2008, 2011). These two models display a typical bell shape and are similar in terms of simplicity and number of parameters; however, they rely on different assumptions. More specifically, they apply to different regimes of aphid infestation: the Matis et al. (2007) model describes cases in which aphid density is high enough to exhaust plant resources, while the Costamagna et al. (2007) model refers to moderate aphid densities for which resource availability varies seasonally and is controlled mostly through plant phenology. These models provide a reliable and simple approach to characterize aphid population dynamics, which may help to predict aphid peak abundance and to develop management strategies. For example, they have been used to characterize maximum aphid populations in studies investigating the impacts of cultural practices (Matis et al., 2008, 2011) and plant growth stage (Catangui et al., 2009) on pest populations. To our knowledge, these models have not been used to assess the impact of natural enemies, such as parasitoids, on aphid populations.

In the context of pest management, a common practice is to estimate yield loss from the cumulative aphid-days (CAD) per plant over a threshold period, i.e. the period during which the threshold is valid, usually until a specific phenological stage of the plant is reached (Hansen, 2000; Kieckhefer et al., 1995; Ragsdale et al., 2007; Sanchez et al., 2007). However, in practice, CAD-based thresholds are often converted into, or provided along, aphid density thresholds (Catangui et al., 2009; Hansen, 2000; Ragsdale et al., 2007) as they are more convenient for farmers. To achieve practical utility, the estimation of parasitoid impact on aphid population must be expressed according to these metrics.

In this study, we first developed the propagated mortality analysis (PMA), a simple method to quantify the impact parasitoids may have on the development of their host populations over time. The method is built upon the aphid population dynamics model developed by Costamagna et al. (2007) and emphasizes the evaluation of the parasitoid impact at either peak aphid densities or through CAD over the pest management threshold period. The PMA was next tested, over two years under field conditions, using the biological model composed of the soybean aphid *A. glycines* and of its principal parasitoid, *Aphelinus* sp. (Hymenoptera: Aphelinidae).

2. The propagated mortality analysis

2.1. Theoretical foundation

2.1.1. Aphid population dynamics in absence of parasitism

Population dynamics models by Costamagna et al. (2007) and Matis et al. (2007) both provide a simple representation of aphid densities that is essential for calculating and interpreting the suppressive effect of parasitoids. We developed our method using the Costamagna et al. (2007) model because it (i) postulates that an aphid population is not highly detrimental to the host plant and (ii) benefits from more accessible regression methods. The model represents the aphid density per plant $N(t)$ as the bell-shaped function

$$N(t) = N(t_0)\exp\left[r_0\left(t-t_0\right)\left(1-\frac{1}{2}a\left(t-t_0\right)\right)\right]. \quad (1)$$

Eq. (1) corresponds to the solution of the following differential equation with respect to N:

$$\frac{dN}{dt} = Nr_0(1-a(t-t_0)), \quad (2)$$

which describes the intrinsic growth rate of aphid density linearly decreasing with time (t). The parameter r_0 (identified as r_{max} in Costamagna et al. (2007)) defines the intrinsic growth rate at a reference time t_0 and a characterizes the slope of the decrease with time. A natural choice for t_0 is the onset of infestation. Indeed, Costamagna et al. (2007) fixed time of infestation as $t_0 = 0$, which is appropriate when plants are artificially infested. However, when natural plant colonization by aphids occurs, t_0 likely differs among years and sites.

Colonization time t_0 thus refers to the arrival of the first aphids in the field but, because relying on few observations might not be accurate, we suggest defining it as when $N(t)$ has reached an arbitrary low density, for instance one aphid per plant. The ability to vary $N(t_0)$ while fixing t_0, in Costamagna et al. (2007), is then replaced by one to vary t_0 while fixing $N(t_0)$. Although this change in representation does not alter the prediction on $N(t)$, it affects parameter values, making them more relevant biologically when aphid colonization happens at different dates during the growing season. The model predicts the peak aphid densities $N(t^*) = N(t_0)\exp(r_0/2a)$ to be obtained at $t^* = t_0 + 1/a$.

2.1.2. The impact of parasitism

The effect of parasitism on aphid populations can be assessed by comparing aphid densities when parasitoids are present (N_p) vs. absent (N). For this purpose, Eq. (2) can be modified to consider mortality from parasitism through time by including the mummification rate $m(t)$ (the number of aphid mummies formed per plant and per unit time),

$$\frac{dN_p}{dt} = N_p r_0(1-a(t-t_0))-m(t). \quad (3)$$

The analytical solution to this equation is also a unimodal function of aphid density

$$N_p(t) = N_p(t_0)\exp\left[r_0(t-t_0)\left(1-\frac{1}{2}a(t-t_0)\right)-\int_{t_s}^{t} m(x)/N_p(x)dx\right], \quad (4)$$

with t_S representing the time from which we want to compare N and N_p; it would correspond to the beginning of sampling and ideally precede detection of mummies. In presence of the parasitoid, the host density can therefore generally be expressed as a proportion of the host density in the parasitoid's absence,

$$N_p(t) = \gamma(t)N(t) \text{ with}$$
$$\gamma(t) = \exp\left[-\int_{t_s}^{t} m(x)/N_p(x)dx\right]. \quad (5)$$

The parasitoid impact $\gamma(t)$ represents the proportional reduction of host density by the parasitoid, arising directly through mortality and indirectly through the subsequent failure of dead aphids to reproduce. The temporal progression of $\gamma(t)$ is strictly decreasing and may help to identify when the parasitoids contribute the most to regulating the aphid population.

2.1.3. Estimates of control

In case thresholds are expressed as aphid density, a proper estimate of aphid control by the parasitoid correspond to $\gamma(t)$ at peak aphid density,

$$\gamma(t^*) = \frac{N_p(t^*)}{N(t^*)}. \quad (6)$$

According to the model by Costamagna et al. (2007), aphid populations would naturally decrease beyond the peak aphid density and any parasitoids would not contribute to maintaining aphids under the density threshold. However, it is worth nothing that if the threshold

period does not encompass peak density, the maximum aphid density rather corresponds to the highest value at one of the threshold period limits.

In case thresholds are specified as cumulative aphid-days (CAD), an equivalent estimate of aphid control corresponds to a reduction in CAD associated with the parasitoid, as expressed by the following ratio:

$$r_{CAD} = \frac{CAD_p(t_E)}{CAD(t_E)}, \tag{7}$$

where $CAD_p(t_E) = \int_{t_{E0}}^{t_E} N_p(x)dx$ and $CAD(t_E) = \int_{t_{E0}}^{t_E} N(x)dx$ are continuous representations of CADs between the threshold period limits (t_{E0},t_E), respectively, in the presence and absence of the parasitoid. The lower bound of integrals (t_{E0}) can be chosen as the onset of sampling (t_S) when both happen before or at aphid colonization. The integrand $N(t)$ can be estimated from experimental $N_p(t)$ and $\gamma(t)$. Although r_{CAD} relates the importance of the parasitoid in suppressing the aphid, one might be interested in calculating the yield gain ($Y_G = y - y_p$) associated with the parasitoid, with y_p and y the relative yields in proportion to maximum yield, in presence vs. absence of the parasitoid. However, the yield response to CAD must be known, and in practice it may adopt different forms (Catangui et al., 2009; Larsson, 2005; Ragsdale et al., 2007; Sanchez et al., 2007). When yield responds linearly to CAD with slope k, the yield gain corresponds to $Y_G = k(CAD - CAD_p)$ or equivalently $Y_G = k \cdot CAD(1 - r_{CAD})$.

2.2. Statistical model

The Costamagna et al. (2007) model is a deterministic model expected to represent the temporal dynamics of the average aphid densities (μ) in the field. The biological parameters (a,r_0,t_0) are *a priori* unknown and must be estimated through a regression on the experimental aphid densities. For this purpose, a statistical model that can independently consider the distribution and the prediction of aphid density is needed. Generalized linear models (GLMs) fulfill this requirement and are characterized by three components: the distribution, a linear predictor (η) corresponding to a linear combination of the predictor variables, and a link function g relating the average μ of the response variable to the linear predictor, $\mu = g^{-1}(\eta)$.

The distribution, for count data such as aphid density per plant, can be chosen as a negative binomial because it generalizes the Poisson distribution, allowing variance to differ from the mean. For the model by Costamagna et al. (2007) in presence of the parasitoid, Eq. (4) can be represented by a log link function ($\mu = \exp(\eta)$) and a nearly quadratic linear predictor in time ($\eta = b_0 + b_1 t + b_2 t^2 - \gamma(t)$), with b_0, b_1, b_2 parameters determined through regression and $\gamma(t)$ estimated *a priori*. One can show that the biological parameters (a,r_0,t_0) can be calculated from the linear predictor parameters, and reciprocally, as follows:

$$\begin{aligned} b_0 &= \log(N_0) r_0 t_0 \left(1 + \tfrac{1}{2} a t_0\right), \\ b_1 &= r_0(1 + a t_0), \\ b_2 &= -\tfrac{1}{2} a r_0, \end{aligned}$$

$$\begin{aligned} \min t_0 | 0 &= b_0 - \ln N(t_0) + b_1 t_0 + b_2 t_0^2, \\ r_0 &= b_1 + 2 b_2 t_0, \\ a &= -2 b_2 / r_0. \end{aligned} \tag{8}$$

Predictions of aphid density through time $N(t)$ as well as peak density $N(t^*)$ and its time of occurrence t^* can then be calculated from the aforementioned equations. Variances of biological parameters, $N(t^*)$ and t^* are estimated through error propagation from those of the linear predictor parameters; details are provided in Supplementary Material. The use of GLM to estimate biological parameters differs from the polynomial regression on the log transformed mean of $N(t)$ used by Costamagna et al. (2007), but allows for easier handling of zeros from raw count data. The use of time, instead of aphid degree-days, is favored to simplify the analysis of the parasitoid impact on aphid density, and especially to be consistent with existing works on CAD which are computed on a day-to-day basis (Hansen, 2000; Ragsdale et al., 2007; Sanchez et al., 2007).

2.3. The analysis

The propagated mortality analysis (PMA) requires the assessment of field mummification rate and aphid density at the same dates. The analysis is then achieved in three steps: (1) compute the impact $\gamma(t)$ from mummification rates and average aphid densities, (2) predict aphid density in absence of the parasitoid through regression using $\gamma(t)$ and (3) calculate a measure of aphid control by the parasitoid, either γ at peak aphid density or r_{CAD} at the end of the threshold period, with the corresponding yield gain Y_G.

The deviance-based R^2_{DEV} developed by Cameron and Windmeijer (1996) is appropriate for a negative binomial distribution and could serve to assess the goodness of fit of the statistical model. In addition, the statistical model representing the Costamagna et al. (2007) model in presence of the parasitoid can be compared to a null model with a zero-order linear predictor ($\eta = b_0$) through a likelihood ratio test.

Code to perform PMA is available in Supplementary Material and was built under R software version 3.3.2 (R Core Team, 2016). Integrations for $\gamma(t)$ and $CADs(t)$ are performed numerically by first interpolating the integrands by cubic B-splines.

3. The case study

Following the arrival of the soybean aphid in North America in 2000, soybean yield was shown to decrease linearly with cumulative aphid density at a rate of 6.88% per 10,000 CAD with respect to maximum yield (Ragsdale et al., 2007). This led to the establishment of an economic injury level (EIL) of 5563 CAD per plant (Ragsdale et al., 2007), which remains valid until the soybean reach full seed (stage R6). For practical purposes, this threshold was converted into a density-based EIL of 674 aphids per plant and into an economic threshold (ET) of 250 aphids per plant, the latter allowing for one week to implement pest control before reaching EIL (Ragsdale et al., 2007, 2011).

In its native Asia, the soybean aphid rarely reaches these thresholds, as populations are controlled by a community of natural enemies (Ragsdale et al., 2011). The importance of generalist predators in the suppression of soybean aphid populations in North America has often been recognized (Costamagna et al., 2008; Rhainds et al., 2007), but efficient parasitoids were considered to be lacking (Heimpel et al., 2010). Augmentative and classical biological control efforts have been undertaken to compensate for the lack of parasitoids but thus far without great success (Gariépy et al., 2015; Ragsdale et al., 2011).

In 2005, the parasitoid *Aphelinus certus* Jasnosh was first detected attacking the soybean aphid in soybean fields in USA (Heimpel et al., 2010). This species was subsequently observed in 2006 in Ontario (Frewin et al., 2010) and in 2010 in Québec (Gariépy, 2011), and has since become the most common parasitoid of the soybean aphid in Canada (Xue et al., 2012). Its biology and potential as a biological control agent has been investigated in a few studies (Frewin et al., 2010; Gariépy, 2011; Hopper et al., 2017; Hopper and Diers, 2014) but no attempt has yet been made to estimate the impact of *A. certus* on soybean aphid populations in the field. In this study, we compared two estimates of aphid mortality and conducted a propagated mortality analysis (PMA) of *Aphelinus* sp., most likely *A. certus*, on the soybean aphid.

3.1. Material and methods

3.1.1. Field survey

The seasonal abundances of soybean aphid and *Aphelinus* mummies were assessed in 2012 and 2013 in three large, intensively managed, commercial soybean fields in the Montérégie region, Québec, Canada. Fields were planted with different cultivars and were insecticide free. Sites were surveyed twice a week, from the arrival of the soybean aphid in the field (end of June), through the growing season, until their density decreased to approximately 1 per plant (early September).

In 2012, we followed the whole-plant survey protocol of the Québec plant protection warning network for the soybean aphid (Martelle and Marcoux, 2005), except that we inspected five plants from eight, rather than six, sampling locations per field on each sampling date (i.e., a total of 40 plants per sampling date, per field). Sample locations were at least 10 m from field edges, separated by 100 m within rows, and by 40 m between rows. To further separate sampling locations, samples from adjacent rows were offset by 50 m. Within a location, sampled plants were separated by approximately 10 m and selected randomly on zigzag courses. A complete census of all living aphids, nymphs and adults, was performed on each plant and leaves containing aphid mummies were collected and brought back to the laboratory. Soybean growth stage was evaluated from eight plants per field, randomly selected within sampling locations; a given stage was attributed to the field when at least half the plants had reached it.

In 2013, the protocol was modified slightly to obtain a more balanced sampling effort with respect to aphid mummies, while compensating for low insect densities early in the season. The number of plants sampled per location was adjusted throughout the season to aim for the collection of approximately 50 intact mummies, i.e. mummies from which neither parasitoids nor hyperparasitoids had emerged, and which had no visible predation damage. In the absence of mummies, a minimum of one and a maximum of 20 plants per location were sampled to limit the effort, while the number of locations was held at eight to preserve the experimental design. When more than 10 plants were examined per sampling location, the survey was separated into two parallel zigzag courses to maintain distance between adjacent sampling locations.

3.1.2. Rearing of Aphelinus mummies

Mummies were isolated in gelatin capsules and held in a growth chamber set to 21 ± 1°C and a photoperiod of 16:8 (L:D). Parasitoid emergence was tallied once a day in 2012 (beginning at 16:00) and twice a day in 2013 (once at 8:00 and once at 16:00). Observations continued for a minimum of 19 days, a period about twice the development time between mummification and emergence of *A. certus* at 21 °C (9.3 days), as estimated by Frewin et al. (2010). Wasps emerging from *Aphelinus* mummies were classified as either genus *Aphelinus*, or hyperparasitoids. *Aphelinus* sp. specimens were presumed to belong to *A. certus*, the latter being a cryptic species (Heraty et al., 2007). In a previous study conducted in the same area, *A. certus* was the only species sampled (Gariépy, 2011). Voucher specimens were deposited in the Ouellet-Robert entomological collection at the Université de Montréal.

3.1.3. Mummification rate estimates

The mummification rate is defined as the number of mummification events per unit of time and per plant. In our case study, we compared two estimates of mummification rate differing only in the procedure used to acquire each of their components. As parasitoids failing to emerge can lead to the accumulation of non-emerged mummies in the field, only emerged mummies were used in the calculation of both mummification rate estimates.

Many studies of aphid parasitoids consider the number of mummies from which parasitoids emerged on a given sampling date, without measuring the remaining development time of individual parasitoids in laboratory (e.g. Maisonhaute et al., 2017; Sigsgaard, 2002; Sturza et al., 2012). We therefore considered an *approximate mummification rate* defined as the number of emergences, including hyperparasitoids, from a sampling date as a whole, divided by the number of plants sampled and by a period corresponding to the time required for development after mummification. The effect of temperature on *A. certus* developmental rate from mummification to adult emergence has been characterized by Frewin et al. (2010). Hourly field temperatures were obtained from the CÉROM Grains Research Center's meteorological station located within 12 km of surveyed sites.

In addition to the approximate mummification rate, an *accurate mummification rate* was calculated by retroactively deducing when aphids had mummified in the field from the duration of parasitoid development in the laboratory. To consider timescale, the season was first divided into time intervals, which we defined from sampling dates. To associate a number of plants with an interval, we counted plants from previous sampling dates that could have allowed the detection of mummification over the entire interval. Then, the number of mummification events corresponding to both the interval and the associated plants was estimated retroactively from *Aphelinus* sp. emergence and from the relationship between development rate and temperature. Mummies taking more than the expected time to emerge were considered to have mummified at sampling. Because the timing of mummification could not be assessed for mummies containing hyperparasitoids, mummification events were weighted by the ratio of total emergence to *Aphelinus* sp. emergence at the sampling date.

3.1.4. Comparison of mummification rate estimates

A GLM was performed to relate the accurate mummification rate, as a predictor variable, to the approximate mummification rate, as a response variable. Identity link function ($\mu = \eta$) and a first order linear predictor in term of accurate mummification rate were chosen to impose a linear relationship between both mummification rates; however, regression parameters were estimated through quasi-likelihood, assuming proportional dependence between mean and variance ($\sigma^2 = a\mu$) to properly represent the error structure. A likelihood ratio-test was performed to test whether the statistical model was significantly different from the null model with a constant linear predictor. Two-tailed t-tests tested the equality of the intercept to zero (constant bias) and the slope to one (proportional bias). The level of significance was chosen as $\alpha = 0.05$ for all tests in this study. The regression was performed using the functions glm {stats} from R. Linear regression on log-transformed scales was avoided because it is not appropriate for rates of zero and because it alters the structure of biases through the relation between both mummification rates. The coefficient of determination R^2_{DEV} of Cameron and Windmeijer (1996) remains valid for quasi-likelihood and was calculated to assess the goodness of fit of the model.

3.1.5. Propagated mortality analysis

Propagated mortality analyses (PMA) were performed using only the accurate mummification rate for concision. Analyses were conducted as described in Section 2 and independently for each site. Colonization time was defined as the date at which aphid density reached one aphid per plant and estimated from the linear predictor parameters using Eq. (8). Yield relationship to CAD was considered linear based on Ragsdale et al. (2007).

3.2. Results

3.2.1. Aphelinus sp. mummification rates

In 2012, a total of 4569 parasitoids emerged from *Aphelinus* mummies, of which 4063 were *Aphelinus* sp. and 506 were hyperparasitoids. In 2013, a total of 1647 parasitoids emerged from *Aphelinus* mummies, of which 1556 were *Aphelinus* sp. and 91 were hyperparasitoids. A few *Aphidius* mummies were also collected during surveys in 2012 and 2013, from which only one and three parasitoids emerged, respectively.

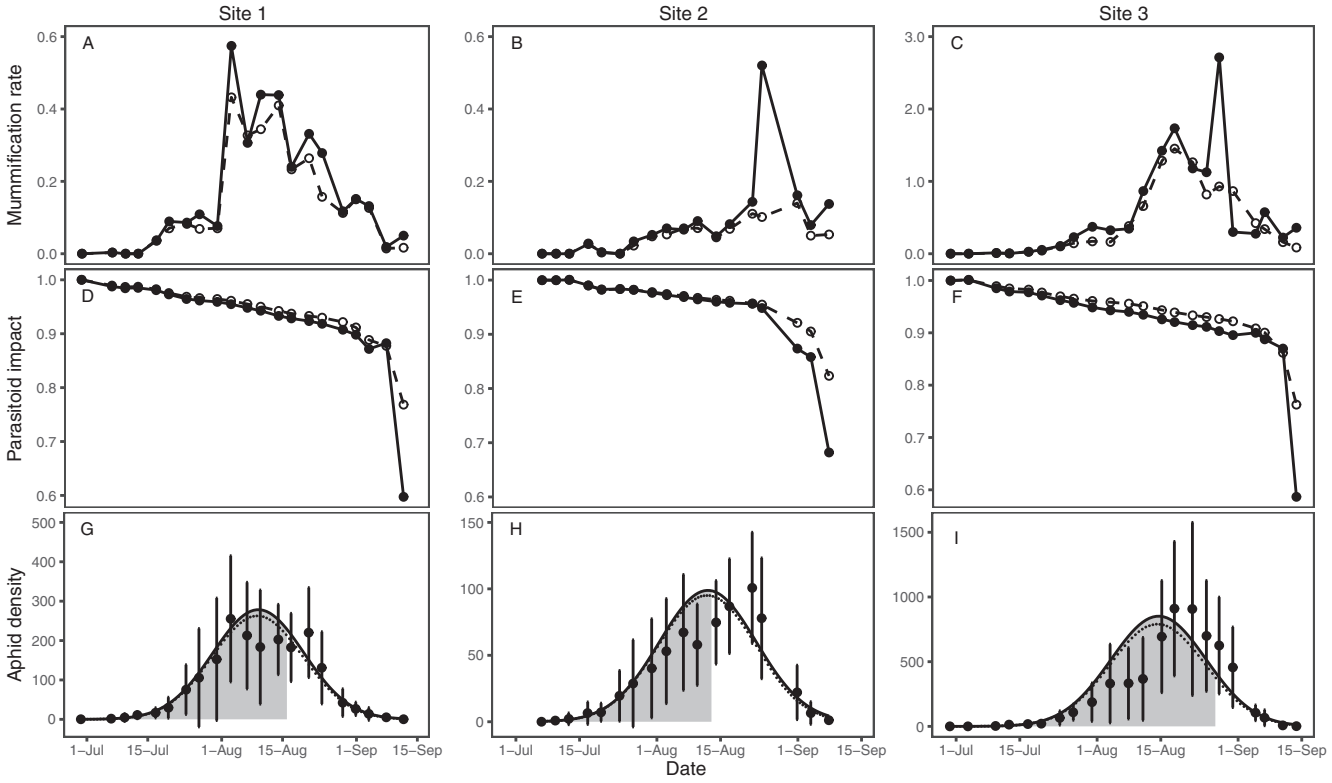

Fig. 1. Propagated mortality analysis for 2012. Important steps of the PMA are illustrated. A–C. Accurate (filled circles) and approximate (open circles) mummification rates (per day and per plant) are calculated from the same data at sampling dates. D–F. Parasitoid impact ($\gamma(t)$) calculated from accurate (filled circles) and approximate (open circles) mummification rates. G–I. Average aphid densities (per plant) and associated standard errors (filled circles and error bars) are compared to the predictions from the GLM representing the model by Costamagna et al. (2007) when considering the parasitoid impact as calculated from the accurate mummification rate. Predictions in presence (full line) and in absence (dotted line) of *Aphelinus* sp. are shown. The grey area correspond to the estimated CAD in absence of the parasitoid and over the threshold period, i.e. until soybean reach the full seed (stage R6). Units of mummification rate are mummies per plant per day, those of aphid density are aphids per plant while γ bears no units.

Overall, mummification rates were more or less unimodal with maxima occurring from early to mid August, i.e. during or after soybean aphid densities started to decrease, except for site 1 in 2013 which first peaked in mid July (Figs. 1 and 2). The GLM of the approximate mummification rate in function of the accurate mummification rate showed a R^2_{DEV} of 0.866. The statistical model was significantly different from the null model with a constant linear predictor (LR-tests: $\chi^2(\text{df} = 1)$, $p < .001$). The intercept of 0.007 (SE = 0.003) was small but statistically different from zero (*t*-test: df = 130, $p = .02$) while the slope of 0.732 (SE = 0.043) was unambiguously distinct from one (*t*-test: df = 130, $p < .001$).

3.2.2. Propagated mortality analysis of Aphelinus sp.

The seasonal progression of $\gamma(t)$ as well as soybean aphid density predictions in presence and absence of *Aphelinus* sp. are shown in Figs. 1 and 2 for the accurate mummification rate. The statistical model representing the Costamagna et al. (2007) model modified to account for the presence of parasitoids is detailed for each site in Table 1. Model predictions described well the observed soybean aphid densities per plant (R^2_{DEV} = 0.562–0.724; Table1), although some asymmetry was observed, particularly for site 3 in 2012 and site 1 in 2013 (Figs. 1 and 2). For all sites, the statistical model was significantly different from the null model with a constant linear predictor (LR-tests: $\chi^2(\text{df} = 2)$, $p < .001$). The average estimated aphid colonization time (t_0) happened on July 7 (SD = 2.52 days) in 2012, and 15 days earlier, on June 22 (SD = 2.52 days), in 2013. The intrinsic growth rate of aphid density at colonization time r_0 and its rate of decrease a were similar in both years and averaged 0.292 (SD = 0.042) per day and 0.0274 (SD = 0.0020) per day, respectively. A constant rate of decrease implies that peak aphid densities occurred at approximately the same period after colonization.

Analysis of peak aphid density and their control estimates are shown in Table 2. On average, the maximum aphid density occurred on August 11 (SD = 2.52 days) in 2012 and on July 30 (SD = 2.89 days) in 2013, 12 days earlier, but within the threshold period (Figs. 1 and 2, Table 3). In the absence of parasitoids, the estimated average for this maximum was of 286.8 (SD = 287.9) aphids per plant but reached 851.6 (SD = 484.5) aphids per plant for site 3 in 2012. Parasitoid impacts at peak density, $\gamma(t^*)$, were on average 0.944 (SD = 0.017) in 2012 and 0.988 (SD = 0.003) in 2013. The discrepancy seems to arise from a better synchrony of *Aphelinus* sp. with aphid populations in 2012. The highest impact was achieved at site 3 in 2012, with $\gamma(t^*)$ reaching 0.927.

Analyses of cumulative aphid-days and their control estimates are shown in Table 3. The threshold period ended when soybean reached stage R6 in mid to late August, with a global average of August 18 (SD = 5.29 days). In the absence of parasitoids, cumulative aphid-days at the end of the threshold period $CAD(t_E)$ was estimated to be on average 6051 (SD = 6009) aphids per plant, but reached 17,863 aphids per plant at site 3 in 2012. Parasitoid control of aphids at the end of the threshold period was higher in 2012, with an average $r_{CAD}(t_E)$ of 0.950 (SD = 0.023) compared to an average of 0.987 (SD = 0.005) in 2013. This aphid control by *Aphelinus* sp. was associated to average yield gains (Y_G) of 0.363% (SD = 0.476) in 2012 and of 0.037% (SD = 0.009) in 2013. Yield gain reached its highest value of 0.906% at site 3 in 2012, corresponding to a $r_{CAD}(t_E)$ of 0.926.

In terms of thresholds, peak aphid density in the absence of parasitoids exceeded the density-based EIL of 674 aphids per plant only at site 3 in 2012 (Table 2); in comparison, the CAD-based EIL of 5563 CAD per plant was reached for site 3 in 2012 and for site 1 in 2013 (Table 3). The presence of *Aphelinus* sp. reduced aphid density according to $N_p(t^*) = \gamma(t^*)N(t^*)$ and CAD according to $CAD_p(t_E) = r_{CAD}CAD(t_E)$,

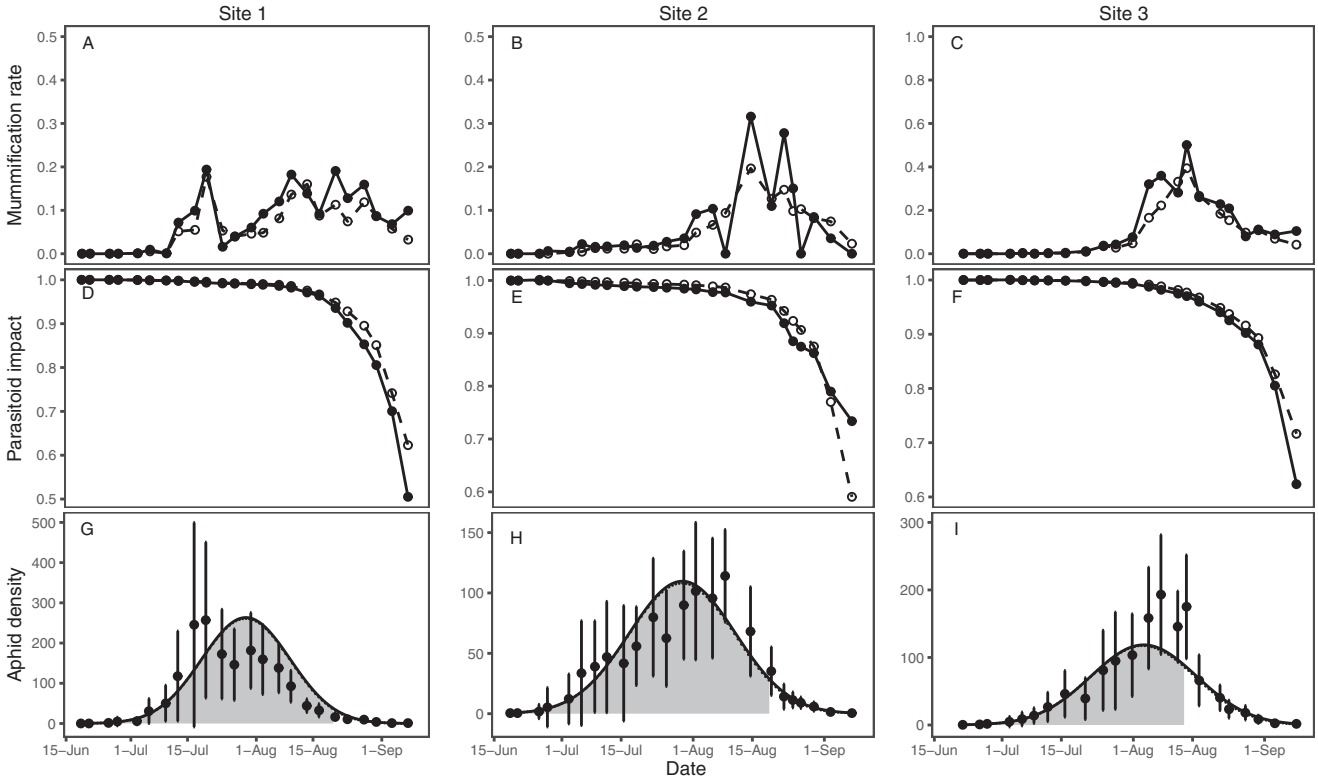

Fig. 2. Propagated mortality analysis for 2013. Important steps of the PMA are illustrated. A–C. Accurate (filled circles) and approximate (open circles) mummification rates (per day and per plant) are calculated from the same data at sampling dates. D–F. Parasitoid impact ($\gamma(t)$) calculated from accurate (filled circles) and approximate (open circles) mummification rates. G–I. Average aphid densities (per plant) and associated standard errors (filled circles and error bars) are compared to the predictions from the GLM representing the model by Costamagna et al. (2007) when considering the parasitoid impact as calculated from the accurate mummification rate. Predictions in presence (full line) and in absence (dotted line) of *Aphelinus* sp. are shown. The grey area correspond to the estimated CAD in absence of the parasitoid and over the threshold period, i.e. until soybean reach the full seed (stage R6). Units of mummification rate are mummies per plant per day, those of aphid density are aphids per plant while γ bears no units.

from Eqs. (6) and (7). In any case, these lower densities or CADs did not drop below thresholds (not shown).

4. Discussion

The development of the propagated mortality analysis (PMA) provides a new tool to quantify control of aphid populations by parasitoids throughout the season. We first utilized the population dynamics model developed by Costamagna et al. (2007) to characterize the temporal dynamics of aphid densities. In the process, we offered an alternative parameterisation of the model to consider unknown colonization time and advocated the use of an alternative method of regression, using GLM, to account for aphid density distribution. Second, we built upon the model of Costamagna et al. (2007) to estimate the impact of aphid parasitoids on aphid density. This impact is represented by $\gamma(t)$, which provides the ratio of the expected aphid density in the presence or absence of the parasitoid. The calculation of $\gamma(t)$ is based on both aphid densities and the rates at which aphid mummification occurs. Therefore, $\gamma(t)$ is unbiased toward parasitoid development time, as opposed to percent parasitism or absolute mummy counts; furthermore, it takes into account the timing of parasitoid-induced mortality with aphid population dynamics, as opposed to mummification rate alone. The method assumes that the Costamagna et al. (2007) model describing seasonal variations in aphid densities remains valid in the presence of

Table 1
Soybean aphid population dynamics. A GLM on observed aphid densities, while considering parasitoid impact $\gamma(t)$ computed from accurate mummification rates, provides a statistical representation of the aphid population dynamics model by Costamagna et al. (2007) adapted in presence of a parasitoid. The regression allows to estimate the colonization time (t_0), defined as when aphid density reach one aphid per plant, the population intrinsic growth rate at the colonization time (r_0) and the rate of linear decrease in intrinsic growth rate (a). The goodness of fit of the model is represented by the deviance-based R^2_{DEV}, which generalize R^2 for non normal distributions. Likelihood ratio tests (not shown) always indicate the model to be significantly better than the null model ($\chi^2(\text{df} = 2), p < .001$). Biological parameters (t_0, r_0, a) and their standard errors (SE) are calculated from the regression parameters, while the standard deviation (SD) is provided for means. Units of t_0 are days while those of r_0 and a are per day.

Sites		t_0	±	SE (SD)	r_0	±	SE (SD)	a	±	SE (SD)	R^2_{DEV}
2012	1	Jul-05	±	0.99	0.321	±	0.017	0.0285	±	0.0018	0.724
	2	Jul-10	±	1.82	0.284	±	0.029	0.0309	±	0.0035	0.610
	3	Jul-07	±	1.05	0.351	±	0.019	0.0260	±	0.0016	0.716
2013	1	Jun-22	±	0.32	0.305	±	0.007	0.0274	±	0.0008	0.670
	2	Jun-20	±	0.32	0.244	±	0.005	0.0260	±	0.0007	0.562
	3	Jun-25	±	0.44	0.247	±	0.007	0.0258	±	0.0010	0.653
Mean	2012	Jul-07	±	(2.52)	0.319	±	(0.033)	0.0285	±	(0.0025)	–
	2013	Jun-22	±	(2.52)	0.265	±	(0.034)	0.0264	±	(0.0008)	–
	Global	Jun-29	±	(8.52)	0.292	±	(0.042)	0.0274	±	(0.0020)	–

Table 2
Peak aphid density control. Estimates of peak aphid density ($N(t^*)$) and its time of occurrence (t^*) in absence of parasitoid are estimated through GLM on observed aphid densities by removing the parasitoid impact $\gamma(t)$, as calculated from the accurate mummification rate. Parasitoid impact at peak density $\gamma(t^*)$ is an estimate of control for aphid density which represents the ratio of the expected peak soybean aphid densities in the presence vs. absence of *Aphelinus* sp. Standard error (SE) is calculated by propagation of error from regression parameters at the site level, while standard deviation (SD) is provided in the cases of means. Units of t^* are days, those of $N(t^*)$ are aphids and $\gamma(t)$ has no units but ranges between 0 and 1.

Sites		(t^*)	±	SE (SD)	N(t^*)	±	SE (SD)	$\gamma(t^*)$	±	(SD)
2012	1	Aug-09	±	1.50	278.4	±	132.7	0.944		–
	2	Aug-12	±	2.29	98.8	±	71.5	0.962		–
	3	Aug-14	±	1.68	851.6	±	484.5	0.927		–
2013	1	Jul-29	±	0.97	263.6	±	54.2	0.990		–
	2	Jul-29	±	0.98	109.8	±	17.6	0.985		–
	3	Aug-03	±	1.21	118.7	±	25.7	0.990		–
Mean	2012	Aug-11	±	(2.52)	409.6	±	(393.2)	0.944	±	(0.017)
	2013	Jul-30	±	(2.89)	164.0	±	(86.3)	0.988	±	(0.003)
	Global	Aug-05	±	(7.00)	286.8	±	(287.9)	0.966	±	(0.027)

Table 3
Cumulative aphid-days control. Cumulative aphid-days (CAD), estimated in absence of the parasitoid from GLM on observed aphid densities by removing parasitoid impact $\gamma(t)$, are provided at the end of the pest management threshold period (t_E), i.e. when soybean reach full seed (stage R6). The estimate of control for CAD is the ratio $r_{CAD}(t_E)$ of cumulative aphid-days per plant in the presence vs. in absence of *Aphelinus* sp. at the end of the threshold period. The corresponding soybean yield gain associated to the parasitoid (Y_G) corresponds to the prevention of losses assuming a known linear relation between CAD and yield. Standard deviations (SD) are provided for means. Units of t_E are days, those of CAD are aphids days while $r_{CAD}(t_E)$ have no units and Y_G is expressed in terms of percentage with respect to maximum yield.

Sites		t_E	CAD (t_E)	±	(SD)	r_{CAD} (t_E)	±	(SD)	Y_G (%)	±	(SD)
2012	1	Aug-16	4732		–	0.951		–	0.161		–
	2	Aug-13	1104		–	0.972		–	0.021		–
	3	Aug-27	17,863		–	0.926		–	0.906		–
2013	1	Aug-20	5946		–	0.990		–	0.039		–
	2	Aug-19	3329		–	0.981		–	0.044		–
	3	Aug-13	3331		–	0.988		–	0.027		–
Mean	2012	Aug-18	7900	±	(8817)	0.950	±	(0.023)	0.363	±	(0.476)
	2013	Aug-17	4202	±	(1510)	0.987	±	(0.005)	0.037	±	(0.009)
	Global	Aug-18	6051	±	(6009)	0.968	±	(0.025)	0.200	±	(0.350)

natural enemies other than those studied, which seems to be the case for a common level of abundance of natural enemies. Third, we defined two estimates of control: (1) the parasitoid impact at peak aphid density, $\gamma(t^*)$; and (2) the ratio of cumulative aphid-days in presence vs. absence of the parasitoid at the end of the threshold period, $r_{CAD}(t_E)$. If the relation of CAD to yield is known, the yield gain associated with the presence of the parasitoid, Y_G, can be calculated and serve to estimate its economic value. Propagated mortality analysis only requires aphid densities and mummification rates to be available at the same dates and can be readily computed through the provided R code (Supplementary Material).

The method is simple and could facilitate the conceptual integration of aphid parasitoids into pest management programs. For instance, the impact of parasitoids could be incorporated into existing economic thresholds or could serve to establish thresholds that are specific to inundative release strategies. The required number of parasitoids to release could therefore be significantly reduced while aiming for aphid population suppression early in the season (Neuville et al., 2016). In our case study, we referred to experimental mummification rates while estimating parasitoid impact, without assuming any population dynamics for the parasitoid. Such an advantage, however, makes the estimated impact specific to the observed levels of aphid and parasitoid populations. The method could become predictive, and serve to optimize inundative release strategies, if the mummification rate could be calculated from the parasitoid's known functional response, i.e. the oviposition rate as a function of host density, and adult mortality rate in the field. Inundative releases strategies can be interpreted using PMA because parasitoid impact on aphid population dynamics, from the Costamagna et al. (2007) model, is already considered through $\gamma(t)$. The effect of insecticides on aphid populations could be similarly incorporated into aphid population dynamics if one knows their impact from efficacy trials. The central idea behind the propagated mortality analysis is to consider the repercussion of parasitoid-induced mortality on host dynamics. In this perspective, the method is not restricted to the model of Costamagna et al. (2007) and can be developed for aphid species, or host-parasitoid associations, that possess different population dynamics. The propagated mortality analysis could also be extended to incorporate other aphid natural enemies. With an aphid suppression estimate $\gamma(t)$ that is invariant with respect to the population dynamics of natural enemies, the method offers interesting opportunities to compare their efficacy in reducing pest populations in the field.

Comparison of mummification rate estimates through regression ($R^2_{DEV} = 0.866$) showed that use of the approximate mummification rate of *Aphelinus* sp. on the soybean aphid leads mostly to a proportional underestimation of parasitoid-induced mortality ($m_{approximate} \simeq s \cdot m_{accurate}$ with $s = 0.732$). The approximate mummification rate estimate consists of an average of former mummification events and is likely to be lower than the accurate mummification rate when the latter is increasing. Considering this discrepancy, the accurate mummification rate estimate is required to establish the impact of parasitoids on aphid populations. Still, the approximate mummification rate remains more accessible and could be used either directly as a magnitude of parasitoid-induced mortality, or after correction for the proportional error when available ($m_{accurate} \simeq 1/s \cdot m_{approximate}$). The correction can be propagated directly to $\gamma_{accurate}(t) = \gamma^{1/s}_{approximate}(t)$, from Eq. (5), but PMA estimates of control and yield gain associated with the parasitoid must be recalculated. R code provided in Supplementary Material to perform PMA facilitates the incorporation of such corrections.

Soybean aphid mummification rates by *Aphelinus* sp. were globally low (< 0.3–3.0 mummies per plant per day) over the two years of the study (Figs. 1 and 2). Maisonhaute et al. (2017) recently observed

average densities of 2.33–8.55 *Aphelinus* mummies per plant in soybean fields. These densities correspond to mummification rates that are similar to those of the present study, considering that the development time of *A. certus* mummies ranges roughly from 5 to 10 days between 20 and 30 °C (Frewin et al., 2010). Many aphid parasitoid species only exploit a fraction of hosts available in the field (Brodeur and Rosenheim, 2000; Müller et al., 1999), usually between 1 and 10% (Brodeur et al., 2017; Mackauer and Völkl, 1993), although intermediate levels of parasitism (< 20%) have been reported in grains (Schmidt et al., 2003, 2004; Thies et al., 2005; Lumbierres et al., 2007; Holland et al., 2008; Traugott et al., 2008; Lumbierres et al., 2011) with high percentages often representing late season parasitism, once aphid densities have dropped. Only a few studies have reported high parasitism levels when aphid populations were high (Sigsgaard, 2002; Sturza et al., 2012).

Increases in mummification rates also lagged behind the soybean aphid population growth and reached its maximum at or after peak aphid density. The increase in mummification rate late in the season suggests low levels of field colonization early in the season by *Aphelinus* sp., despite the fact that *A. certus* is known to exit winter diapause from late May to early June in Québec (Gariépy, 2011). Late colonization by parasitoids has been recognized as problematic in annual crops, due to high levels of seasonal perturbation (Neuville et al., 2016), and is also influenced by landscape composition (Gardiner et al., 2009; Maisonhaute et al., 2017). Alternatively, the late increase in mummification rates could indicate a poor retention of parasitoids at low soybean aphid densities, which is likely if the surrounding landscape is rich in alternative hosts, as supported by the marginal value theorem (Charnov, 1976). Subsequent efforts to examine the impact of *Aphelinus* sp. as a biocontrol agent of the soybean aphid should focus on factors that determine its establishment and efficiency early in the growing season.

Low mummification rates and their late season increase may help to explain why estimates of soybean aphid control by *Aphelinus* sp. remained poor, with $\gamma(t^*)$ in the range 0.927–0.990 and $r_{CAD}(t_E)$ in the range of 0.926–0.990. Density-based and CAD-based estimates of control both remained in the same range in our case study, which is surprising as t^* and t_E differed greatly (Figs. 1 and 2, Tables 2 and 3). Nonetheless, a $r_{CAD}(t_E)$ value of 0.926 represents a decrease of 7.4% in CAD, and is associated with natural control from only one species of natural enemy that arises at no cost. Because the relation of CAD to yield is linear for the soybean aphid, it also translates into the equivalent in yield loss prevention due to aphids. However, when expressed in term of total soybean production, yield loss (Y_G) fell below 1% (Table 3), mostly because aphid levels in our study decreased yield only slightly.

Underestimation of aphid control arises when the mummification rate is assessed only from emerging parasitoids because post-mummification mortality of parasitoids may occur (Brodeur and Rosenheim, 2000; Desneux et al., 2009); although these are not counted at emergence, they killed their aphid host. In addition, other parasitoid-induced host mortality factors are not considered when only mummification rates are analyzed. These include host feeding, ovipositor probing trauma, paralysis without oviposition, and host sterilization (Abram et al., 2016; Jervis and Kidd, 1986; Van Driesche, 1983). However, if one can establish a relation between mummification rate and these mortality factors, the overall mortality induced can be estimated accordingly (Van Driesche et al., 1990). When this relation remains roughly constant through time, the same proportional correction ($m_{overall} \simeq 1/s \cdot m_{measured}$) as between accurate and approximate mummification rate estimates can be applied to calculate corrected estimates of control and yield gain, with s the survival rate associated with mortality factors not measured.

Estimates of soybean aphid control by *Aphelinus* sp. can be corrected accordingly for post-mummification mortality. Hyperparasitism has already been accounted for in mummification rates, whereas rough mortality estimates can be acquired from other studies. Intraguild predation (IPG) on mummies averaged 18.1% in soybean fields (Costamagna et al., 2008), while the intrinsic mortality of *A. certus* during the mummification phase reached about 12% in laboratory experiments (Frewin et al., 2010; Hopper and Diers, 2014), with no effect of temperature between 15 and 30 °C (Frewin et al., 2010). Considering intrinsic mortality and IPG to be approximately constant throughout the season, at the aforementioned values, the combined survival rate s reach (1–0.12) (1–0.181) ≃ 0.72. Using data from site 3 in 2012, which conferred the highest control in this study, the corresponding corrected $\gamma(t^*)$, $r_{CAD}(t_E)$ and Y_G would respectively have reached at best 0.900, 0.899 and 1.28%.

During the two-year field study, the model of Costamagna et al. (2007) in presence of the parasitoid tended to represent the soybean aphid density well (R^2_{DEV} = 0.562–0.724). However, some asymmetry in the observed aphid densities could engender a certain lack-of-fit. The inclusion of t_0 in the model, allowing aphid colonization to occur at different dates, greatly increased our ability to interpret the results. Aphid establishment occurred later in 2012 than in 2013, but so did peak aphid densities. This effect was observed among sites in general (Table 1), with a quasi-constant soybean aphid population decrease in intrinsic growth rate a, independent of aphid pressure (Tables 2 and 3). This observation supports the idea that the decrease in the soybean aphid intrinsic growth rate a is temporal rather than depending on the cumulative number of aphids throughout the season, thereby justifying the use of the model of Costamagna et al. (2007) rather than the one of Matis et al. (2007).

This decrease in intrinsic growth rate a is not seasonal, however, because of its relation with the time of colonization t_0, and also cannot be attributed solely to plant phenology, as soybean reached full seed (stage R6) at approximately the same date in both years (Table 3; Figs. 1 and 2). Other natural enemies, especially predators, play a prominent role in regulating soybean aphid populations in North America, (see Ragsdale et al. 2011 for a review), and could contribute more than initially expected (Costamagna et al., 2007) to the mid-season decline of aphid populations. Although we focused on measuring parasitoid-induced mortality in this study, integrating other types of natural enemies would isolate their contribution to a and explain the observed asymmetry in soybean aphid population dynamics.

5. Conclusion

We developed a method, designated as the propagated mortality analysis (PMA), to assess the impact of parasitoids on growing aphid populations. Estimates of control are provided for both aphid density and cumulative aphid-days and can be compared with their respective thresholds. The yield gain associated with parasitoid impact on aphid populations can also be calculated and used to estimate their economic benefit. The PMA should apply to most aphid-parasitoid associations, and we encourage its utilization in future studies by providing R code for its implementation. As the PMA is invariant to the population dynamics of parasitoids, it could greatly increase predictability in the use of biological control agents and serve to compare the contributions of multiple natural enemies.

Our results showed that *Aphelinus* sp. did not contribute greatly to control of soybean aphid populations in the field. Their late colonization in soybean fields seems to be the probable cause for their poor impact on soybean aphid populations. However, other elements of the parasitoid biology are likely to be involved. The intrinsic potential of *Aphelinus* species as biological control agent of aphid pests remains unclear in the literature, especially compared to aphidiine braconids. Several biological traits differ significantly between the two groups. For instance, *Aphelinus* have lower reproductive capacity, longer handling time and poorer dispersive capacity than aphidiine parasitoids, but they benefit from prolonged longevity and can also kill aphids by host feeding (Hopper and Diers, 2014). Future studies should focus on

characterizing the distinct roles play by *Aphelinus* sp. and other natural enemies on the control of soybean aphid populations. Particular attention should be made in decoupling the effects of natural enemies abundance, their individual suppressive potential (e.g. voracity, fecundity), and elements of their seasonality (e.g. synchrony, voltinism) on the regulation of aphid populations.

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Appendix A. Supplementary Material

Supplementary Material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocontrol.2018.01.002.

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