Simulating the effectiveness of three potential management options to slow the spread of emerald ash borer (*Agrilus planipennis*) populations in localized outlier sites

Rodrigo J. Mercader, Nathan W. Siegert, Andrew M. Liebhold, and Deborah G. McCullough

Abstract: The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is a devastating, invasive insect pest of ash trees, *Fraxinus* spp., in North America. Using a simulation model, we evaluated three potential management options to slow the spread of *A. planipennis* in discrete outlier sites: (*i*) removing ash trees to reduce available host phloem resource, (*ii*) girdling ash trees to attract ovipositing female beetles and destroying the trees before larvae complete development, and (*iii*) applying a highly effective systemic insecticide. Simulations indicate that systemic insecticide applications provided the greatest reduction in the radial spread of *A. planipennis*. In simulations in which management options were applied only within a 300 m radius from the origin of the infestation, insecticide applications reduced the radial spread by 30% and larval consumption of ash phloem by 40% beyond the treated area. In contrast, girdling ash trees reduced the radial spread by 15% and larval consumption of ash phloem by 20% beyond the treated area. Both of these management options significantly reduced the spread of *A. planipennis* when treatments were applied 1 to 4 years after infestations were initiated. Reducing ash phloem by removing ash trees decreased population size within treated areas but did not reduce the radial spread, population size, or larval consumption of ash phloem beyond treated areas.

Résumé : L'agrile du frêne, *Agrilus plenipennis* Fairmaire (coléoptère, buprestidés), est un insecte nuisible envahissant qui est dévastateur pour le frêne, *Fraxinus* spp., en Amérique du Nord. À l'aide d'un modèle de simulation, nous avons évalué trois options potentielles de lutte pour ralentir la propagation d'*A. plenipennis* dans différents sites enclavés : (*i*) l'élimination des frênes pour réduire la ressource disponible que constitue le phloème de l'hôte, (*ii*) l'annélation des frênes pour attirer les insectes femelles durant la période d'oviposition et éliminer les arbres avant que les larves complètent leur développement et (*iii*) l'application d'un insecticide systémique très efficace. Les simulations indiquent que les applications d'insecticide systémique réduisent le plus la propagation radiale d'*A. plenipennis*. Dans les simulations où les options de lutte ont été appliquées seulement à l'intérieur d'un rayon de 300 m du point d'origine de l'infestation, les applications d'insecticide ont réduit la propagation radiale de 30 % et l'alimentation dans le phloème du frêne par les larves de 40 % au-delà de la zone traitée. Par contre, l'annélation des tiges de frêne a réduit la propagation radiale de 15 % et l'alimentation dans le phloème du frêne par les larves de 20 % au-delà de la zone traitée. Ces deux options de lutte ont significativement réduit la propagation d'*A. plenipennis* lorsque les traitements étaient appliqués un à quatre ans après le début des infestations. L'élimination des frênes pour réduire la quantité de phloème disponible a diminué la taille de la population à l'intérieur des zones traitées mais n'a pas réduit la propagation radiale, la taille de la population, ni l'alimentation dans le phloème du frêne au-delà des zones traitées.

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Introduction

Nonindigenous invaders threaten biodiversity (Mack et al. 2000) and may profoundly affect evolutionary (e.g., Strauss et al. 2006) and community–ecosystem processes (e.g., Krushelnycky and Gillespie 2008). Invasive pests in forested and urban forest settings cost plant-based industries, regulatory agencies, and property owners billions of dollars annually (Pimentel et al. 2005; McCullough 2011). The process by which biological invasions proceed can be divided into three phases: arrival, establishment, and spread (Lockwood et al. 2007; Liebhold and Tobin 2008). Early intervention targeted at the two initial phases is generally regarded as the most cost-effective management option for invasive species (Myers et al. 2000; Leung et al. 2002). However, although international trade regulations and inspections

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have undoubtedly reduced the arrival of nonindigenous species, increases in world trade and travel have led to a corresponding increase in the introduction of exotic species (e.g., Work et al. 2005; Liebhold et al. 2006; McCullough et al. 2006).

Since the discovery of established populations of emerald ash borer (*Agrilus planipennis* Fairmaire; Coleoptera: Buprestidae) in Michigan and Ontario in 2002, there has been growing recognition that this insect represents a serious ecological and economic problem (Poland and McCullough 2006). *Agrilus planipennis* females lay eggs on the bark of ash trees (*Fraxinus* spp.), and larvae bore into the tree, where they feed on phloem and cambium, disrupting the vascular system and eventually killing the tree (Cappaert et al. 2005). The lack of resistance in native hosts (Anulewicz et al. 2008; Rebek et al. 2008) indicates that this insect could effectively eliminate most North American *Fraxinus* species if its range expands across the entire continent. Ash trees are an important component of many North American forests and urban and suburban communities (Poland and McCullough 2006). Potential costs of *A. planipennis* over the next 10 years in developed communities alone were projected to be US$10.7 billion (Kovacs et al. 2010). Given the high economic impact associated with ash resources, particularly in urban settings, considerable expenditures may be justified to slow the spread of this insect (Kovacs et al. 2010).

Once established, the spread of many invasive species, including *A. planipennis*, is characterized by stratified dispersal (also known as stratified diffusion). Stratified dispersal occurs in organisms with at least two separate mechanisms of dispersal, resulting in both short- and long-distance dispersal (Shigesada and Kawasaki 1997). This leads to a spread process marked by the establishment of satellite colonies ahead of the main invasion front. These satellite colonies typically grow, coalesce, and ultimately increase the speed of the invasion front. Consequently, any action to reduce their formation or growth can significantly decrease the spread of an invasive species (e.g., Shigesada and Kawasaki 1997; Sharov and Liebhold 1998; Liebhold and Tobin 2008). In addition, the small population sizes typical of newly formed, isolated populations may make successful management more practical.

Agrilus planipennis larvae develop under the bark for 1 to 2 years, depending on host vigor (Siegert et al. 2007; Tluczek 2009), and nonhuman-mediated spread is limited to the localized dispersal of gravid females. Taylor et al. (2010) recorded the average flight capacity for *A. planipennis* in flight mills as 1.3 km/day. However, the distance traveled is likely considerably lower. In a random-walk model based on the same data, 2 km of flight led to a total displacement of approximately 250 m (Taylor et al. 2010). In addition, field studies have indicated that over 90% of eggs laid by *A. planipennis* females occur on trees within 500 m of the beetles' emergence point (Mercader et al. 2009; Siegert et al. 2010). In contrast, anthropogenic transport of infested trees or wood can lead to long-distance dispersal events and the development of satellite colonies far beyond the main invasion front (Cappaert et al. 2005). Numerous satellite colonies in Michigan were established through movement of ash nursery stock, logs, and firewood prior to the discovery of *A. planipennis* in 2002 and subsequent establishment of quarantines (Cappaert et al. 2005; Siegert et al. 2010). As of September 2010, satellite populations of *A. planipennis* had been found in at least 15 states and two Canadian provinces. The high specificity of *A. planipennis* for ash tree hosts (Cappaert et al. 2005; Anulewicz et al. 2008) leads to a strong influence of ash distribution on the localized dispersal of *A. planipennis* (Siegert et al. 2010; Mercader et al. 2011).

Potential management options proposed to slow the nonhuman-mediated spread of *A. planipennis* from localized outlier sites include (*i*) harvesting or removing ash trees to reduce the phloem available for larval development, (*ii*) girdling ash trees to attract ovipositing female beetles and subsequently destroying the trees before progeny develop, and (*iii*) applying a highly effective systemic insecticide to create passive population sinks (McCullough and Poland 2010). Potential production of *A. planipennis* beetles depends on the phloem area available for larval development (McCullough and Siegert 2007). Harvesting or destroying ash trees will reduce the potential maximum *A. planipennis* population size in a defined area. This would presumably reduce the spread of the population by reducing the maximum number of dispersing beetles. In addition, removing trees of merchantable size can generate an economic benefit from a resource that is otherwise likely to be lost.

Girdling and destroying trees is less likely to generate direct economic benefits and typically requires more labor. However, girdling and destroying trees has the potential to directly reduce local *A. planipennis* population size in an outlier site and consequently affect spread. Girdled ash trees are significantly more attractive than healthy trees to ovipositing *A. planipennis* females (McCullough et al. 2009*a*, 2009*b*), particularly in areas with low *A. planipennis* densities. Therefore, girdled trees may be used to concentrate the future cohort of *A. planipennis* larvae into a known area, facilitating their removal from the population and limiting the spread of the population.

The third management option that we evaluate here, the application of an effective insecticide, offers an important advantage. It is the only option that protects existing live ash trees, which can be of significant economic benefit in residential or commercial areas (Kovacs et al. 2010). Recent studies have shown that the use of the relatively new systemic insecticide emamectin benzoate, applied as a trunk injection, provided nearly 100% control of *A. planipennis* larvae for at least 2 years (Herms et al. 2009; McCullough et al. 2010). Control extended over 2 years offers some economic and logistical advantages for incorporating systemic insecticides into management strategies targeted at reducing the spread of *A. planipennis*.

Despite the potential of these three management options to reduce *A. planipennis* spread, limited information on the effectiveness of these management options currently exists. Here, we use simulations to contrast the potential for these three management strategies to slow the spread of *A. planipennis* in recently detected satellite populations. In particular, we use a spatially explicit simulation model of the spread of *A. planipennis* based on field-collected data from satellite populations in the Lower Peninsula of Michigan, USA. Dispersal in this model is limited to movement of *A.*

planipennis females by flight and anthropogenic movement is not included.

Materials and methods

General model of *A. planipennis* spread

The underlying model that we used to examine the effect of the three management options on localized spread is a spatially explicit, coupled lattice model of *A. planipennis* population growth and spread from small, isolated colonies described in Mercader et al. (2011). The lattice is composed of a "phloem grid", which consists of a matrix of cells with values for available ash phloem in each cell. The model couples population processes relevant to the spread of *A. planipennis* onto matrices that record the quantity of available ash phloem and the number of *A. planipennis* larvae that develop in 1 or 2 years. Population processes linking these matrices include (*i*) emergence of adult beetles in a particular year, (*ii*) dispersal of adult beetles, and (*iii*) population growth and loss of ash phloem through consumption by developing *A. planipennis* larvae, which were determined and parameterized using data collected from multiple field sites (see Mercader et al. 2011).

Emergence of adult beetles in a particular year represents a combination of the number of larvae developing in 1 and 2 years from eggs laid in the previous 1 and 2 years, respectively. The proportion of larvae developing in 1 or 2 years is dependent on host quality, with stressed ash trees leading to a faster development than healthy ash trees (Siegert et al. 2007; Tluczek 2009). Because of the increase in stressed trees as *A. planipennis* populations build, there is also an increase in the proportion of 1-year larvae. Here the proportion of *A. planipennis* developing in 1 or 2 years is determined using a function describing the proportion of 2-year larvae in relation to population density. This function was developed using data collected from 208 ash trees in nine sites in seven Michigan counties consisting of state forests, campgrounds, and highway right-of-ways. Density of *A. planipennis* in these areas ranged from very low (<10 larvae/m^2) to sites where trees were heavily infested and severely declining (>90 larvae/m^2).

Following emergence, adults in the model disperse throughout the matrix, avoiding or exiting cells devoid of ash trees. Adult dispersal was determined using a negative exponential function estimated from data gathered from an infestation originating from a single point source in an isolated area in Livingston County, Michigan, and validated using data from a second site located in Lenawee County, Michigan (Mercader et al. 2009). Following dispersal, the number of larvae developing from eggs laid by females is determined based on population growth estimates quantified for an outlier population in Ingham County, Michigan (Mercader et al. 2011). Finally, the quantity of phloem consumed by individual larvae during their development was estimated from McCullough and Siegert (2007) to be 0.0113 m^2 of phloem per larva. Population growth in the model is not allowed to exceed the maximum number of larvae that can develop from the available ash phloem resource.

The R code for the original model can be found in Mercader et al. (2011). The adapted code, including the management options described below, can be found in Supplemental Appendix S1[2].

Local harvest or removal of ash trees

Efforts to eradicate *A. planipennis* populations in outlier sites have been largely unsuccessful due to the difficulty of accurately delimiting *A. planipennis* infestations and the flight capabilities of mated *A. planipennis* females. Flight mill studies have indicated that the average flight capacity of mated adult females is 1.3 km/day and, for some females, may be up to 7 km/day (Taylor et al. 2010). In addition, *A. planipennis* larvae can develop in ash trees that are only 2.5 cm in diameter, requiring an extensive effort to remove all potential host resources. For these reasons, a reduction, rather than elimination, of available ash phloem has been proposed as a means to reduce overall population size and consequently decrease the number of beetles that could disperse from newly established outlier sites. Ash inventory data collected from several sites in Michigan indicated that approximately 50% of the available ash phloem was contained within trees ≥ 27.9 cm (11 in.) in diameter at breast height (DBH) (McCullough and Siegert 2007). These large trees, however, accounted for only 6.2% ± 1.0% of the stem count (McCullough and Siegert 2007). Removing the large, merchantable trees, therefore, could be a practical approach for substantially reducing host phloem in an outlier site. Here, we assume that all phloem reduction would occur during the fall or winter, after oviposition and initial larval development but before adult emergence. This treatment was simulated by reducing the phloem estimated to be present in trees ≥ 27.9 cm DBH (50% of available phloem) for each treated cell prior to adult dispersal and removing any larvae expected to be in the phloem.

Girdled trees

Girdled ash trees are more attractive to egg-laying *A. planipennis* females, presumably due to an overall attraction to changes in volatiles and possibly visual cues associated with stressed trees (McCullough et al. 2009*a*, 2009*b*). This attraction provides an opportunity to use girdled trees as population sinks, effectively employing an "attract and kill" strategy. Girdled trees are simulated in the model by removing the phloem area and the number of larvae expected to be in the girdled tree. As *A. planipennis* density increases in an area, however, the proportion of stressed trees also increases. Consequently, the attractiveness of girdled trees relative to nongirdled trees is likely to diminish over time. Larval densities on girdled ash trees and untreated ash trees of similar size, age, and growing conditions were recorded at several Michigan sites from 2003 to 2007 during studies related to *A. planipennis* biology (Tluczek 2009) and detection methods (McCullough et al. 2009*a*, 2009*b*).

To determine the relationship between the relative attractiveness of girdled trees and the *A. planipennis* density in a site, we performed a linear regression between the ratio of larvae on girdled and untreated trees and the larval density in untreated trees recorded in these sites. A power function provided an adequate fit ($r^2 = 0.87$): $y = 20.5x^{-0.56}$, where y

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[2] Supplementary data for this article are available on the journal Web site (http://cjfr.nrc.ca).

is the ratio of larvae on girdled and nongirdled trees and x is the larval density in control trees (Fig. 1). We used this relationship to estimate the proportion of larvae expected to be removed from the population per square metre of ash phloem present in each cell.

An important constraint to the use of girdled trees is that not all ash trees in an area will be suitable or accessible for girdling. For comparison purposes, here we assumed that, as with ash removal, only trees ≥ 27.9 cm DBH would be used as trap trees. To simulate this constraint, we modeled the quantity of phloem available to be girdled as phloem present in trees ≥ 27.9 cm DBH at the start of each simulation, with a default value of 50% of the available phloem. For simplicity, we also assumed that all trees ≥ 27.9 cm DBH were of equal size (27.9 cm DBH) and only a single tree was treated per cell every year.

To illustrate the effect of the above constraints on the effectiveness of girdled trees as a management strategy, we simulated the spread of *A. planipennis* when girdled trees ≥ 27.9 cm DBH (10.32 m^2 of phloem) are applied in four scenarios: (*i*) as described above, (*ii*) excluding the limitation that only a proportion of available trees can be girdled, (*iii*) excluding the loss in relative attractiveness in girdled trees as sites become increasingly infested, and (*iv*) excluding both the limitation that only a proportion of trees are available for girdling and the loss in relative attractiveness of girdled trees.

Application of systemic insecticides

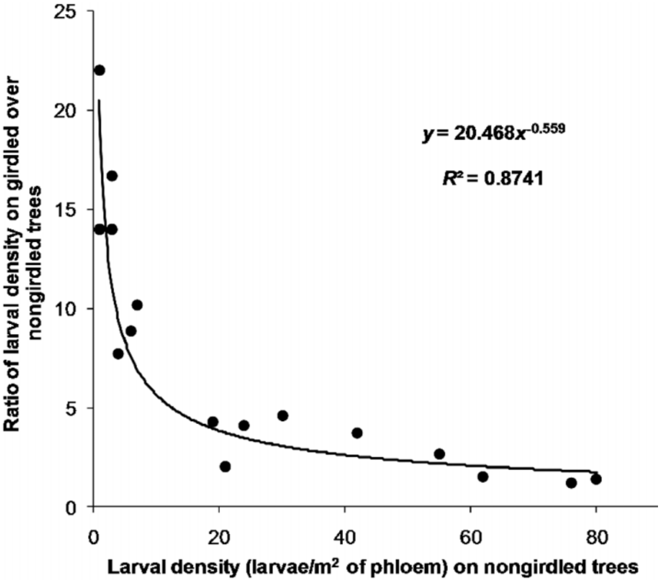
Because of costs and logistical considerations of applying a trunk-injected systemic insecticide, we assumed that the number of trees that could be treated in any given area is limited. For comparison purposes, we again assumed that insecticide applications would target trees ≥ 27.9 cm DBH (default = 50% of available ash phloem). In our simulations, only the proportion of phloem determined to be in trees ≥ 27.9 cm DBH at the start of a simulation was treated. Insecticide applications were assumed to completely protect trees and to exhibit no repellency effects. Therefore, the proportion of larvae killed by the insecticides was considered to be the proportion of treated phloem per cell, and the phloem contained in treated trees ≥ 27.9 cm DBH was not consumed by *A. planipennis*.

Insecticide applications were simulated in the model by subtracting the number of larvae expected to be in treated ash phloem. As with trees available for girdling, phloem available in trees ≥ 27.9 cm DBH and phloem available in trees < 27.9 cm DBH were accounted for separately in each cell. Once insecticide treatments were applied to chosen cells, the larvae developing in the proportion of phloem contained in treated trees were assumed to be eliminated from the population as early instars, so that the phloem area present in treated trees would be unaffected by larval feeding.

Beetle attraction to areas containing stressed or girdled trees

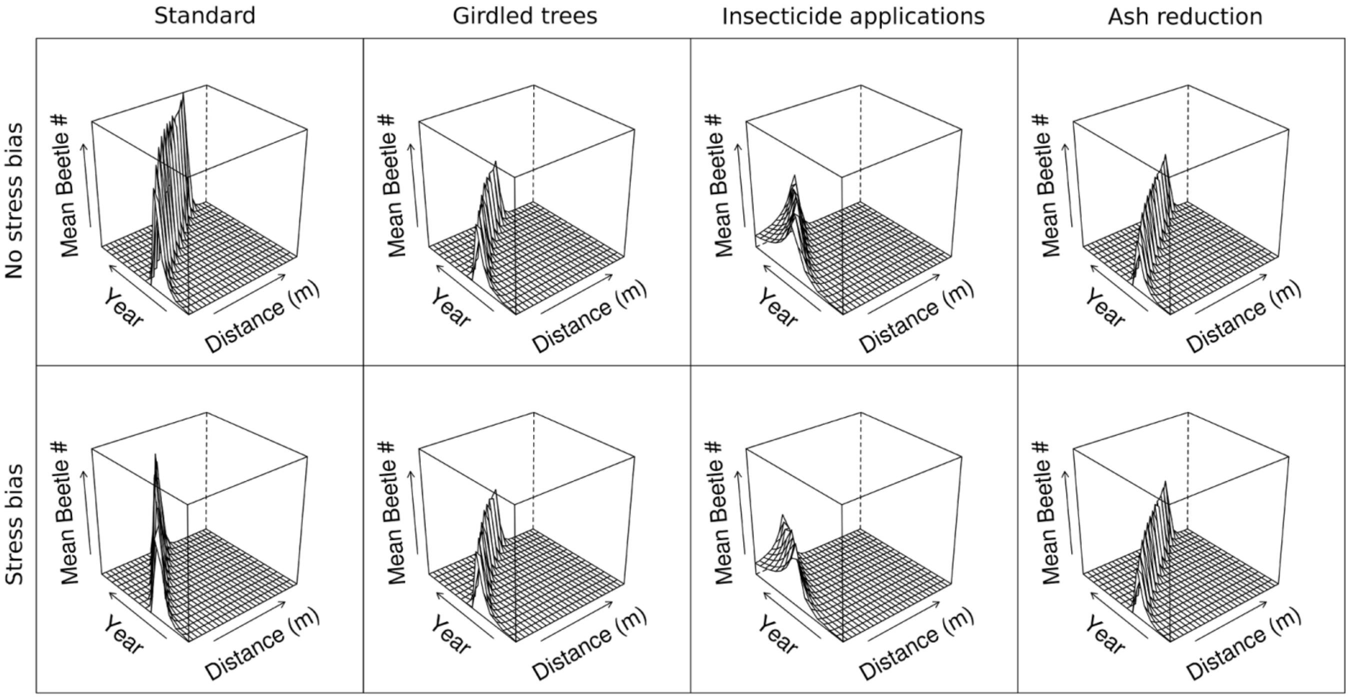
An important component of understanding the spread of an organism is the potential for directed movement to influence spread, which may affect the relative efficacy of management options. In addition to being more attractive compared with neighboring healthy trees, movement of *A. planipennis* populations towards areas containing girdled trees has been observed in low-density sites (Siegert et al. 2009). As previously noted, attraction to girdled trees is presumed to be a consequence of an overall attraction to stressed trees, potentially leading to a general attraction towards areas with stressed trees. Previous simulations (Mercader et al. 2011) indicated that inclusion of attraction to stressed trees leads to a reduction in the radial spread of the population. This influence on spread could presumably be important when considering the efficiency of management options. Here, we simulate the attraction of *A. planipennis* to areas containing trees stressed by girdling or by damage induced by *A. planipennis* larvae, following the methods described in Mercader et al. (2011). Preliminary results from field studies (Siegert et al. 2009) indicate that the presence of girdled trees can increase the attraction of an area containing girdled trees relative to an adjacent area without girdled trees up to sevenfold. To simulate the potential influence of this effect on spread, here we assumed that cells containing girdled trees or cells in which more than 33% of the initial phloem was consumed would contain sufficiently stressed trees to generate a sevenfold increase in attraction. Based on this assumption, we increased the attraction of cells containing a girdled tree by a factor of seven. For cells without girdled trees, we increased the attraction to cells containing stressed trees as a linear function of the proportion of phloem consumed by larvae (100% when no phloem was consumed, 700% when greater than 33% of available was phloem consumed).

Fig. 1. Ratio of *A. planipennis* larvae on girdled trees to larvae on nongirdled trees as a function of larval density in nongirdled trees in 16 outlier sites in Michigan, USA.



It is important to note that within the spread model, dispersal between cells is simulated in the model as a proportion (Mercader et al. 2011; Supplemental Appendix S1[2]); therefore, an increase in the attractiveness of a cell is dependent on the status of other cells in the environment. For example, the proportion of gravid females exiting a cell containing a girdled tree and entering an adjacent cell contain-

Fig. 2. Mean number of *Agrilus planipennis* beetles (mean beetle #) by distance for simulations with no treatments (standard) or when girdled trees, insecticide applications, or ash reduction treatments are applied. All treatments were applied to the entire artificial environment. Simulations were performed without any bias in movement towards areas containing stressed trees (no stress bias) and with a bias in movement towards areas containing stressed trees (stress bias).



ing another girdled tree is identical to the proportion exiting a cell not containing a girdled tree and entering an adjacent cell also not containing a girdled tree.

Simulations

Radius of treatment

Two sets of simulations applying each of the management options outlined above were performed varying the distance from the origin of the infestation to which treatments were applied. Treatments were applied to all cells within a specified distance from the origin of the infestation, referred to from here on as the "radius of application". For these simulations, the specified distances (i.e., radii of application) were varied from 0 to 1700 m in 50 m increments (i.e., one cell). The first set of simulations was designed to evaluate effects of varying the intensity of treatments applied per cell. The intensities of the three treatments rely on the quantity of phloem (trees) being treated. For this reason, we varied the proportion of phloem available to be treated in each cell from 0% to 90%, in addition to varying the radius of application. In the second set of simulations, the proportion of phloem available to be treated was maintained at 50%, but treatments were initiated 0, 1, 2, 3, and 4 years after the start of infestations to simulate variation in detection thresholds of outlier populations.

Both sets of simulations were conducted in homogeneous environments consisting of a matrix of 100 × 100 cells, where each cell was 50 × 50 m in size and contained 200 m^2 of ash phloem. The 200 m^2 of ash phloem per cell was based on ash densities observed in intensively sampled sites in Midland Coounty, Michigan. All infestations were initiated at the center of the environment, with an initial population size of 100 adult beetles and assuming a 50:50 sex ratio.

Spread beyond treated area

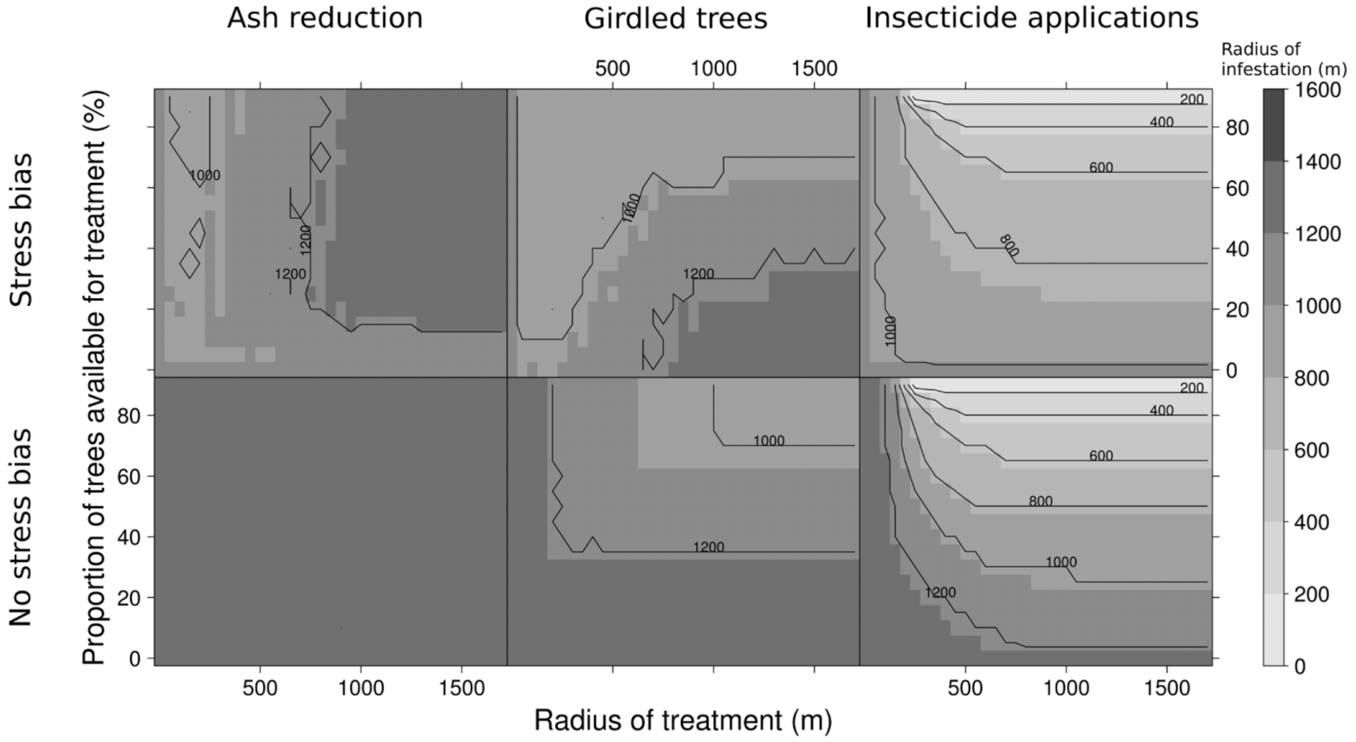
We assumed that an important goal of the three management options was to reduce the spread of *A. planipennis* and protect ash trees beyond the managed area. Here, we simulated the spread of *A. planipennis* at a site to which the above treatments were applied to a 300 m radius from the origin of the infestation and observed the spread beyond this area for a 15-year period. These simulations were conducted in a two-dimensional homogeneous environment consisting of a lattice of 100 × 100 cells, each of which was 50 × 50 m in size and contained 200 m^2 of ash phloem. As before, infestations were initiated in the center of the environment, with an initial population size of 100 adult beetles, assuming a 50:50 sex ratio.

Results

Local harvest or removal of ash trees

Reducing ash phloem led to a small increase in the radial spread of the population (<3%), which was substantially greater when a movement bias induced by stressed trees was included (Figs. 2, 3, and 4). The mean number of beetles by distance was uniformly lower in simulations that included ash removal than in the no-treatment (standard) simulations (Fig. 2). However, we also noted that the distance at which beetles were present did not differ (Fig. 2), and spread was actually increased when a movement bias towards stressed trees was included (stress bias). In addition, when ash reduction was applied to all cells within 300 m of

Fig. 3. Radius of *A. planipennis* infestation after a 15-year period when ash reduction, girdled trees, or insecticides were applied on a radius of 0 to 1700 m from the origin in a homogeneous environment in which 0%–75% of trees were available for treatment. Simulations were run including a bias towards cells containing girdled trees or beetle-induced injury (stress bias) and without the bias (no stress bias).



the origin of the infestation, the number of beetles present outside the treated area was not reduced (Fig. 4). Likewise, allowing up to 90% of trees per cell to be harvested (i.e., assuming that 90% of phloem was contained in trees of merchantable size) and increasing the area treated up to a 1700 m radius around the source of infestation did not reduce the radius of infestation (Fig. 3). Delaying the initiation of local harvest or removal of ash trees by up to 4 years did not greatly increase or decrease the efficiency of this treatment in terms of the radial spread of *A. planipennis* (Fig. 5).

Girdling trees

As noted in previous studies (McCullough et al. 2009*a*, 2009*b*), results from field sites indicated that the higher proportion of larvae in girdled trees relative to healthy trees diminishes as population density increases (Fig. 1). In particular, a rapid decline in the differential proportion of larvae in girdled trees was observed as densities reached 20 larvae/m^2. Including this effect in the simulation model decreased the effectiveness of this tool as a management option (Fig. 6). Likewise, limiting the proportion of trees that may be girdled (i.e., only trees ≥ 27.9 cm DBH), or the combination of these two limitations, led to lower decreases in population size and spread rate associated with the use of girdled trees (Fig. 6).

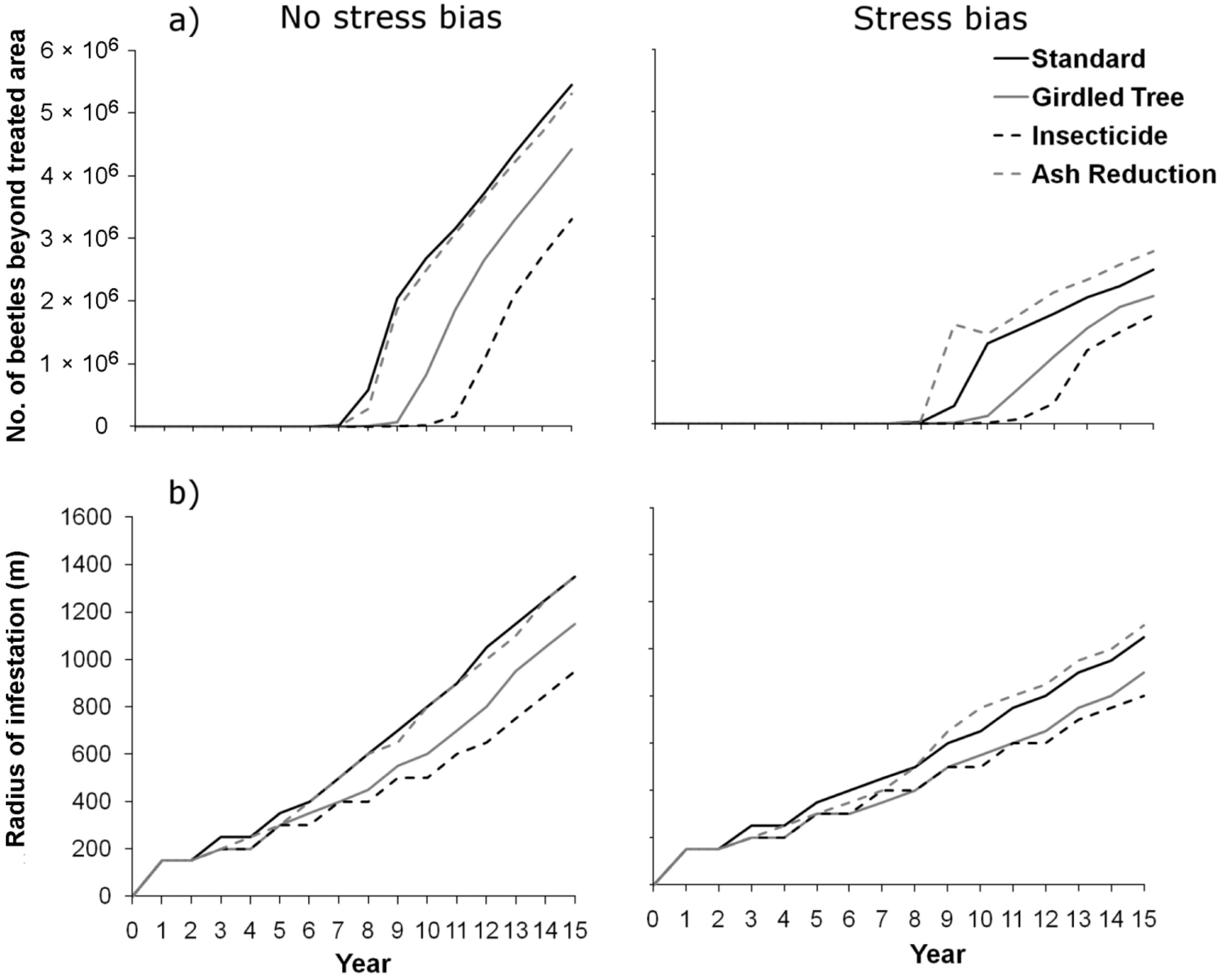
However, despite the reduction in effectiveness with increasing population size and limited number of available trees for treating in simulations, girdling trees did reduce the population size and radial spread rate of the *A. planipennis* (Figs. 2 and 3). During the first years of the simulation, both the population size and the distance at which beetles are present were lower (Fig. 2). However, towards the end of the simulation, only the size of the population was lower (Fig. 2). Increasing the initial area in which trees were girdled led to a greater reduction in the radial rate of spread, but a rapid decrease in added benefit was observed as trees ≥ 27.9 cm DBH became exhausted. This effect can be observed in the increase in the radius of infestation as the proportion of trees that could be girdled decreased (Fig. 3). Specifically, as the number of trees available for girdling was reduced, the effect of increasing the radius of application diminished. In addition to a potential decrease in benefit, when a movement bias towards areas containing stressed or girdled trees was included, increasing the area in which trees were girdled diminished the reduction in the radial rate of spread associated with increasing the distance at which treatments were applied (Figs. 3 and 5).

In simulations in which trees were girdled in all cells within 300 m of the initial infestation source, reductions in the radial spread (15%) and population size (40%) were observed after 15 years (Fig. 4). The reduction in radial spread delayed the movement of *A. planipennis* beyond the treated area by 3 years in these simulations (Fig. 4). In addition, girdling trees 1, 2, 3, and 4 years after the infestation was initiated also reduced the spread rate when a dispersal bias towards areas containing stressed trees was not included (Fig. 5). However, when a bias towards areas containing stressed trees was included, the reduction in radial spread observed when the radius of treatment is <500 m was diminished (Fig. 5).

Application of systemic insecticides

Simulated applications of a highly effective systemic in-

Fig. 4. (*a*) Number of *Agrilus planipennis* beetles found beyond a 300 m treatment radius and (*b*) radius of infestation for simulations run applying girdled trees, insecticides, or ash reduction out to a 300 m radius from the center of an infestation. Simulations were run including a bias towards cells containing girdled trees or beetle-induced injury (stress bias) and without the bias (no stress bias).



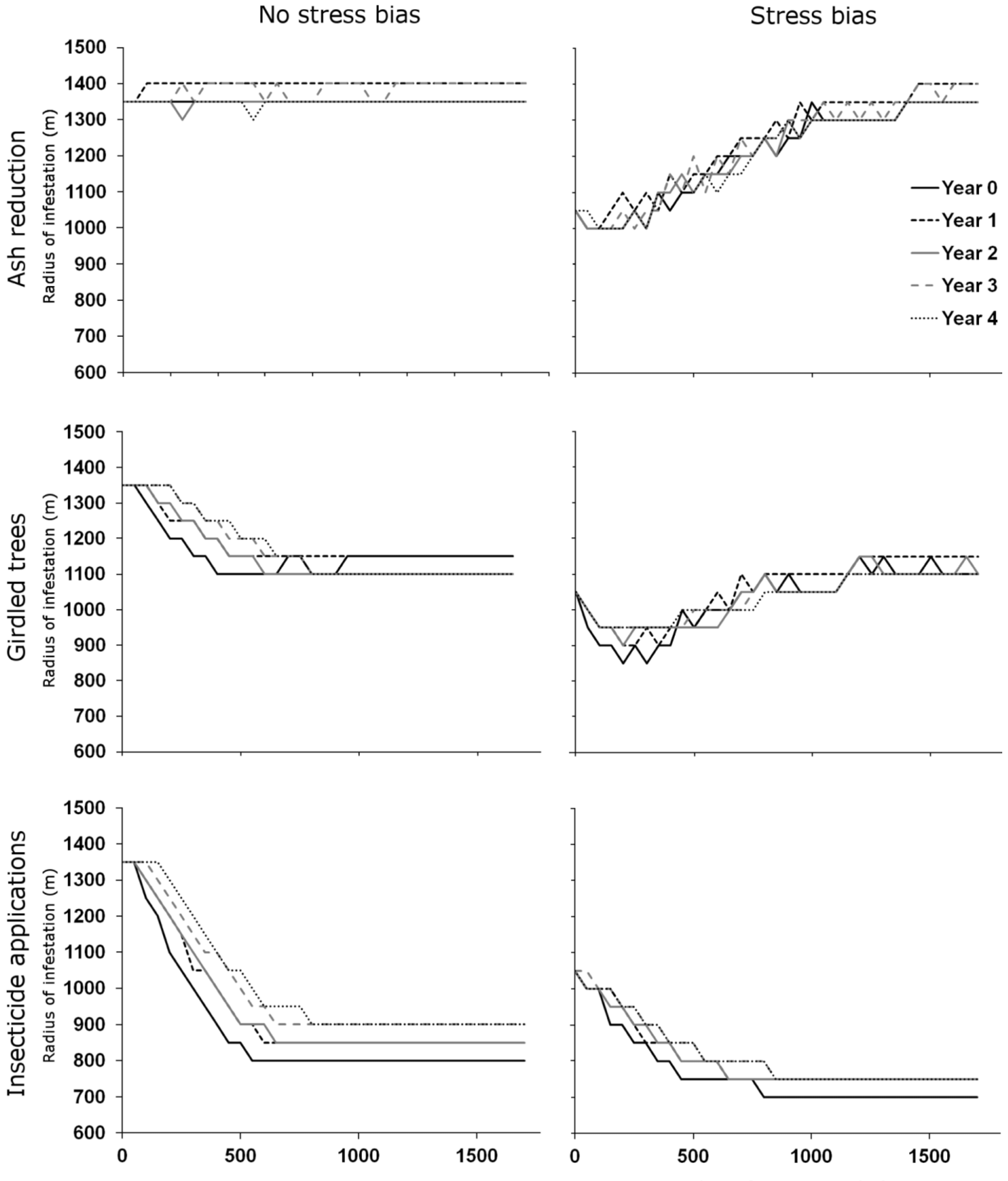
secticide generated the strongest reduction in the radial spread (Figs. 2, 3, and 4) and population size (Figs. 2 and 4) of all treatments considered. Insecticide applications led to the greatest reduction in the radius of infestation at any level of application (Fig. 3). The effect of insecticide applications was observed with and without the inclusion of an attraction to stressed trees (Figs. 2 and 3). Applying insecticides within a 300 m radius from the infestation point source led to a significant reduction in the population size (40%) and radial spread (30%) beyond the treated area after 15 years (Fig. 4). In addition, simulations indicated a reduction in the spread rate when detection of the infestation was delayed up to 4 years, whether or not a dispersal bias towards areas containing stressed trees was included (Fig. 6).

Discussion

Ash trees grow throughout much of North America, comprising an important component of forests across a wide geographic range, and can be locally abundant, particularly in eastern deciduous forests. The near-total loss of this valuable resource appears possible without active management to reduce the spread of *A. planipennis* and slow the progression of ash mortality (Knight et al. 2008). The simulations presented here indicate that two currently available management options are likely to provide at least a moderate reduction in spread rate. Specifically, simulations indicate that use of a highly effective systemic insecticide (e.g., emamectin benzoate) is likely to reduce the local spread of *A. planipennis*. The use of insecticides not only led to a reduction in population size and in the radial spread of *A. planipennis* within treated areas, but also reduced the number of beetles exiting a 300 m treated area over a 15-year period. Furthermore, insecticide use is likely to remain an effective management option to reduce the radial spread when infestations are detected up to 4 years after an infestation has become established.

However, the use of insecticides may not be a viable option in some regions due to local environmental concerns (e.g., threatened and endangered insect species), cost, and (or) habitat idiosyncrasies. In these cases, the use of an alternative option such as girdled trees may be a more attractive option. Employing sacrificial plants or "trap crops" in pest management has a long tradition in entomology, partic-

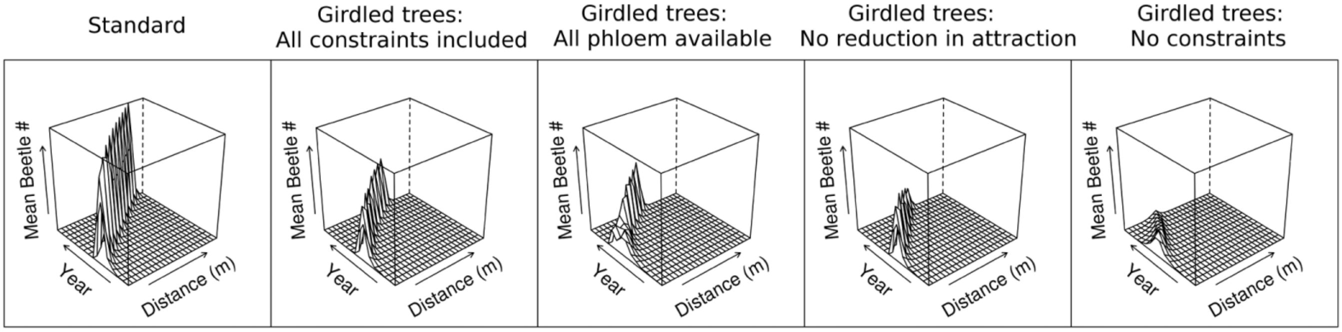
Fig. 5. Radius of *A. planipennis* infestation after a 15-year period from simulations applying (*a*) girdled trees, (*b*) insecticide applications, and (*c*) ash reduction to a radius of 0 to 1700 m from the origin in a homogeneous environment. Treatments were applied at 0, 1, 2, 3, and 4 years after establishment of *A. planipennis*. Simulations were run including a bias towards cells containing girdled trees or beetle-induced injury (stress bias) and without the bias (no stress bias).



ularly in agriculture (e.g., Bouché (1834) cited in Curtis (1860); Hokkanen 1991; Shelton and Badenes-Perez 2006). In general, this technique has been used to protect neighboring resources or as a monitoring tool, and the simulations presented here indicate that this strategy may also effectively reduce the localized spread of *A. planipennis*.

It is important to note that the design used to deploy girdled trees across an environment can have a substantial influence on the effectiveness of this management option. Because the relative attractiveness of girdled trees as an ovipositional substrate is maximized when *A. planipennis* density is low, placing girdled trees at the leading edge of the

Fig. 6. Distribution of *Agrilus planipennis* by distance for simulations without girdled trees (standard) or with 27.9 cm DBH girdled trees including all constraints (all constraints), assuming that all trees are available for girdling (all phloem available), assuming the relative attraction to girdled trees does not decrease with increases in population density (no reduction in attraction), and assuming that neither constraint is present (no constraints). Mean beetle #, mean number of beetles.



spreading population would be ideal. However, delineating the leading edge may be difficult, and girdling trees too far ahead of the spreading population could waste resources and exhaust the trees that are accessible and available for girdling prior to the arrival of *A. planipennis* individuals. More significantly, if *A. planipennis* oviposting females are strongly attracted to areas containing girdled trees, placing a large girdled tree (or several small girdled trees) too far ahead of the leading edge could potentially increase the radial spread of *A. planipennis*. The results from these simulations emphasize the need for a better understanding of *A. planipennis* dispersal and how it is influenced by host stress level.

Although local ash removal did reduce the maximum number of *A. planipennis* larvae developing within a given area, it did not reduce the predicted spread of *A. planipennis* in these simulations. Before completely discounting local ash removal as a management option, three important considerations need to be taken into account when considering the output of this model: (*i*) *A. planipennis* dispersal is known to be affected by the environment, (*ii*) *A. planipennis* mated females may engage in long-distance dispersal flights despite the presence of available local and nearby ash trees (Siegert et al. 2010), and (*iii*) the model does not account for density-dependent effects on the population growth rate. Because *A. planipennis* dispersal in homogeneous environments is expected to be lower than in heterogeneous environments (Siegert et al. 2010; Mercader et al. 2011), the radial spread is expected to differ between environments. However, simulations altering the dispersal kernel used in the model and adding variability in the environment indicate that the qualitative results described here remain consistent (Supplemental Appendix S2)[2].

The effect of differences in long-distance dispersal can significantly influence the efficiency of the management options presented and may potentially affect local population dynamics sufficiently for local ash reduction to be a viable management option to reduce the spread of *A. planipennis*. If individuals engage in long-distance dispersal independent of host resource availability, reducing population size by removing available resources could lead to a lower rate of spread. However, if individuals engage in long-distance dispersal as a function of population density (measured as population size per square metre of ash phloem), then reducing available resources would increase the proportion of beetles that disperse long distances. Dispersal patterns observed in sites with a continuous distribution of ash predicted a considerably lower dispersal distance of *A. planipennis* than what was observed in a heterogeneous site with only a small quantity of ash phloem present near the point of emergence (Mercader et al. 2011). This discrepancy may be an indication of an increased propensity to engage in long-distance flights when ash phloem is not present (or present at very low densities) near the point of *A. planipennis* emergence.

Removing ash trees of merchantable size in an area will lead to the majority of phloem being present in small, but numerous, point sources (i.e., small trees). A shift towards a preponderance of resources in small trees is likely to lead to a change in the local quality, distribution, and variability of available host resources, which can influence population dynamics (e.g., Price et al. 1980; Awmack and Leather 2002; Underwood 2004, 2007). Mortality rates and the relationship between the proportion of larvae that develop in 1 or 2 years and larval density for a site will likely be affected by the diffuse distribution of ash phloem. These effects could be important, and altering either of these two parameters within the simulation model could significantly affect the predicted spread rate (Mercader et al. 2011). Currently, however, there is no evidence to determine whether local ash reduction decreases population growth rate or the number of potential long-distance dispersal events.

For comparison purposes, here we assumed that treatments would not be applied to small trees and saplings and that the available phloem was distributed equally among trees of merchantable size. These assumptions allow for direct comparisons of the treatments presented. However, logistical concerns and variability in size classes present in the field may shift the relative efficiency of insecticide and girdled trees as management tools. Furthermore, although the simulations presented here compare the individual effectiveness of the three options for reducing *A. planipennis* spread, these options are not mutually exclusive and could readily be integrated at an outlier site. Treatments imposed on individual sites will undoubtedly be dependent on local socioeconomic and ecological conditions. Insecticides, for example, will likely play a dominant role in slowing *A. planipennis* spread in developed urban areas, whereas girdled sink trees might play a more significant role in forested areas. Implementation of tactics would ideally be geared to the conditions specific to individual sites. For example, in rural sites, small ash trees could be girdled to act as sink trees and large ash trees could be harvested for timber to increase the efficacy of the small girdled trees and to provide an economic benefit to landowners. Alternatively, in a suburban site, trees in unmanaged wooded areas could be girdled to act as sink trees and systemic insecticides could be applied to landscape ash trees to protect property values and to establish buffers around the clusters of girdled sink trees.

Ultimately, further work will be needed to address how these strategies might be utilized over a large scale and across varied environmental conditions and habitats to manage the spread of this insect across North America. A large-scale management plan such as the one developed for slowing the spread of the gypsy moth in the eastern US (Sharov et al. 2002) would entail integrating local management strategies such as those explored here with a large-scale survey program. Furthermore, bioeconomic analyses will be needed to evaluate and optimize intervention strategies that provide the most effective approach to reducing spread and ultimately minimizing costs and impacts (Sharov and Liebhold 1998: Epanchin-Niell and Hastings 2010).

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