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A model to simulate the spread and management cost of kudzu (*Pueraria montana* var. *lobata*) at landscape scale☆

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ABSTRACT

Invasive plant species are a global problem causing damaging ecologic and economic impacts valued in billions annually and requiring agencies and local governments to contain, eradicate, or otherwise manage them. The spread of invasive species is complex and involves spatially and temporally variable processes. The life history characteristics of invasive species are frequently poorly known. This makes the development of effective strategies problematic. Spatially explicit population models, offering a virtual platform to test the implications of life history hypotheses or alternative management strategies can therefore provide valuable and inexpensive support on which to base management decisions. However, two problems limit the use of such models in the actual management of invasive species: (1) field practitioners and management groups often lack the expertise (or funds) to develop their own models and (2) existing invasive species models are often too cryptic to be readily understood and modified by novices.

We present a model simulating the spread and population dynamics of kudzu and illustrate its potential through a case study application. The model, which could be adapted to fit the characteristics of other invasive plant species, couples species biology, dispersal and local management practices to generate local and regional scale outcomes that can be compared to identify those most effective given the level of available resources. This model could be further expanded, improved, and utilized as a medium through which the weed management, modeling, and decision-making communities could collaboratively increase the knowledge pool and effectiveness of their management decisions.

1. Introduction

Invasive plant species are one of the world's greatest environmental threats (Olson, 2006; Pyšek and Richardson, 2010). Their impacts cost billions of dollars every year whether measured in terms of direct or indirect ecological impacts, loss of ecosystem services (Funk et al., 2013), economic damages or costs of control (Olson, 2006; Pimentel et al., 2005). Examples of invasive species having widespread ecological and economic impact include kudzu (*Pueraria montana* var. *lobata*) (Forseth and Innis, 2004b), gypsy moths (*Lymantria dispar*) (Campbell and Sloan, 1977; Herrick, 1981) and zebra mussels (*Dreissena polymorpha*) (Khalanski et al., 1997; MacIsaac, 1996; Ricciardi et al., 1998). Many agencies and local governments are confronted with limiting their spread, eradicating them, or otherwise managing them. With limited financial resources and manpower, the development of effective management strategies is essential and poor, inadequate, or incorrect management decisions can have important financial, political, and/or ecological consequences.

The problem of invasive plant species is complex. Ecologists recognize four major sequential stages operating in an invasion: arrival, establishment, spread, and saturation (Kolar and Lodge, 2001; Lockwood et al., 2007; Richardson et al., 2000; Sakai et al., 2001; Shigesada and Kawasaki, 1997). Because each stage may be facilitated by human action as well as by the biology of the potentially invading species, and because their distribution across landscapes involves spatially and temporally variable processes, the development of management strategies becomes a complex, non-trivial exercise. This is the case because key elements controlling the spread of many of these organisms, e.g. flowering period, seedbank life expectancy, seed dispersal, reproductive rate, dispersal distance, or land-use disturbance factors are often poorly known (Bradley et al., 2010) especially at the local or regional scale. Focusing on early control is important, but prevention efforts are never completely successful and high levels of effort for prevention can be very costly. Furthermore, appropriate prevention levels depend on the expected costs and damages of established invaders, so identifying optimal management of established invasions is

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☆ The views expressed are the authors' and do not necessarily correspond to those of the European Commission.

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also important for choosing optimal levels of prevention and detection effort (Leung et al., 2002).

The spatial pattern of an invasion plays a key role in the rate of spread of the species and understanding this can lead to significant cost savings when designing efficient control strategies (Murphy et al., 2013). Spatially explicit models provide a virtual platform to test implications of particular life history hypotheses or management options and thus offer a valuable support structure on which to base invasive species management decisions (Vilà et al., 2011). Recent developments in analytical methods and computer processing power have also led to the development of several types of spatially explicit models such as dispersal kernels, individual based models, cellular automata, Gaussian plumes, trajectory models, network models, metapopulation models, and potential distribution models. Each of these model types has different characteristics and capacity to simulate particular processes (see the work of Parry et al., 2013 for more detail). Indeed, many models simulating the dispersal and/or cost associated with the spread of invasive species can be found in the literature. Certain models are theoretical and focus on fictitious species and virtual landscapes (Cacho et al., 2010; Rebaudo and Dangles, 2013). Some models focus on specific species, such as the emerald ash borer (Yemshanov et al., 2012), rhododendron (Harris et al., 2011), potato (Crespo-Pérez et al., 2011) or black night Buddleia (*Buddleaj davidii*) (Pitt et al., 2011). Other models are general and applicable to multiple species, such as invasive plants (James et al., 2011), beetle or fungal pathogens (Savage and Renton, 2014) dispersing at the parcel level, the economic impacts of invasions (Epanchin-Niell and Hastings, 2010; Holmes et al., 2010; Marco et al., 2011), human-mediated movement of plant species (Stanaway et al., 2011), the dispersal of harmful non-indigenous species (Carrasco et al., 2012), or the spread and detection of invasive insects (Carrasco et al., 2010).

The use of such models in actual management of invasive species, however, appears very limited. We believe this infrequent use of modeling technology can be attributed to two main reasons: (1) “on the ground” invasive species management groups often lack the resources (expertise and/or funds) to develop their own models and (2) existing invasive species models are often too cryptic to be understood and modified by people without advanced computer coding experience or require the use of expensive patented software.

While some published models provide equations describing key processes, access to the full model code is rarely offered (exceptions include Stanaway et al., 2011, who proposed making their code (developed in R) available to readers upon request, and Savage and Renton (2014), whose code (developed in Python and C) can be downloaded). As no code is generally provided, the potential next user is expected to re-code the model from the published equations. Most published models do not share their utilized equations and many even neglect to supply basic information about the software package or programming language used for model development. Notable exceptions include use of R (Stanaway et al., 2011), C++ within the MDiG dispersal-modeling framework (Harris et al., 2011), C++ and Matlab in the model of above- and below-ground kudzu biomass (Hughes et al., 2014), C and Python in the GMBI (Savage and Renton, 2014), and Java (Carrasco et al., 2010; Carrasco et al., 2012)).

We believe the absence of shared model information, both in its development and utilization, is a strong impediment to widespread application of spatial modeling technology in invasive species management. We present a NetLogo-based model simulating the dispersal and management of the invasive plant kudzu for which we provide full code access. This model represents complex spatial and temporal patterns of invasion to predict quantitatively the impact of these factors on the invasion dynamics of kudzu at local and regional scales. Most previously published modeling work on kudzu dispersal has been on climate-based species distribution models (Geerts et al., 2016; Jarnevich and Stohlgren, 2009) or spatially implicit optimization models (Hughes et al., 2013). We believe this model is one of the first investigating kudzu potential dispersal and management options through a spatially explicit agent based model.

This paper briefly describes the structure of the kudzu model (a more complete description can be found in the additional material). We illustrate its potential through a case study examining plausible spread and management options for kudzu during a 50-year period at the landscape scale. The model also simulates the effects and costs of alternative management scenarios.

2. Material and methods

2.1. Modeling environment

Among various types of spatially explicit models, Parry et al. (2013) identified the characteristics of individual-based models and cellular automata as most suited to account for environmental heterogeneity and population dynamics and mechanistically model the spread of invasive organisms. We chose the NetLogo multi-agent programmable modeling environment (Wilensky, 1999) to develop our kudzu model. NetLogo is a relatively user-friendly, yet powerful open source agent-based modeling platform. It does not require users to be advanced programmers in computer languages such as Java, C, R, or Python. Furthermore, NetLogo enjoys strong support from the programming community and the availability of several sample models allows new users to experiment and modify existing procedures to their own needs. NetLogo is also platform-independent (available for Windows, Mac, and Linux users) and very well documented. With a GIS extension, NetLogo has the capacity to read-in and output spatial data, and actual landscape data (such as the U.S. National Land Cover Dataset (NLCD) (Jin et al., 2013) or the CORINE land cover dataset from the European Environment Agency) can easily be input. The NetLogo interface allows users to visualize model outputs, query the status of variables, and change model parameters during simulations. This facilitates rapid model debugging, easy interpretation of results, and creates opportunities for incorporating short-term interactive simulations within group decision-making activities. Another NetLogo advantage is that, apart from spatial data sources, the entire model (including the user interface) can be contained within a text file (see Additional material) and easily shared with others.

2.2. Overview of the model structure:

The model's objective is to provide a platform where users can bring together what is known about kudzu and where the implication of possible, yet undocumented, life history traits or management strategies can be investigated in an interactive manner. This spatially explicit model, brings together a combination of modeling procedures that represent essential “building blocks” to allow the simulation, on a weekly time step, of kudzu movement across landscapes. These procedures do the following functions:

1. Read-in spatial data and for each location (patches), associate specific variables such as habitat preferences/carrying capacity, etc.
2. Simulate, in each patch, population dynamics: germination, death, reproduction, and transition between different life stages. The model distinguishes between four life stages: seeds, seedlings, saplings (reproduce vegetatively) and adults (reproduce both vegetatively and produce seeds).
3. Simulate plant dispersal (seed dispersal and local expansion via vegetative propagules).
4. Allow users to define the type and location of management strategies and simulate their impact on the plant population.
5. Calculate costs associated with management activities.
6. Export the outputs of the model into tables and raster format for analysis and visualisation.

Table 1
Summary of local and global model variables.

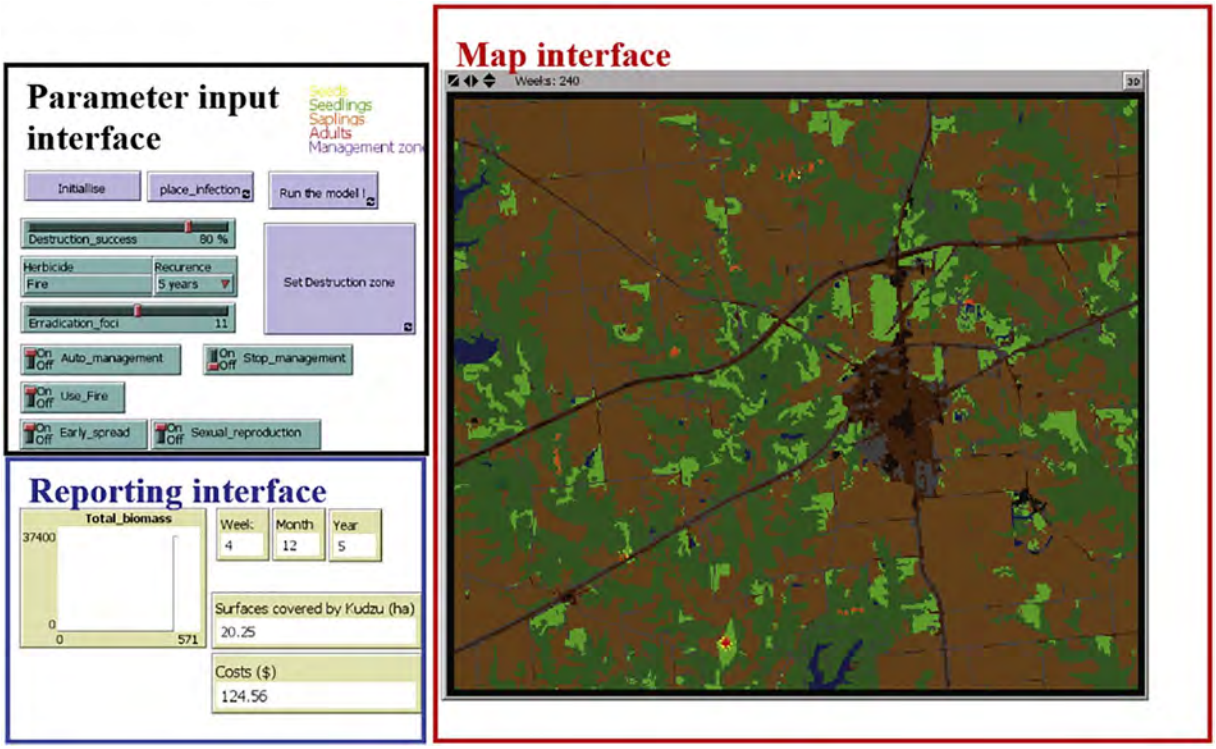
Variable	Description	Level of relevance of the variable
Carrying capacity	Maximum biomass of kudzu that can grow at a specific location.	Specific to each land use type
Delay to adulthood	Number of years required for kudzu saplings to reach the adult stage	Specific to each land use type
Fresh seeds	Number of fresh seeds present in a patch	Specific to each pixel
Seed bank	Number of seeds present in the seed bank of a patch	Specific to each pixel
Seedlings	Number of seedlings in a patch	Specific to each pixel
Saplings	Number of saplings in a patch	Specific to each pixel
Adults	Number of adult in a patch	Specific to each pixel
Germination rate	Germination rate of seeds in a patch	Specific to each pixel
Seed produced	Number of seeds being produced per patch	Specific to each pixel
Life stage specific biomass	Total biomass of seedling, sapling or adult kudzu plants per patch	Specific to each pixel
Management	Array of values containing (1) the year, (2) month and (3) week when management started (4) the recurrence (in years) to which management is applied (5) the target life stage and (6) the destruction success of the management.	Specific to each pixel
Cost	Amount (in $) spend on kudzu management	Specific to each pixel
Life stage specific reference biomass	Average biomass of an kudzu seedling, sapling or adult plant	Identical for all pixels
Fraction of seedbank available for germination	Proportion of the seeds present in the seed bank that can germinate each year.	Identical for all pixels
Life stage specific disease and predation rate	Specific death rate of seeds, seedlings, saplings or adults associated with predation and disease	Identical for all pixels
Life stage specific sprouting rate	Average number of vegetative sprout produced by each sapling or adult	Identical for all pixels
Adult seed production rate	Average number of seeds produced by each adult kudzu plant	Identical for all pixels
Prop adults moving out	Proportion of adult kudzu plant in a cell which can send saplings in neighboring cells	Identical for all pixels
Percent seed exported	Proportion of seeds produced in a cell spread to neighboring cells	Identical for all pixels

A summary of the most important model variables is presented in Table 1. A more detailed description of all model variables, input parameters, and procedures, as well as its program code, can be found in the online Appendix.

Users can interact with the model via a graphic user interface, composed of a map, a reporting section, and a parameter/action section (Fig. 1). The map interface allows users to visualize the landscape of interest by associating different colors to each land-use class. Kudzu populations at each life stage are displayed in a color scale ranging from yellow (seeds) to red (adults). Users can also directly interact with the map interface, in combination with the parameter interface to initialize infestations at specific locations or specify management zones and types.

In the parameter interface, users specify and change model parameters at any time during the course of a simulation. These parameters include the:

(1) Location of initial infestations of the focal invasive species; in this



Destruction_success 80 %
Herbicide Fire
Recurence 5 years
Erradication_foci 11
Week: 4
Month 12
Year 5
Surfaces covered by Kudzu (ha) 20.25
Costs ($) 124.56

Fig. 1. Initial interface of the model.

example, adding a population of 100 seedlings to each selected cell.

(2) Occurrence (or not) of early vegetative spread from saplings and adults.
(3) Occurrence (or not) of seed production and dispersal.
(4) Extent and location of management actions, destruction success, and repeat interval (recurrence) of management activities.

Users visualize temporal changes in variables of interest via graphic and numeric reporters at the reporting interface. Lastly, a data export option allows weekly map outputs to be saved in GIS format for later analysis.

The modeling procedures (functional building blocks) at the core of our model, simulate population dynamics, reproduction, and dispersal and link these processes in a two dimensional landscape. This provides functionalities that are similar to the discrete spatially explicit general model of biological invasion (GMBI) described by Savage and Renton (2014). But unlike the GMBI, our model allows for the modeling of the impact of various management strategies that can target specific patches and/or life stages. It also allows stakeholders to interact directly and in real time with the model interface to affect the outcomes of the simulation.

2.3. Kudzu

Kudzu, (*Pueraria montana* var. *lobata* (Willd.) Sanjappa & Predeep), is a highly invasive perennial vine with an extraordinary growth capacity of as much as 25 to 30 m per year (Sasek and Strain, 1989), allowing it to overgrow most existing vegetation and leading to the formation of large mono-specific stands (Forest Invasive Plants Resource Center, 2005; Lindgren et al., 2013; Sharkey and Loreto, 1993). Extensively planted throughout the southern U.S. in the mid-1930s (Bordner and Hymowitz, 2002; Frankel, 1989), before being recognized as a noxious weed in 1970, kudzu currently infests approximately 3 million ha across twenty-two states in the U.S. It is also found in Ontario, Canada (Chittenden, 1997). Kudzu constitutes a major problem in the southeastern United States, where it decreases the productivity of plantation forests, damages power lines, outcompetes native vegetation, and smothers orchards and crops. Its economic impact in the United States is estimated between $100–500 million per year in lost forest productivity and yearly management costs are estimated at $500 per hectare, which may exceed annual per hectare profits (Britton et al., 2002; Forseth and Innis, 2004a).

Kudzu appears to be extending its geographical range towards higher latitudes (Bradley et al., 2010; Jarnevich and Stohlgren, 2008) and alpine areas (Follak, 2011). Since kudzu benefits from elevated CO_2 (Sasek and Strain, 1988, 1989), it is likely to become a widening problem as global change continues. The potential geographic distribution of kudzu has been predicted using habitat and climate suitability models under current and future climate conditions. Modeling indicates areas of the Pacific Northwest and Montana are susceptible to invasion under predicted 2035 climate scenarios (Jarnevich and Stohlgren, 2009). Bradley et al. (2010) projected northward range expansions into Pennsylvania, New York, and New England, and into coastal Washington and Oregon by 2100. Other modeling studies predict suitable climate conditions for kudzu expansion in Switzerland, Italy, Austria, and Slovenia (Follak, 2011).

The reproductive behavior of kudzu is unclear. Kudzu was long assumed to reproduce only vegetatively and not to be able to set seed at northern latitudes. It was also thought to die off as a result of freezing temperatures (Bordner and Hymowitz, 2002; Erickson et al., 2001; Sorrie and Perkins, 1988). However, more recent studies have shown that not only do kudzu populations not die back in winter in central and southern Illinois, they could flower, bear fruit and produce viable seeds (McClain et al., 2006).

The importance of seed dispersal in the spread of kudzu is not clear and while some sources report kudzu seeds disperse less than six meters from the mother plant (Hipps, 1994; Pappert et al., 2000), others note potential dispersal across moderate distance via mammals and birds (EPPO, 2007). Anecdotal evidence indicates kudzu seedlings have been found hundreds of meters away from known source populations, suggesting possible seed dispersal (Boyda, 2013). The uncertainty in the reproductive and dispersal potential of kudzu has strong implications in terms of its potential impact in the landscape. Indeed, this risk was already highlighted by McClain et al. (2006) who stated “the continuous increase of kudzu, coupled with an effective seed dispersal agent, could result in a population explosion, particularly in southern Illinois” and could become a local problem, causing concern for rural landowners.

The model was parameterized to match known life history characteristics of kudzu by incorporating information from the published literature. This information included data on the timing of transition between different life stages, their specific biomass, reproductive rate and death rates, as well as the germination rate of seeds (see additional material for details). To account for the uncertainties associated with the dispersal of kudzu, the model included procedures to simulate (1) vegetative spread, where kudzu plants can spread via propagules into adjacent patches, and (2) seed dispersal, where seeds are spread at a distance of up to 150 m using a simple dispersal kernel (see additional material for details).

2.4. Case study application

To illustrate the potential of our model, it is configured to simulate a plausible scenario of kudzu spread across an actual landscape in the state of Illinois, U.S.A.

2.5. Study region

In Illinois, a total of 78 populations of kudzu were recorded from 28 counties in 1997 (McClain et al., 2006). The extent of infestations was later decreased following a coordinated eradication (Shimp, 2009). In 2005, a local news article reported kudzu populations in six Illinois counties, all located in the southern half of the state: Clark, Cumberland, Macon, Peoria, Shelby and Tazewell (http://www.news.illinois.edu/news/05/1020kudzu.html).

Our model was applied to simulate the spread of kudzu in a portion of Clark County, located near the town of Marshal (illustrated in Fig. 2), covering an area of approximately 20,000 ha. The land-use data input for the model was obtained from the freely-accessible 2006 National Land Cover Data (NLCD) land-use dataset (Jin et al., 2013). The obtained raster dataset was clipped using ESRI ArcGIS 10 (but an open-source GIS software could also be used) and exported as an ASCII file that can be read directly into NetLogo. The created dataset consisted of a grid of 497 × 430 cells having a resolution of 30 m and origin coordinates of x = 697,115.0898 and y = 1,842,499.218 (USA Contiguous Albers Equal Area Conic projection). The 497 × 430 grid file was imported into NetLogo using the GIS extension to create a world of 497 × 430 patches using a bottom left corner location of origin and no horizontal or vertical wrap. Although our study region is small, NetLogo has the capacity to handle significantly larger datasets (particularly the 64 bit version), which is limited only by the amount of RAM memory (the authors having successfully tested it with several million cells).

2.5.1. Scenario investigated

Kudzu model users specify and modify model parameters interactively during the course of the simulation. However, in order to illustrate the effects of varying parameter estimates (for example those involving mortality, reproductive, and dispersal rates), a set of fixed elements common to all scenarios was defined for further investigation, including the initial kudzu population, a set of “auto” management strategies (see Appendix Section 3.1.4.2 for detail) that applied a recommended herbicide specific to each land-use type and achieving a

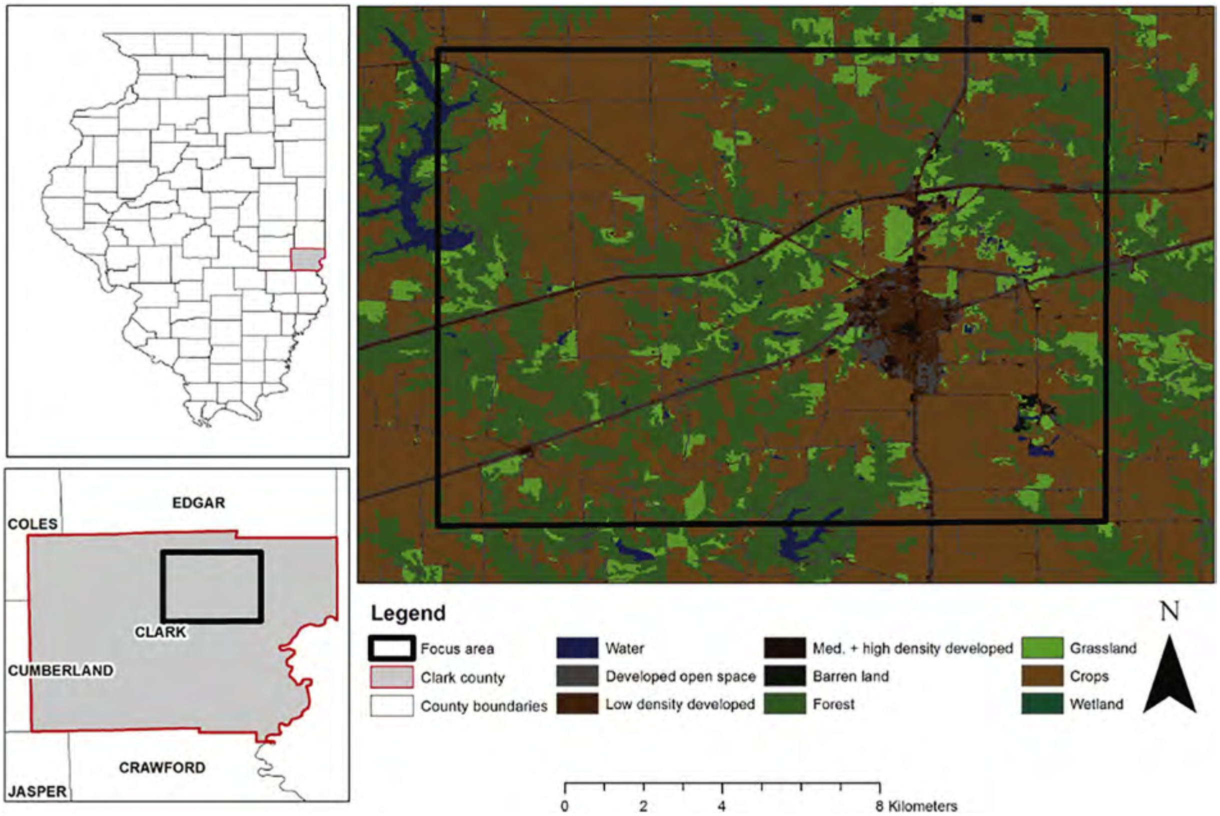


Fig. 2. Focus area for the spatial incursion simulation model.

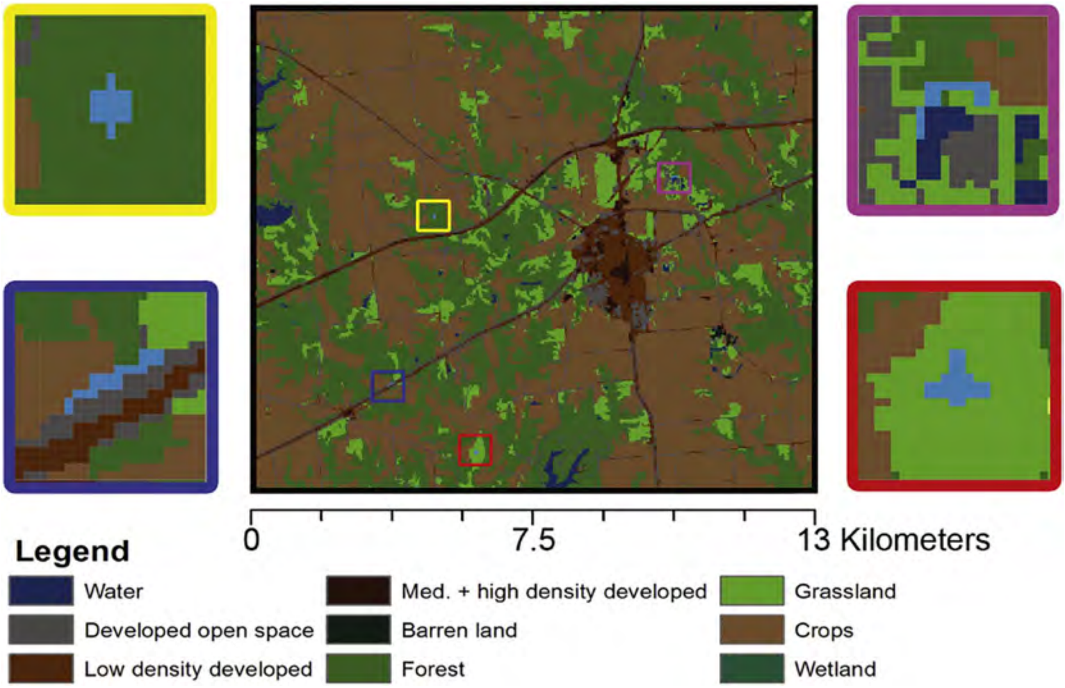


Fig. 3. Illustration of the model interface displaying the initial founding kudzu infestations for scenario analyses. Kudzu populations appear in light blue. The square images on the left and right side of the map surrounded by yellow, blue, pink and red boundaries correspond to zoomed portions of the map (squares of the matching color) and are shown for illustrative purpose only. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

particular destruction rate, and recurrence year common to all cells. Although the model includes a management option using fire, which kills seedling, saplings and adult kudzu plants, but increases germination rate (see Section 3.4 of the Appendix for detail), this management option was not considered in our example.

2.5.1.1. Initial populations. Data on the presence of invasive species is often reported at the county level. In the absence of GPS coordinates specifying the exact location and extent of existing kudzu infestations, we created a plausible scenario based on available information. In Illinois, kudzu is found in five types of habitat: road-side, open field,

Table 2
Life history characteristics considered for the "no management" scenario.

Scenario name	Description
No seed	Vegetative spread via adult kudzu plants
Early no seed	Vegetative spread via adults and saplings
Seed dispersal	Seed production by adults and seed dispersal to neighboring cells with vegetative spread via adult plants
Early seed dispersal	Seed production by adults and seed dispersal to neighboring cells with vegetative spread via adults and saplings
Seed no dispersal	Seed production by adults with no seed dispersal to outside cells with vegetative spread via adult plants only
Early seed no dispersal	Seed production by adults with no seed dispersal to outside cells with vegetative spread via adult plants and saplings

Table 3
Life history characteristics considered for the nine management strategies.

Scenario name	Description
No seed early	Vegetative spread via adult and saplings
Seed dispersal early	Seed production by adults and seed dispersal to neighboring cell with vegetative spread via adult plants and saplings
(No seed no dispersal early	Vegetative spread via adults only
Seed no dispersal early	Seed production by adults with vegetative spread via adult plants only

woodland, strip mine, and water edge (McClain et al., 2006). To simulate similar starting conditions, four founding kudzu populations were placed within corresponding land-uses in our study environment (Fig. 3). Each of the founding populations was composed of 11 cells, each containing a population of 100 kudzu seedlings. The land area within the 11 cells is equivalent to 1.6 ha, the mean area for all kudzu populations reported in Illinois (McClain et al., 2006).

2.5.1.2. Parameter combinations investigated. The potential spread of kudzu across the study region was initially investigated under a "no management - let it be scenario" for a period of 50 years. Using the NetLogo "behavior space" functionality, six possible kudzu life history characteristics (described in Table 2) were considered.

Subsequently the effectiveness (estimates based on surfaces of kudzu infestations) of nine different management strategies (applied with a recurrence of 1: one a year, 2: every other year, and 5: every fifth year and eradication success of 80, 90, and 95%) as well as their associated costs (including herbicides cost) over a 50 year-period was investigated. For these assessments, four kudzu life history characteristics (described in Table 3) were considered.

Stochasticity is an important component of biological dispersal models (Savage and Renton, 2014) and our model included stochastic processes in both its demographic (germination, reproduction, death) and dispersal (vegetative and by seeds) components (see Sections 3.2, 3.4, 3.5, 3.6, 3.9, 3.13 Appendix for more detail). To investigate the impact of this stochasticity on model behavior, each scenario was run for 30 iterations.

3. Results

3.1. Simulation monitoring

During the course of a simulation, users can visualize the progression of the spread of the modeled species in real time. They also can "intervene" in the simulation by changing model parameters or even by manually selecting particular mapping regions in which to apply management measures. Fig. 4 shows the viewer interface during a kudzu simulation.

3.2. Spread under no management scenario

The results of the no management simulation are presented in Fig. 5. Box plots indicate the extent of land area occupied by kudzu after 50 years across each set of 30 iterations. The relatively small variation within each life history scenario indicates the model's imbedded

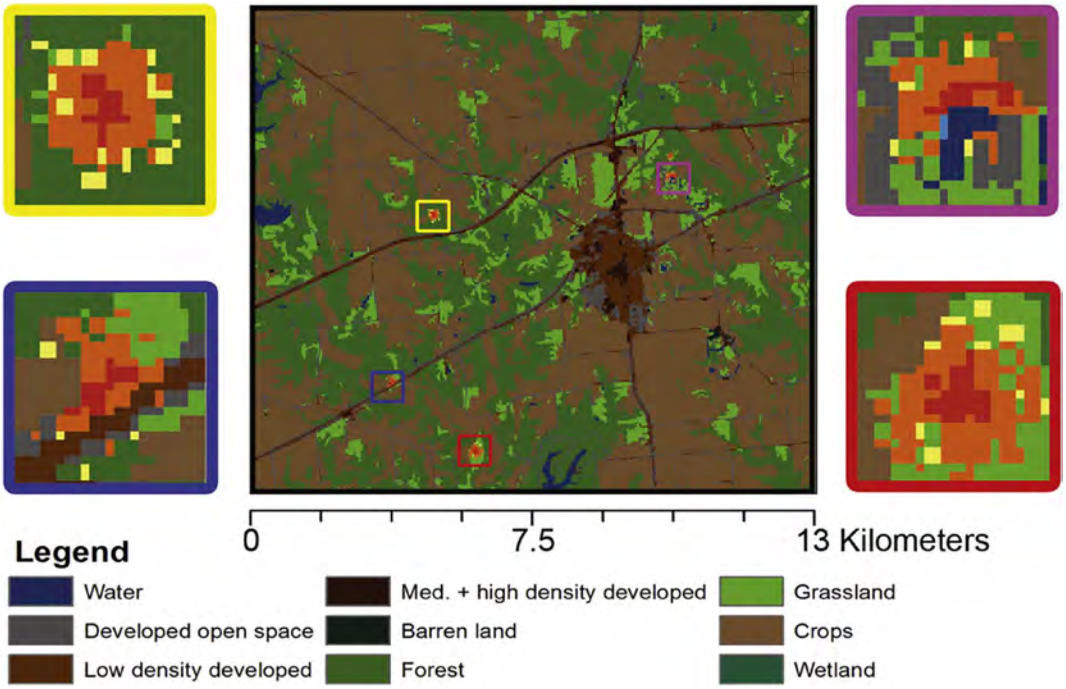


Fig. 4. Illustration of the model interface during the course of a simulated kudzu infestation. Adult kudzu populations appear in red, saplings in orange, seedlings in bright green, and seeds in yellow. The square images on the left and right side of the map surrounded by yellow, blue, pink and red boundaries correspond to zoomed portions of the map (squares of the matching color) and are shown for illustrative purpose only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

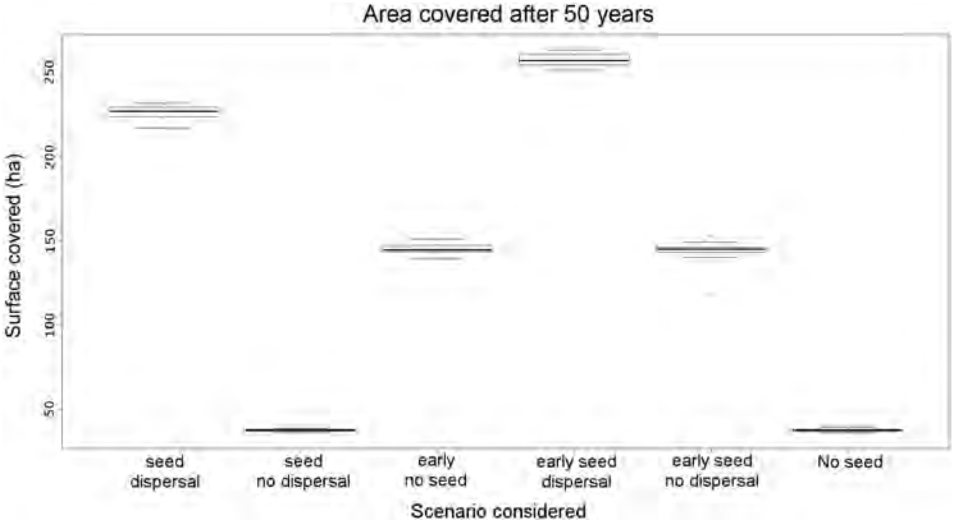


Fig. 5. Total area covered by kudzu populations after a 50-year period under six life history scenarios and no-management actions.

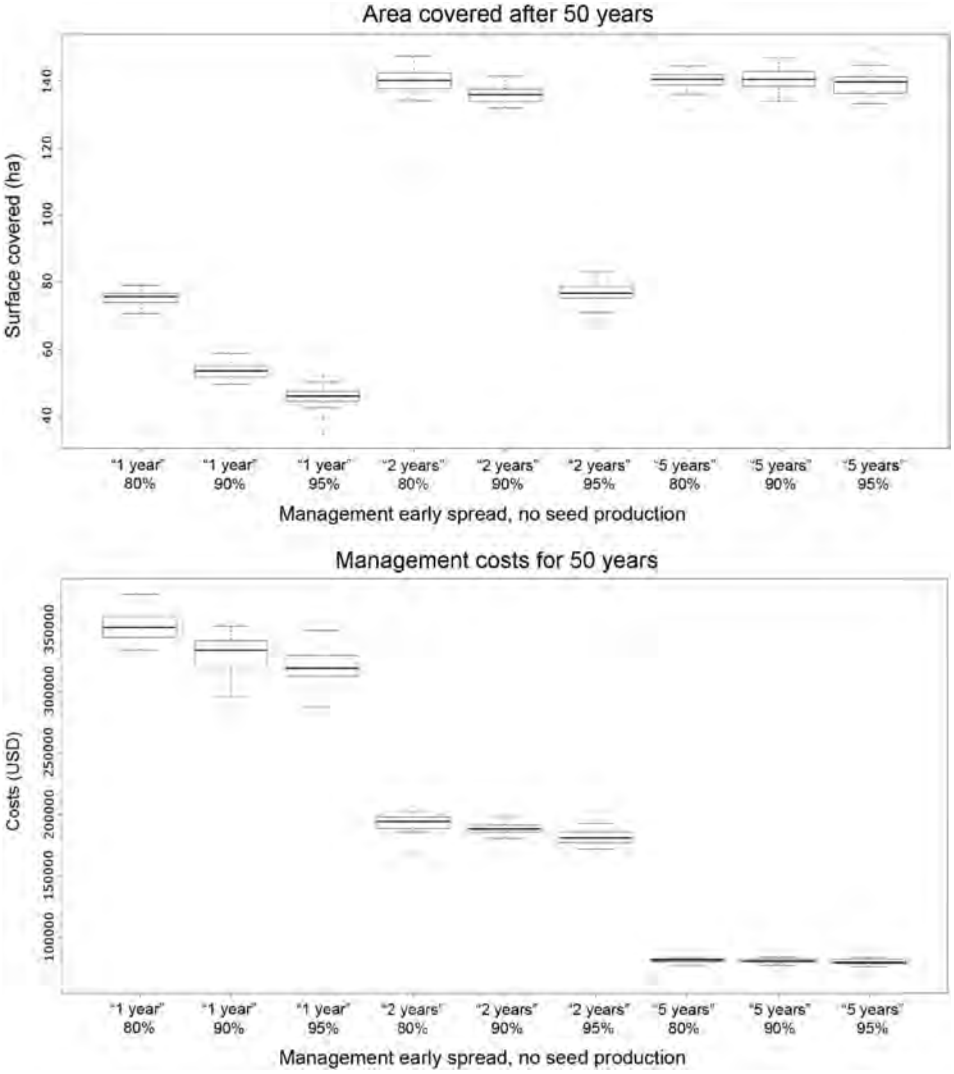


Fig. 6. Impact (top) and costs (bottom) of various management strategies on the spread of kudzu infestations assuming a "no seed early" scenario.

stochasticity had minimal impact on its general behavior. As expected, more variability was observed in scenarios where longer distance seed dispersal occurred.

The occurrence of sexual reproduction (seed production) without associated dispersal to neighboring cells (seed no dispersal) led to landscape coverages nearly identical (around 40 ha) to those observed without seed production (no seed). Consequently, the production of seed by itself is likely to have minimal impact on kudzu's capacity to expand.

The occurrence of vegetative spread by saplings (early scenarios)

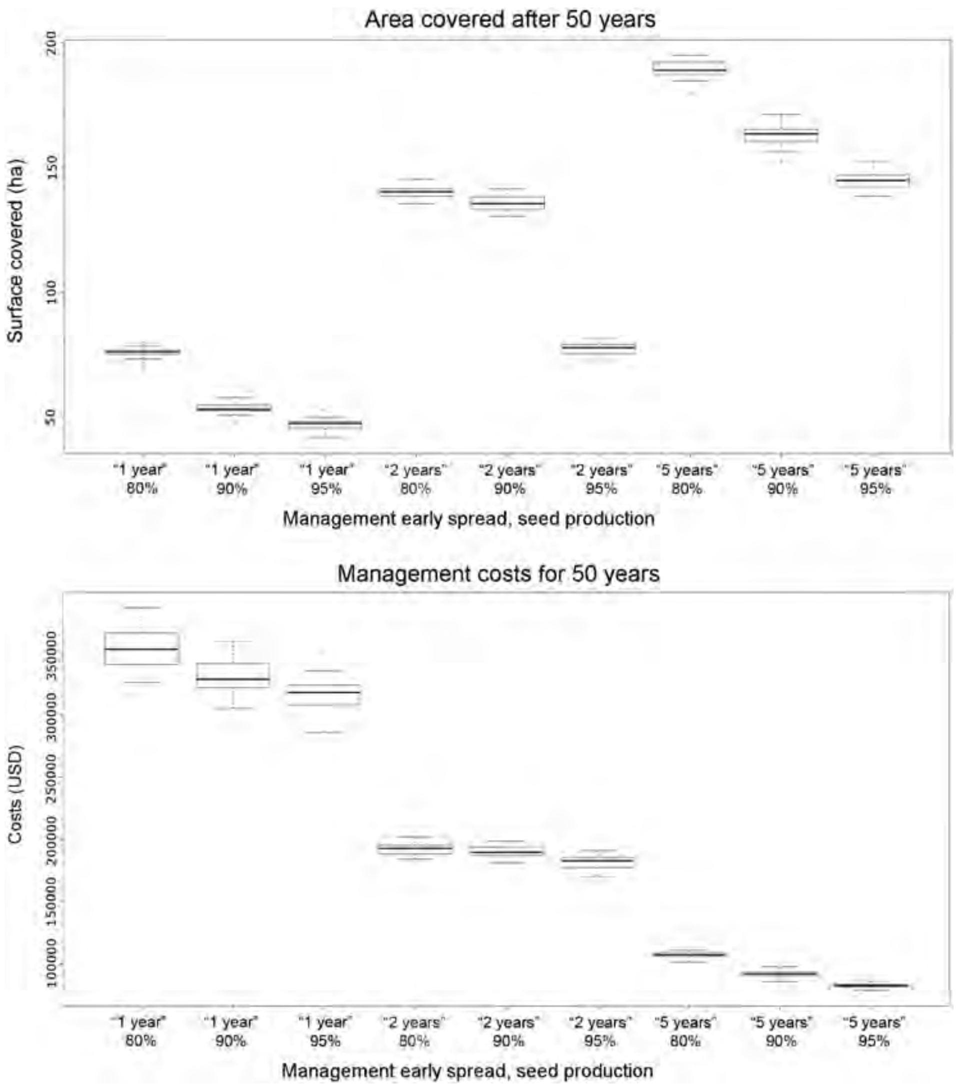


Fig. 7. Impact (top) and costs (bottom) of various management strategies on the spread of kudzu infestations assuming early vegetative spread of saplings and seed production and dispersal (seed early).

had a major impact on the capacity of kudzu to colonize new areas. The occupation of nearly fivefold greater land area (around 200 ha) occurred only when adults were able to spread vegetatively to nearby cells. Again the "seed no dispersal" and "no seed scenarios" generated similar outcomes.

The occurrence of seed dispersal (seed + dispersal scenarios) also had a positive effect on spread, allowing kudzu to occupy six times (240 ha) the area covered under scenario conditions of no seed dispersal and no early vegetative spread. This "multiplying" effect was less pronounced, however, in scenarios in which saplings could provide propagules to neighboring (seed dispersal early), increasing their area of coverage by 1.25 above that of the seed dispersal scenario.

3.3. Impact and cost of management strategies

Figs. 6 through 9 show the outcomes, including management costs and land areas occupied by kudzu, when simulating the effects of nine different management strategies and four life history characteristics.

3.3.1. Management and early spread no seed production: (no seed early) (Fig. 6)

For each application frequency, 1 (every year), 2 (every other year) and 5 (every fifth year), herbicide applications consistently produced a higher destruction rate leading to smaller remaining infestations and lower costs. Interestingly the use of an herbicide achieving a 95% destruction rate on an every other year application schedule led to a much better control of kudzu population than the 90%, but this effect was much less pronounced for yearly and every fifth year schedules.

Low management recurrences also led to significantly lower costs, with 5-year recurrence (every fifth year) expenses roughly one half the 2-year recurrence (every other year) and 3.5 less than yearly management recurrences.

For a 95% destruction success rate, yearly applications constrained the infestation to 50 ha, while the every other year spread led to about 75 ha and every fifth year led to spread of 140 ha. Eradication of kudzu could not be achieved under the investigated scenarios, but optimal cost benefit seems to occur on a 2-year recurrence (every other year) using herbicides providing a 95% destruction rate.

3.3.2. Management and early spread combined with seed production (seed early) (Fig. 7)

This scenario showed very similar patterns to the previous one (Fig. 6), with more frequent management effort leading to more containment success. Kudzu eradication could not be achieved under the investigated scenarios, but again the 2-year recurrence 95% destruction rate appeared to be the most cost effective measure to contain kudzu.

3.3.3. No early spread no sexual reproduction (no seed no dispersal early) (Fig. 8)

Under this scenario, kudzu eradication was achievable in four of the

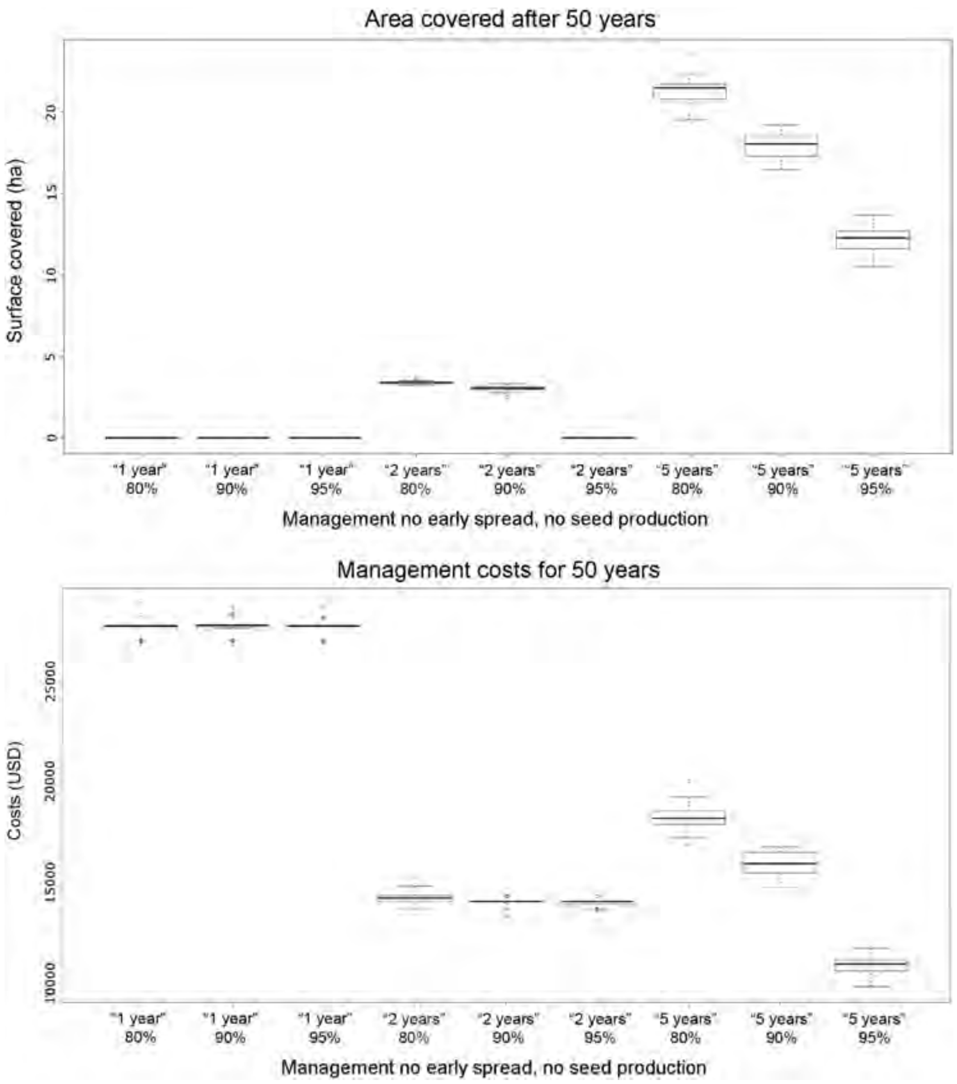


Fig. 8. Impact (top) and costs (bottom) of various management strategies on the spread of kudzu infestations assuming vegetative spread of adults only and no seed (no seed no dispersal).

nine considered scenarios: all management scenarios using yearly management recurrence and every other year management with 95% destruction rate. Again the most effective cost benefit option was at 2 year recurrence (every other year) and 95% eradication rate achieving eradication for approximately $15,000. Interestingly this option was even cheaper than the 5-year management recurrence option with destruction rates of 80 and 90%.

3.3.4. No early spread sexual reproduction (no spread seed) (Fig. 9)

In this scenario, kudzu eradication was possible in four cases, all yearly management schedules and the 2-year management recurrence using a 95% destruction rate. This last option was also the cheapest of all management options.

4. Discussion

We proposed an interactive, spatially explicit model of kudzu to help habitat managers investigate the implications of unknown life history traits and develop and test management strategies in a virtual representation of the real world where sophisticated technical expertise, deep budgets, and access to extensive computing facilities are not needed. The model was used to explore various scenarios for managing kudzu within an Illinois (U.S.A.) landscape and demonstrated its potential use as a planning tool. In a no management scenario (Fig. 5) seed production without dispersal was shown to make no contribution towards expanding area covered by kudzu. The simulation results also highlighted the contribution of vegetative reproduction by young individuals leading to the spread of kudzu across much larger surfaces. Unsurprisingly seed dispersal led to the largest infestations and its effect was compounded with that of early vegetative spread. This example highlights the importance of understanding alternative reproductive pathways within the kudzu life cycle when estimating the risk the species represents.

The model also allowed us to identify a potential "highest return" management strategy. The management strategy using a 2-year (every other year) recurrence 95% destruction rate, provided across scenarios, the most cost effective option to contain and in some cases eradicate kudzu populations. This observed behavior is the result of complex dynamic interactions at patch levels, between seed production, germination, transition between life stages and predation. Although our model incorporated some level of randomness in the occurrence of predation and for rates of sexual and asexual reproduction that provided some variability in the outcomes of the model, it is likely that the use of different model assumption will lead to results different from the one observed in our scenarios. However, this type of sensitivity analysis could help identify parameters of most importance and potentially identify "highest return" options.

There are significant gaps in the scientific literature concerning the knowledge of key parameters influencing kudzu population dynamics, such as seed production, germination rate, dispersal distance, etc. Such

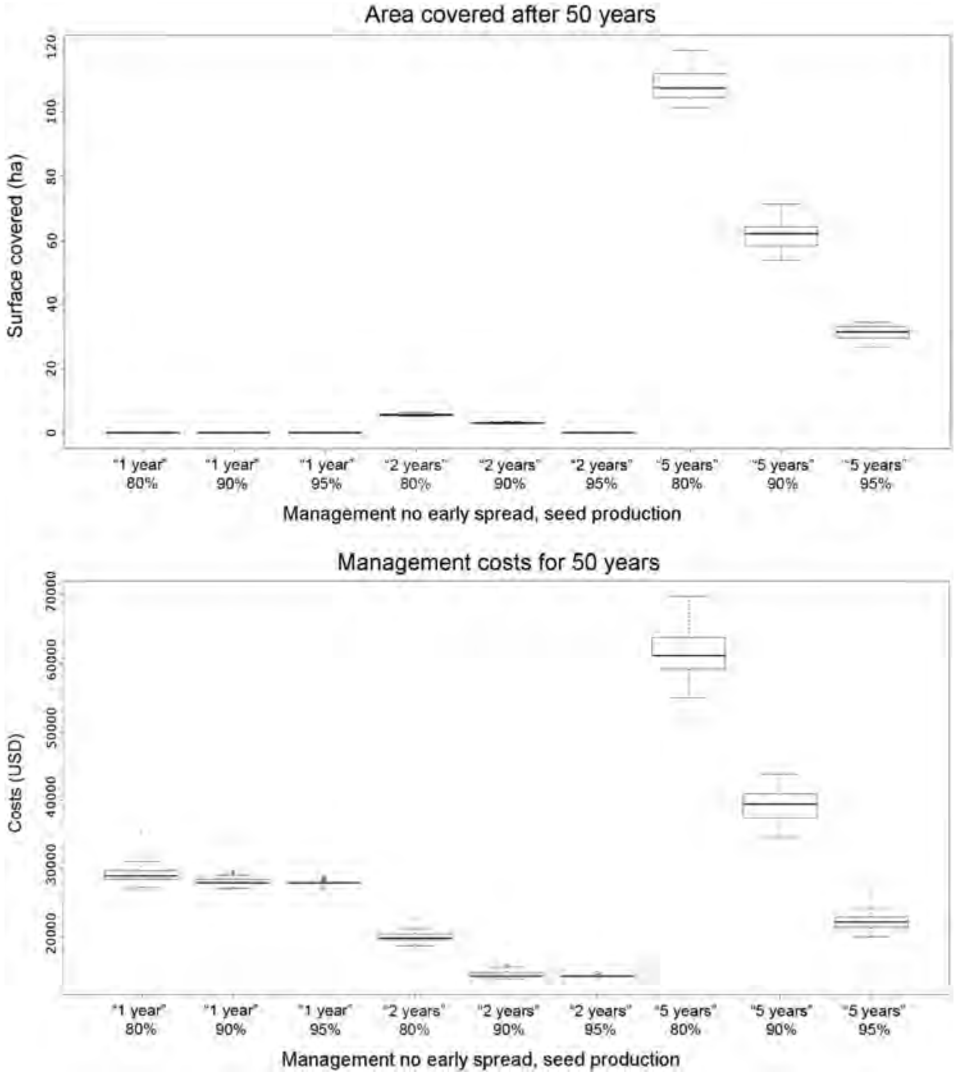


Fig. 9. Impact and costs of various management strategies on the spread of kudzu infestations assuming vegetative spread of adults only and seed production (no spread early seed).

knowledge gaps are very common for most invasive plants species. By combining known information with plausible values for a range of parameters on a platform in which scenarios can be adjusted at any time during a simulation, the outcomes of numerous management actions can be evaluated. The proposed model is not only useful for optimizing management behavior according to available resources or life history characteristics; it also offers potential use within a group-based decision setting such as described by Cook et al. (2016) (who also used a NetLogo based model interface). Although we did not demonstrate this facet of the model in our example, we believe it could prove particularly useful to facilitate cross-organizational discussions of invasive species management. For example, by exploring the financial implications and eradication effectiveness of scenarios of working in a coordinated manner or separately, authorities such as National Park authorities, road maintenance, and private landowners could come together, and through facilitated interactions, identify optimal management strategies.

Although it was developed for kudzu, our model contains the essential building blocks of code necessary to simulate the spread of invasive plants and test the impact and cost of various management strategies. Being written in NetLogo, it could easily be adapted to fit the characteristics of other plant species (by changing model parameters or adding procedures to simulate other processes) by users without advanced computer coding experience. Through our example application, we have demonstrated the potential use of this model to test the implications, at local scale, of different management scenarios and life history characteristics.

To our knowledge this model is one of only a few providing full access to its code and not requiring advanced software-coding expertise. We hope it will be used, modified and improved by subsequent users and possibly contribute to bridging the gap between the traditional modeler's community and the practitioners who manage invasive plants species in the field.

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