



Modeling Invasive Plant Spread: The Role of Plant-Environment Interactions and Model Structure

Author(s): Steven I. Higgins, David M. Richardson, Richard M. Cowling

Source: *Ecology*, Vol. 77, No. 7, (Oct., 1996), pp. 2043-2054

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/2265699>

Accessed: 07/07/2008 16:53

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=esa>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

MODELING INVASIVE PLANT SPREAD: THE ROLE OF PLANT–ENVIRONMENT INTERACTIONS AND MODEL STRUCTURE¹

STEVEN I. HIGGINS, DAVID M. RICHARDSON, AND RICHARD M. COWLING
*Institute for Plant Conservation, Department of Botany, University of Cape Town,
Private Bag, Rondebosch 7700, South Africa*

Abstract. Alien plants invade many ecosystems worldwide and often have substantial negative effects on ecosystem structure and functioning. Our ability to quantitatively predict these impacts is, in part, limited by the absence of suitable plant-spread models and by inadequate parameter estimates for such models. This paper explores the effects of model, plant, and environmental attributes on predicted rates and patterns of spread of alien pine trees (*Pinus* spp.) in South African fynbos (a mediterranean-type shrubland).

A factorial experimental design was used to: (1) compare the predictions of a simple reaction–diffusion model and a spatially explicit, individual-based simulation model; (2) investigate the sensitivity of predicted rates and patterns of spread to parameter values; and (3) quantify the effects of the simulation model's spatial grain on its predictions.

The results show that the spatial simulation model places greater emphasis on interactions among ecological processes than does the reaction–diffusion model. This ensures that the predictions of the two models differ substantially for some factor combinations. The most important factor in the model is dispersal ability. Fire frequency, fecundity, and age of reproductive maturity are less important, while adult mortality has little effect on the model's predictions. The simulation model's predictions are sensitive to the model's spatial grain. This suggests that simulation models that use matrices as a spatial framework should ensure that the spatial grain of the model is compatible with the spatial processes being modeled.

We conclude that parameter estimation and model development must be integrated procedures. This will ensure that the model's structure is compatible with the biological processes being modeled. Failure to do so may result in spurious predictions.

Key words: alien plants; biological invasions; disturbance; factorial simulation experiment; fynbos; individual-based models; *Pinus*; plant life history; reaction–diffusion models; scaling artifacts; sensitivity analysis; spatially explicit simulation models.

INTRODUCTION

The spread of invasive alien plants threatens the structure and functioning of many ecosystems worldwide (Drake et al. 1989). Unfortunately, syntheses of knowledge on biological invasions (Groves and Burdon 1986, Macdonald et al. 1986, Mooney and Drake 1986, Drake et al. 1989, di Castri et al. 1990, Richardson et al. 1992) have failed to develop any predictive theories of alien invasions (Lodge 1993). Although some workers have begun developing empirical invasion models that predict which species will invade certain environments (e.g., Richardson et al. 1990, Tucker and Richardson 1995, Rejmanek and Richardson 1996), it remains that very little is known about the rates, spatial patterns, and determinants of invasive plant spread (Macdonald 1993). The magnitude and nature of the impacts of alien plants on natural systems demand the development of a framework for predicting alien plant spread.

Predicting rates and patterns of alien plant spread requires, inter alia, the formalization of the relationships between the input and output components of an

invasion system, i.e., a model. Most invasion models use information on the plant and environmental attributes of the invasion system to predict rates and patterns of alien plant spread (Higgins and Richardson 1996). Reaction–diffusion (R–D) models are probably the most widely applied invasion models, and they have been successfully used to predict invasion rates of animal species (Levin 1992). Because R–D models use the formulation of a partial differential equation, they allow the incorporation of spatial and population processes into a single framework that can predict rates of invasion (Holmes et al. 1994). The basic assumptions of R–D models are that populations are large enough so that stochastic effects are not important and that, in the absence of reproduction, the abundance of organisms decreases exponentially around the point of release (Czaran and Bartha 1992, Holmes et al. 1994). In a homogeneous environment, where population growth is density independent, the R–D model predicts that the asymptotic rate of spread, in one dimension, can be described as

$$V \approx \sqrt{4rD} \quad (1)$$

where V is the asymptotic velocity of the invasion, r is the intrinsic rate of population growth, and D is the

¹ Manuscript received 29 June 1995; revised 17 November 1995; accepted 21 November 1995; final version received 20 January 1996.

diffusivity (Andow et al. 1990). The use of r implies that population growth is modeled as a continuous process, and that the rate of population increase is not modeled as a function of the population's age structure or environmental heterogeneity. Similarly, the parameter D implies that dispersal is modeled as a continuous function that is independent of age or environmental heterogeneity.

The assumptions of R–D models prevent the explicit investigation of the interactions between plant attributes, environmental heterogeneity, and stochasticity. Because plant–environment interactions and stochasticity strongly influence invasion rates and patterns, this limits the predictive ability of R–D models (Higgins and Richardson 1996). An additional implication of this limitation is that Eq. 1 only provides an estimate of the rate, and not the pattern, of invasive spread. Many of the limitations of the R–D models have been addressed by modifying the basic R–D model (see Hengeveld 1994, Holmes et al. 1994, Shigesada et al. 1995). Unfortunately, because the complexity of a R–D model increases with increasing realism, many of these modified R–D models either are special cases or are analytically intractable. Since the historical rationale behind pursuing the R–D approach in an invasion context was the promise of an analytical solution, it is clear that alternate model formulations should be investigated. Such an alternative must integrate space, ecological processes, and stochasticity into a single predictive framework. Spatially explicit simulation models meet these criteria (Vance 1984, Huston et al. 1988, Czaran and Bartha 1992, Higgins and Richardson 1996) and they have been applied in plant invasion scenarios (e.g., Auld and Coote 1980, 1990) and spatial problems in ecology in general (e.g., Wiener 1981, Vance 1984, Silvertown et al. 1992). Another advantage of spatially explicit models is that the spatial locations of individual modeling elements are traced. This ensures that context-specific aspects of individual plant behavior can be simulated (Czaran and Bartha 1992) and that the model's predictions can be geographically referenced and hence linked to Geographical Information Systems (GISs) for further analyses. It appears, however, that no attempt has been made to compare the performance of a R–D model with spatially explicit simulation models. Such a comparison will allow the evaluation of model performance, and this is the first objective of this paper.

To achieve this objective, we built a spatially explicit, individual-based simulation (SEIBS) model of alien plant spread. The SEIBS model is constructed to simulate the spread of alien pine trees (*Pinus* spp.) from established commercial plantations into natural fynbos ecosystems, since this is a major management problem in the mountain catchments of the Fynbos Biome of South Africa (Richardson et al. 1992). The literature on pine invasions in fynbos (which covers invasions by *P. halepensis*, *P. pinaster*, and *P. radiata*) suggests

that five factors (adult fecundity, dispersal ability, time to reproductive maturity, the temporal frequency of post-fire recruitment opportunities, and fire survival of adults) are major determinants of spread (Richardson et al. 1990, Richardson and Cowling 1992). The SEIBS model is constructed so that each of these factors can be explicitly modeled. This means that the direct effects and interactive effects of each of these factors on the rates and patterns of pine tree spread can be determined. It follows that the second objective of this paper is to investigate how rates and patterns of plant spread are influenced by these five factors, with the aim of improving the understanding of invasion processes.

Investigating the model's sensitivity to these five factors addresses two additional and important issues. Firstly, as is often the case with ecological systems, empirical data for parameter estimation are not available (Okubo 1980, Crawley 1983, Williamson 1989). The SEIBS model's output will be useful for setting priorities for empirical data collection. Secondly, an analysis of the model's response to different factors and factor levels acts as a sensitivity analysis. Although not always included in simulation studies, sensitivity analyses are imperative for defining the range of conditions for which a simulation model's predictions hold (Caswell and John 1992, Fahrig 1992). Spatially explicit simulation models are also sensitive to the model's spatial grain. However, it appears that few process-based simulation models have explored the importance of this spatial artifact (Costanza and Maxwell 1994); it is therefore the third objective of this paper to investigate the importance of this artifact. It should be noted that since R–D models use continuous parameters, they do not suffer from this grain limitation. Consequently they can, and have been, applied over a range of spatial scales (Hengeveld 1994).

The aims of this paper are to: (1) compare the qualitative and quantitative behaviour of the simple R–D model (Eq. 1) with that of a spatially explicit, individual-based simulation (SEIBS) model; (2) explore the effects, interactions, and therefore the importance of two ecologically realistic levels of five factors (adult fecundity, dispersal distribution, age of reproductive maturity, fire-return interval, and fire survival) on the rate and pattern of spread of pine trees in a homogeneous landscape; and (3) investigate the sensitivity of the SEIBS model's predictions to the spatial grain of the individual modeling elements.

METHODS

Description of the simulation model and the simulation experiment

A 2⁵-factorial experimental design (Table 1) was used to investigate the effects of fire survival (FS), adult fecundity (AF), age of reproductive maturity (ARM), mean dispersal distance (MDD), and fire-return interval (FRI) on the rate and pattern of alien plant

TABLE 1. Factor levels and combinations used in the 2⁵-factorial simulation experiment, and reaction-diffusion model parameter estimates, in a study of models of invasive plant spread.

Factor combination	Factors†					R-D‡	
	FS	AF	MDD	ARM	FRI	λ	D
1	0.4	100	70	6	8	1.586	390
2	0.1	100	70	6	8	1.574	390
3	0.4	10	70	6	8	1.196	390
4	0.1	10	70	6	8	1.179	390
5	0.4	100	20	6	8	1.586	31.8
6	0.1	100	20	6	8	1.574	31.8
7	0.4	10	20	6	8	1.196	31.8
8	0.1	10	20	6	8	1.179	31.8
9	0.4	100	70	15	8	1.168	390
10	0.1	100	70	15	8	1.159	390
11	0.4	10	70	15	8	1.043	390
12	0.1	10	70	15	8	1.029	390
13	0.4	100	20	15	8	1.678	31.8
14	0.1	100	20	15	8	1.159	31.8
15	0.4	10	20	15	8	1.043	31.8
16	0.1	10	20	15	8	1.029	31.8
17	0.4	100	70	6	25	1.465	125
18	0.1	100	70	6	25	1.460	125
19	0.4	10	70	6	25	1.144	125
20	0.1	10	70	6	25	1.137	125
21	0.4	100	20	6	25	1.465	10.2
22	0.1	100	20	6	25	1.460	10.2
23	0.4	10	20	6	25	1.144	10.2
24	0.1	10	20	6	25	1.137	10.2
25	0.4	100	70	15	25	1.187	125
26	0.1	100	70	15	25	1.183	125
27	0.4	10	70	15	25	1.068	125
28	0.1	10	70	15	25	1.063	125
29	0.4	100	20	15	25	1.187	10.2
30	0.1	100	20	15	25	1.184	10.2
31	0.4	10	20	15	25	1.068	10.2
32	0.1	10	20	15	25	1.063	10.2

† FS = fire survival (probability); AF = adult fecundity (recruits); MDD = mean dispersal distance (m); ARM = age of reproductive maturity (yr); FRI = fire-return interval (yr).

‡ λ = finite rate of population increase; D = diffusivity (m²/yr).

spread. A factorial design was used since it is a very efficient way of examining multi-factor experiments and detecting interactions (Montgomery 1984). The SEIBS model considers a two-dimensional grid of sites (150 by 400 locations). Although using a larger grid would be more realistic, computer time limitations prohibited this. Each site is of equal environmental quality, represents a spatial area of 100 m² (the approximate canopy area of an adult pine tree), and can be occupied by one plant. Several assumptions are made about the behaviour of pine trees in these sites:

- 1) Time passes in discrete intervals of 1 yr.
- 2) Fire is a source of environmental heterogeneity. Two fire-return intervals (factor FRI) are considered, an 8-yr and a 25-yr return interval. These two fire regimes are within the extremes (4–45 yr) reported for fynbos systems (van Wilgen 1987). A fire covers the entire modeling landscape, i.e., the spatial heterogeneity of fires is not considered. Burning the entire modeling landscape is consistent with the observed spatial extent of fires in fynbos (Kruger and Bigalke 1984).
- 3) Recruitment is only possible following fires. This assumption is supported by the fact that most invasive

pinus in fynbos are serotinous (Richardson et al. 1992), and that fire provides recruitment opportunities by removing the understory (Bond et al. 1984, Richardson et al. 1992).

4) Only adult trees can reproduce and two scenarios are considered, with adulthood and hence age of reproductive maturity (factor ARM), being reached at either 6 or 15 yr after recruitment. This is consistent with the range of age of reproductive maturity observed in invasive pine trees in fynbos (Richardson et al. 1992).

5) Fire causes mortality and adult mortality is less than juvenile mortality. Anecdotal observations suggest that fire-induced mortality of juvenile pine trees is extremely high (Richardson 1988). Consequently, we set the probability of juvenile fire survival at 0.05 for all simulations. Since fire-induced adult mortality varies with bark thickness (McCune 1988), two probabilities of adult fire survival (factor FS), 0.4 and 0.1, are defined. The model assumes that mortality occurs during fires, i.e., no inter-fire mortality is considered. Individual mortality occurs when a computer-generated uniform random number is greater than the probability

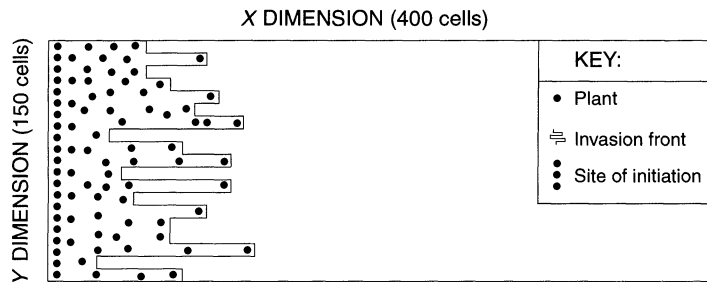


FIG. 1. A schematic representation of the spatially explicit, individual-based modeling environment.

of fire survival for that tree. Adult trees killed in a fire can contribute recruits to the next generation, but the space they occupied becomes available for colonization.

6) Two levels of adult fecundity (factor AF), 10 and 100 recruits per adult plant, were considered. Although empirical data on the fecundity of invading pines is poor, the 10–100 range is in agreement with published accounts of pine invasions in fynbos (van Wilgen and Siegfried 1986, Richardson 1988).

7) The spatial position of a recruit is determined by the position and dispersal ability of the parent plant. It is assumed that the chance of recruitment decreases as a negative exponential function of distance from the parent plant. This is a reasonable assumption, if we accept that: (i) dispersal is a negative exponential function of distance from the parent plant, as is reported in many empirical studies (see Harper 1977, Okubo and Levin 1989 for reviews); (ii) there is a homogeneous spatial distribution of recruitment opportunities for pine trees in fynbos (Richardson et al. 1992); (iii) no secondary dispersal and post-dispersal predation occurs. Using these assumptions, empirical data (van Wilgen and Siegfried 1986, Benkman 1995) and a wind-dispersal model (Greene and Johnson 1989) as calibration, we define the dispersal profile of a heavy-seeded pine species as following a negative exponential distribution with a mean dispersal distance (factor MDD) of 20 m. Similarly, we assume that the dispersal profile for a small-seeded pine would follow a negative exponential distribution with a mean dispersal distance of 70 m. The model's dispersal algorithm involves generating a negative exponential random number (with a mean of either 20 m or 70 m, as is appropriate) to determine the distance of each recruit from the parent plant, and a uniform random number (in the range 0–360°) to determine the dispersal direction of each recruit. Dispersal profiles are truncated at a distance of 1 km from the parent plant, thus excluding the possibility of rare long-distance dispersal events. The distance and direction of each recruitment event is converted to grid co-ordinates, and successful recruitment only occurs if the grid location is unoccupied. This means that preemptive competition (*sensu* Schoener 1983) for sites occurs, and that an individual can only be displaced through mortality (*cf.* assumption 5).

Ten replicated simulation runs of a 2⁵-factorial ex-

perimental design (Table 1) were performed, resulting in a total of 320 simulation runs. Replicates were performed to record the variance in model performance caused by the stochastic elements in the dispersal and mortality rules (*cf.* assumptions 5 and 7). Each simulation run was initiated with a row of mature trees along a Y-dimension edge of the 150- by 400-cell grid (Fig. 1). This row of trees represents the edge of a commercial pine tree plantation. All runs were stopped when a single tree reached the Y-dimension edge opposite the site of initiation or after 1000 simulation years. The X-dimension edges were wrapped, hence removing boundary effects (Gardner et al. 1987). The following response variables were measured from each simulation run:

- 1) Rate of spread, estimated by simple linear regression of the maximum distance of the invasion front from the site of initiation (as defined in Fig. 1) against simulation time.
- 2) The mean and standard deviation of plant density within an invasion focus, expressed as areal cover per unit area of invasion focus.
- 3) The mean and standard deviation of perimeter length of the invasive front, expressed as perimeter length per unit linear length of invasion front in metres.

Parameterizing the reaction–diffusion model

We used the structure and assumptions of the simulation model to construct a life table and population projection matrix for each factor combination. These matrices were used to estimate, using the power method (Caswell 1989), the finite rate of increase (λ) for each factor combination (Table 1). For example, for factor combination 1 we construct a projection matrix with 6 classes (=ARM). Since only the sixth class can reproduce and reproduction can only occur after fires, the annual reproduction of the sixth class is 12.5 recruits/yr (=AF/FRI). Mortality occurs during fires and hence for classes 1–5 only 0.88125 of the population (= [FRI-1]/[juvenile fire survival]) moves into the next class. Similarly, 0.925 of class six survive each year ([FRI-1]/FS). Diffusivity (D , in square metres per year) was also estimated from the structure and assumptions of the simulation model for each factor combination, using the formula provided by Andow et al. (1990). For factor combination 1 the diffusivity is 390 m²/yr ($2MDD^2[\pi \cdot FRI]^{-1}$). This procedure mimics the sam-

pling of a real population over time, by summarizing the underlying determinants of the population's vital rates in two parameters, λ and D . By substituting r for $\ln(\lambda)$, Eq. 1 was used to calculate the R-D model's predicted rate of spread.

Spatially explicit, individual-based simulation model: spatial grain simulation experiment

To explore the effects of spatial grain on aspects of the SEIBS model's performance, we carried out simulations of alien plant spread at different spatial grains. The mean of the two levels of each factor used in the 2⁵-factorial simulation experiment was used to parameterize the runs. Ten replicated simulations were performed for each of seven spatial grains (patch dimensions = 10, 20, 40, 80, 160, 320, and 640 m). Increasing the spatial grain in this manner introduces a conceptual modification into the model's structure, since one no longer models individual plants each of 10 m canopy diameter, but rather individual patches of vegetation of various sizes. The extent of the model was maintained at 150 by 400 cells to avoid any boundary-related artifacts. Apart from these modifications, the scale-dependent simulations runs had the same structure and assumptions as the 2⁵ simulation runs.

RESULTS

Reaction-diffusion model vs. spatially explicit, individual-based simulation model

The mean ($n = 10$ factors) rate of spread for each factor combination of the SEIBS model was compared with the R-D model's estimate (Figs. 2A, B). The two models produced very similar median estimates of spread rate, although the SEIBS model produced a wider range of estimates (range 0–44 vs. 1.6–26.8 m/yr). Comparison of the rate-of-spread estimates for each factor combination for the two models (Fig. 3) revealed that neither model consistently over- nor under-estimated spread rates, suggesting that the patterns observed were not due to parameterization errors. The SEIBS model provided a higher estimate of spread rate for factor combinations 1 to 8, lower estimates for combinations 9 to 16, similar estimates for combinations 17 to 24, and higher estimates for combinations 25 to 32 (Fig. 3). Hence the models differed both qualitatively and quantitatively in behavior.

The main effects and primary interactions of the factors on the predicted rate of spread for these two models (Fig. 4A, B) showed several similarities and differences. The models were similar in that they both highlighted the primary importance of all factors except fire survival. In addition, both models indicated the importance of interactions between the factors in determining the rate of spread. The quantitative details of the importance of the different factors in their effect on spread rate did differ between the models; in particular the SEIBS model emphasized the importance of

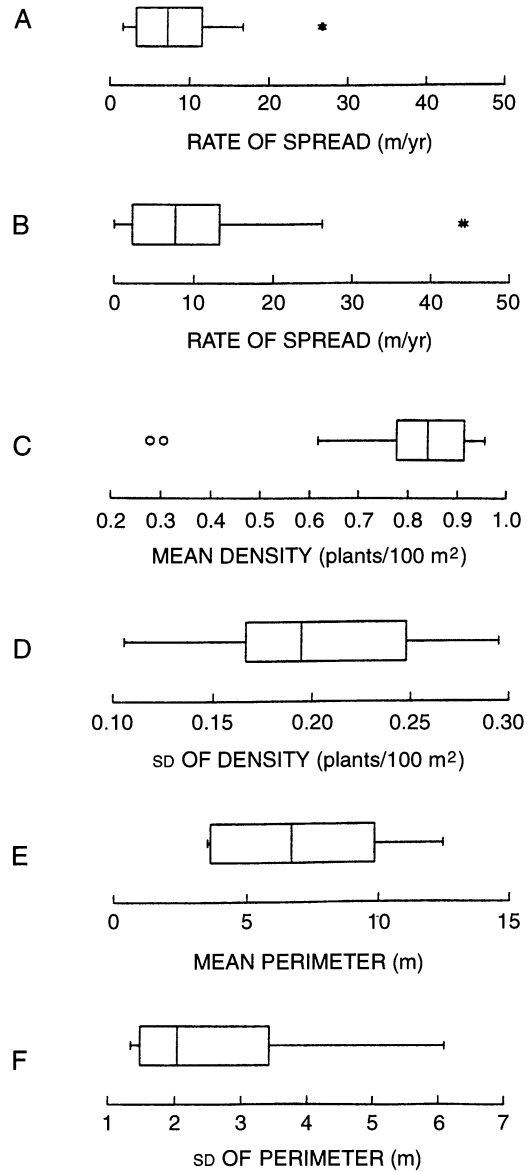


FIG. 2. Box-and-whisker plots of the range of responses for 32 factor combinations (Table 1) of the reaction-diffusion model rate of spread (A); spatially explicit, individual-based simulation (SEIBS) model rate of spread (B); SEIBS model mean density of plants in invasion focus (C); SEIBS model standard deviation of plants in invasion focus (D); SEIBS model perimeter length (E); and SEIBS model standard deviation of perimeter (F), in a study of invasive plant spread. SEIBS responses are the mean of $n = 10$ replicated simulations.

a short time to reproductive maturity (high-level ARM). The magnitude of the primary interactions between the factors illustrated more differences between the models. Large interactions, similar in magnitude to the main effects, were detected by the SEIBS model (e.g., ARM × FRI, ARM × MDD, and ARM × FRI × MDD), but not by the R-D model.

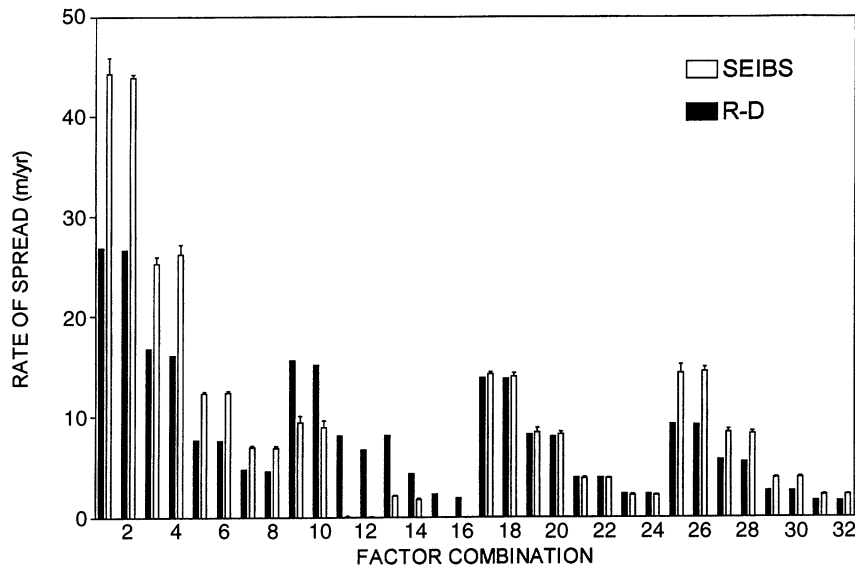


FIG. 3. Comparison of the rate of spread predicted by the reaction–diffusion (R–D) and spatially explicit, individual-based simulation (SEIBS) models for each of 32 factor combinations (Table 1), in a study of models of invasive plant spread. SEIBS values are mean \pm 1 SD ($n = 10$ replicates).

The 2⁵-factorial simulation experiment

The box-and-whisker plots describe the range of responses the SEIBS model produced (Figs. 2B–2F). The rate of spread was right-skewed and ranged from 0 to 44 m/yr (Fig. 2B). The mean density within an invasion focus was left-skewed (range 0.28 to 0.96; Fig. 2C) and the standard deviation of density was normally distributed (range 0.11–0.29; Fig. 2D). The mean perimeter was weakly left-skewed (range 3.5–10.2 m; Fig. 4E); while the standard deviation perimeter was strongly left-skewed (range 1.3–6.1 m; Fig. 4F).

A number of strong correlations between the SEIBS response variables were detected (Table 2). Spread rate was significantly correlated with the standard deviation of plant density within the invasion front, and the mean and standard deviation of perimeter length of the invasion front. We detected a strong correlation between the two related measures, mean perimeter length of the invasion front and standard deviation of the length of the invasion front. We also detected a negative correlation between mean density of plants within an invasion front and the mean length of the perimeter of the invasion front. The standard deviation of density and the standard deviation of perimeter length were positively correlated. All other correlations were weak.

The box-and-whisker plots and effects plots (Figs. 2B and 4B) show that higher levels of all factors resulted in an increased rate of spread. The FS levels chosen for this study did not have a significant effect on the spread rate, and the primary interactions involving FS were not large in magnitude (Fig. 4B). High levels of MDD and ARM resulted in 115 and 98% increases in the mean spread rate respectively. High levels of AF and FRI, while of less importance, in-

creased the mean spread rate by 63 and 54%, respectively. Two of the primary interactions (MDD \times ARM, ARM \times FRI) were of a magnitude similar to the main effects, and they resulted in 54 and 99% respective increases in the mean spread rate, while the secondary interaction between MDD, ARM, and FRI had a large effect on spread rate (55% increase).

The mean density of plants in the invasion focus responded to all five factors, and many primary interactions were large in magnitude (Fig. 4C). High levels of FRI and MDD reduced mean density by 20 and 15%, respectively, while high levels of ARM, AF, and FS increased mean density by 13, 11, and 2% respectively. Four of the primary interactions (ARM \times FRI, AF \times ARM, AF \times FRI, and AF \times MDD) were of a similar magnitude to the main effects, influencing mean density by between 2 and 13%. Two secondary interactions (AF \times ARM \times FRI and AF \times MDD \times FRI) were of large magnitude; the first reduced mean density by 9% and the second increased mean density by 5%.

The standard deviation of plant density within the invasion focus did not produce the same pattern as mean density (Fig. 4C, D). High FS reduced the standard deviation of density by 17%, while high levels of AF, MDD, ARM, and FRI led to increased variations in density (15, 10, 13, and 29% respectively). Five primary interactions were of a magnitude similar to those of the main effects. The FS \times ARM, AF \times ARM, and MDD \times FRI interactions led to decreases in the standard deviation of density of 9, 17, and 11%, respectively. Increases in standard deviation in density were caused by the AF \times FRI and ARM \times FRI interactions (respective increases of 20 and 13%). Two large

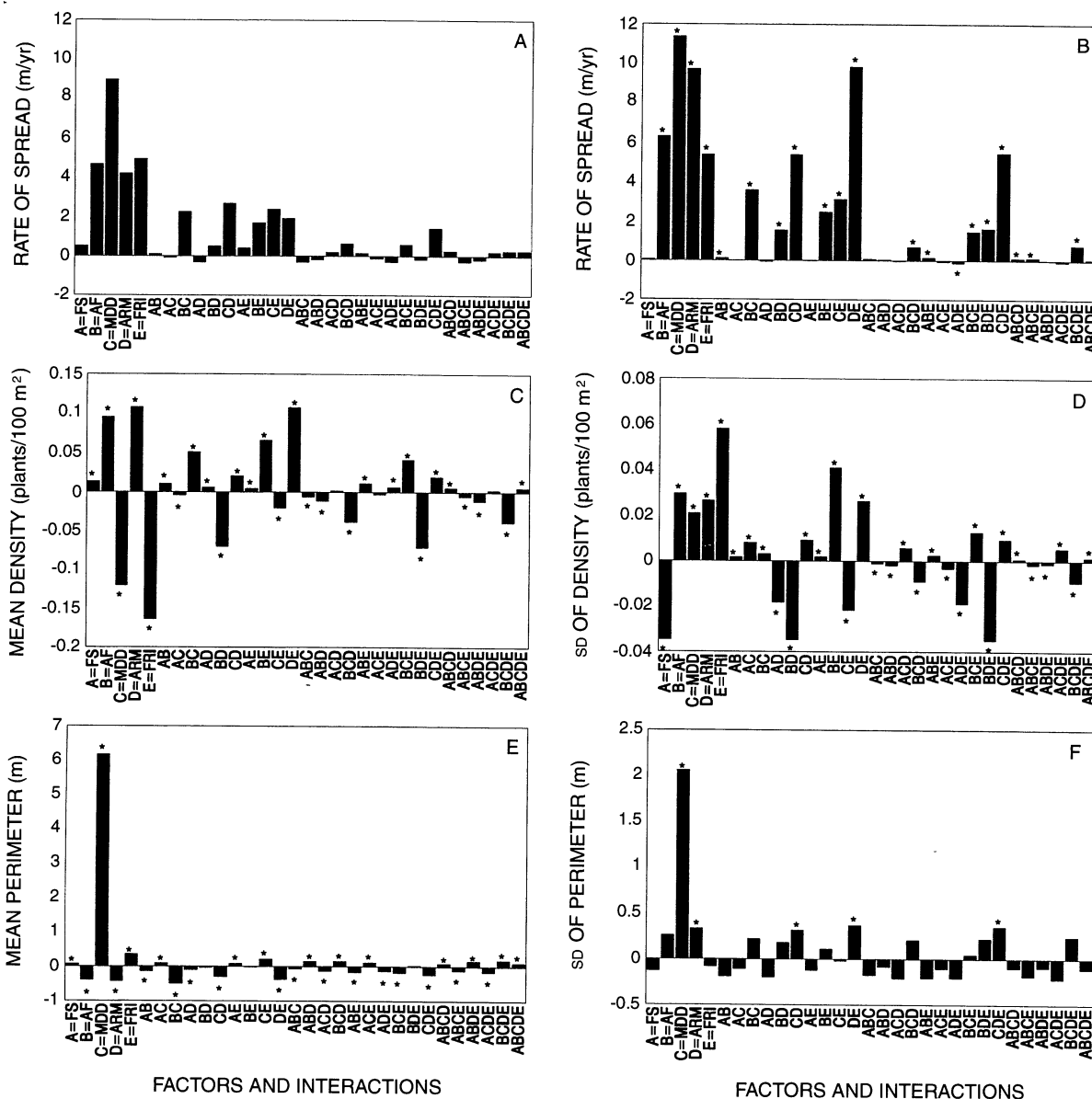


FIG. 4. The mean effect of each factor and interaction on the reaction-diffusion model rate of spread (A); spatially explicit, individual-based simulation (SEIBS) model rate of spread (B); SEIBS model mean density of plants in invasion focus (C); SEIBS model standard deviation of plants in invasion focus (D); SEIBS model perimeter length (E); and SEIBS model standard deviation of perimeter (F), in a study of invasive plant spread. FS = fire survival; AF = adult fecundity; MDD = mean dispersal distance; ARM = age of reproductive maturity; FRI = fire-return interval. * Indicates significant effects ($P < 0.05$).

secondary interactions (FS \times ARM \times FRI and AF \times ARM \times FRI) decreased standard deviation density by 9 and 17%, respectively.

The mean length of perimeter and standard deviation of perimeter (Fig. 4E, F) illustrated the same trends, namely that MDD was the primary determinant of the perimeter length of the invasion focus. This was not surprising, considering the strong positive correlations between these two related measures of invasion pattern (Table 2). The high level of MDD resulted in a 91% increase in the mean perimeter length and an 82% in-

crease in the standard deviation of perimeter length. All other factors and interactions had substantially smaller effects on perimeter length.

Scaling artifacts and the spatially explicit, individual-based model

The correlation matrix revealed that all the correlations between the model's response variables over a range of spatial grains were statistically significant (Table 3). Rate of spread was negatively correlated with mean density and positively correlated with the stan-

TABLE 2. Coefficients of Pearson correlation between response variables of the spatially explicit, individual-based simulation model and means and standard deviations of the response variables for the 320 simulation runs of the factorial experiment, in a study of models of invasive plant spread.

Response variable	Rate of spread	Mean density	SD of density	Mean perimeter	SD of perimeter	Mean	SD
Rate of spread	1					9.848†	10.99†
Mean density	0.104	1				0.808‡	0.157‡
SD of density	0.510	0.161	1			0.202‡	0.058‡
Mean perimeter	0.417	-0.506	0.137	1		6.765	3.143
SD of perimeter	0.483	-0.142	0.166	0.562	1	2.488	1.734

† m/yr; ‡ plants/100 m²; || m.

standard deviation of density, mean perimeter, and standard deviation of perimeter. Mean density was negatively correlated with standard deviation of density, mean perimeter, and standard deviation of perimeter; while standard deviation of density was positively correlated with mean and standard deviation of perimeter. Mean and standard deviation of perimeter were strongly correlated.

The SEIBS model's predictions were not consistent over a range of spatial grains. None of the observed spatial-grain trends were smooth, although this is probably because changing spatial grain in this study also changed the scale at which measurements were made and "rounded off" the location of a recruit to the nearest cell. The predicted rate of spread was relatively stable over a spatial grain from 10 to 160 m, with only a 12.4% decrease in the predicted rate of spread observed (Fig. 5A). Further increase in the spatial grain resulted in substantial decreases in the predicted rate of spread. The mean density of patches within the invasion focus increased rapidly with increasing spatial grain (Fig. 5B). The standard deviation of patch density within the invasion focus decreased slowly with spatial grain in the range 10–320 m, after which it decreased dramatically (Fig. 5C). The mean perimeter length and standard deviation of perimeter length both exhibited a rapid decline with spatial grain that levelled out at 80 m (Fig. 5D, E).

DISCUSSION

Reaction-diffusion vs. spatially explicit, individual-based model

The range of predictions made by the R-D and SEIBS models falls within the lower range of spread rates reported in the literature for invading plant species (see Lee et al. 1991, Lonsdale 1993, Perrins et al. 1993) and for Holocene tree spread rates (Birks 1989). The utility of this comparison is limited since there are few published estimates of rates of spread and since the taxa, environments, and methodologies reported in the literature are likely to yield different spread rates (S. I. Higgins and D. M. Richardson, *unpublished manuscript*). However the result does confirm that the rates of spread predicted by this study are reasonable. The R-D and SEIBS models differ in the range of spread-rate predictions they make and in the predicted effects of plant life history attributes and disturbance frequency. These differences can be attributed to the R-D model's use of two continuous parameters to summarize plant-environment interactions. We show that the use of spatially implicit model formulations and continuous parameters, which summarize many ecological processes into a few parameters, can qualitatively and quantitatively influence a model's predictions. This is well illustrated by the large interaction between age of reproductive maturity and mean dispersal distance in the SEIBS model, where stands of a

TABLE 3. Coefficients of Pearson correlation between response variables of the spatially explicit, individual-based simulation model and means and standard deviations of the response variables for the 70 scale-dependent simulation runs, in a study of models of invasive plant spread.

Response variable	Rate of spread	Mean density	SD of density	Mean perimeter	SD of perimeter	Mean	SD
Rate of spread	1					9.122†	3.861†
Mean density	-0.743	1				0.945‡	0.029‡
SD of density	0.983	-0.745	1			0.155‡	0.050‡
Mean perimeter	0.525	-0.948	0.509	1		2.797	1.784
SD of perimeter	0.405	-0.903	0.392	0.982	1	1.396	0.451

† m/yr; ‡ plants/100 m²; || m.

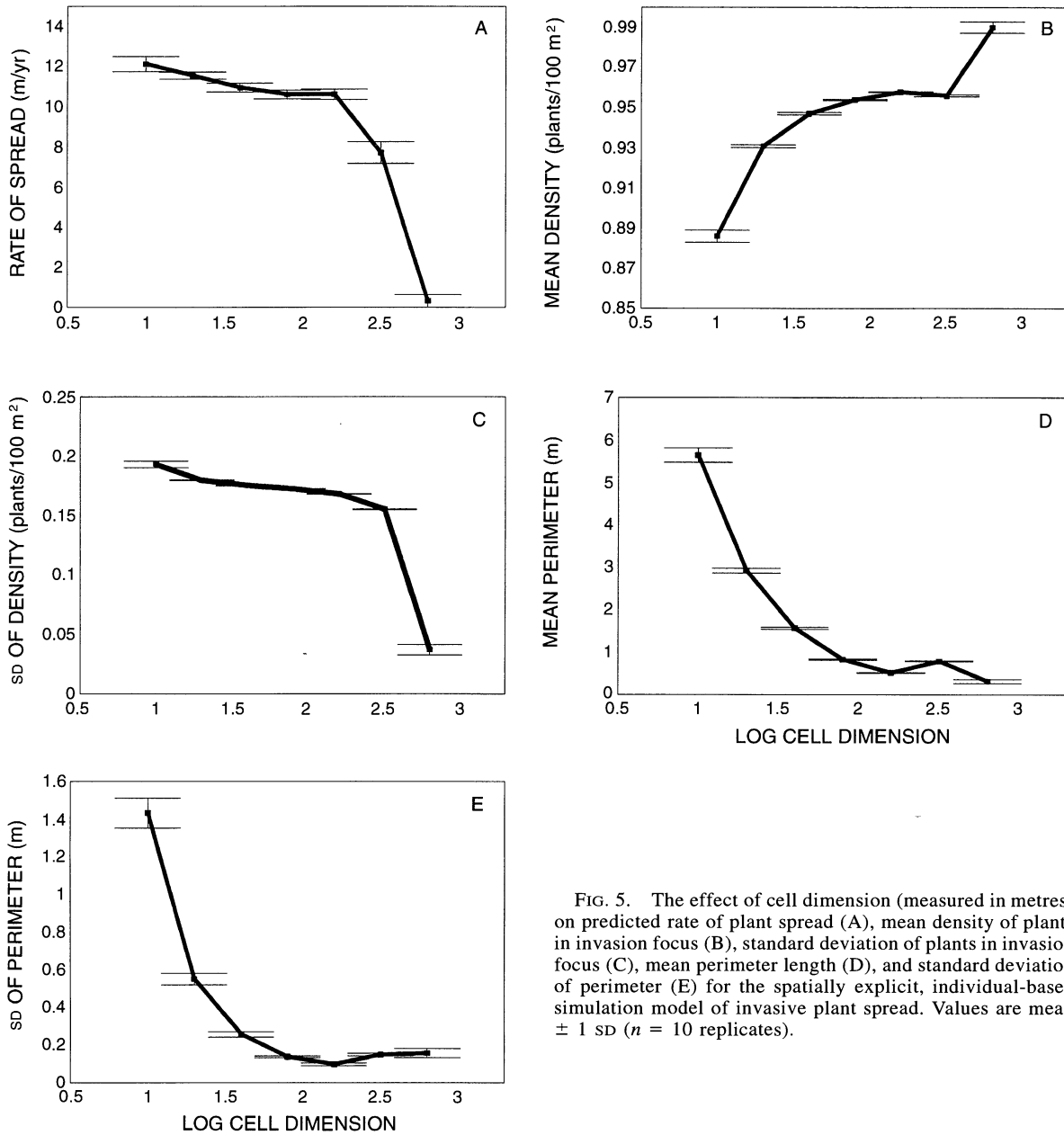


FIG. 5. The effect of cell dimension (measured in metres) on predicted rate of plant spread (A), mean density of plants in invasion focus (B), standard deviation of plants in invasion focus (C), mean perimeter length (D), and standard deviation of perimeter (E) for the spatially explicit, individual-based simulation model of invasive plant spread. Values are mean \pm 1 SD ($n = 10$ replicates).

slow-maturing, short-dispersing species spread more slowly than would be predicted from a knowledge of their mean dispersal distance and age of reproductive maturity alone. This interaction occurs because slow-maturing, short-dispersing species are unlikely to have many adult trees on the edge of an invasion focus when recruitment opportunities occur. Hence, although the R-D model recognizes that invasive success is a function of both the reproductive and dispersal potential of individuals (Skellam 1951), the SEIBS model illustrates that an explicit knowledge of the effects and interactions of factors that influence reproductive po-

tential (indexed by r in the R-D model) is required for predicting spread rates. Several workers have recognized limitations of the R-D approach and this has motivated the modification of the basic R-D model. It seems that these attempts were in vain, firstly because these modifications have not substantially influenced model predictions (e.g., Holmes 1993, Hengeveld 1994), and secondly since our results suggest that these limitations are inherent in the structure of R-D models.

The larger effects of the factor mean dispersal distance in the SEIBS model indicates that the use of a stochastic dispersal rule results in higher predicted

spread rates, implying that the incorporation of stochastic rules can substantially modify a model's predictions for small populations. The same result was found by Goldwasser et al. (1994). Furthermore, the tails of dispersal profiles of wind-dispersed species may not decrease in a negative exponential manner, but rather more gently (Portnoy and Willson 1993, Greene and Johnson 1995). In such circumstances, an alternative dispersal algorithm to the one used here will be needed. These rarer long-distance events can result in the formation of new disjunct invasion foci, which can substantially increase the observed rate of spread as well as change the pattern of spread (Moody and Mack 1988, Shigesada et al. 1995). Since the incorporation of alternative dispersal distributions into the SEIBS model would be technically simple, it follows that effort should be devoted to collecting data on the tails of dispersal profiles.

Determinants of invasive spread

The SEIBS model quantifies the more rapid invasion of plants with shorter juvenile periods, higher fecundity, and longer dispersal distances, which grow in more frequently disturbed environments. Importantly, the model quantifies the effects on rate of spread of the interactions between these factors. This study, therefore, allows for the quantification of how different suites of life history and environmental attributes influence the chance of invasion. This is a progression from previous studies, which merely identified the attributes of invasive plants (e.g., Richardson et al. 1990, Lodge 1993, Rejmanek and Richardson 1996). The large magnitude of the interactions between factors means that all factors, except fire survival, can strongly influence spread rates. The consequence of this is that for most invasion scenarios, effort should be placed on obtaining good empirical data for all factors except fire survival.

The SEIBS model predicts that high levels of adult fire survival, high adult fecundity, short dispersal distances, short time to reproductive maturity, and infrequent fires all lead to increased mean stand density. Predictions of alien plant abundance may be useful for predicting the impacts of alien plants in situations where alien abundance is correlated with alien plant impacts (e.g., Richardson et al. 1989). The plant-environmental traits identified by the SEIBS model (which increase local density) differ from the traits that influence the rate of plant spread. This observation is supported by the poor correlation between rate of spread and stand density (Table 2).

Mean and standard deviation of alien plant density were influenced by some complex interactions that further emphasize the utility of the SEIBS approach. For example, while fecund individuals that mature quickly on average resulted in denser and more variable stand densities, the interaction between these two factors decreased the mean and standard deviation of stand den-

sity. This decrease can be attributed to the reduced availability of establishment sites around parent plants caused by density-dependent effects associated with preemptive competition for establishment sites. Any model that does not consider real coordinate space is unlikely to account for this reduction in safe site density (Perry and Gonzalez-Andujar 1993). The interactions between fire frequency, reproductive age, and adult fecundity provide another example of the importance of interactions for predicting stand density: for slow-maturing plant populations that produce few offspring, a short fire-return interval leads to high levels of mortality, but this same fire-return interval provides recruitment opportunities for a fast-maturing and fecund population.

Spatial grain and the spatially explicit, individual-based simulation model

The SEIBS model's predictions for all response variables were strongly influenced, both quantitatively and qualitatively, by changes in spatial grain. The most sensitive variables were mean plant density and perimeter length, whereas predicted rate of spread and variation in plant density were less sensitive to small changes in spatial grain yet very sensitive to large changes in spatial grain. Since the strength and sign of the correlations between response variables of the scale-dependent simulation runs (Table 3) and the factorial simulation runs (Table 2) differ substantially, we conclude that the correlations identified in the factorial runs are not stable over different spatial grains, and conversely that the trends identified in the scale-dependent runs are a function of the parameter values selected. This can be illustrated by considering that since increasing spatial grain increases the distance a recruit must travel to leave its parent cell, a species with a short dispersal distance will be more sensitive to increased spatial grain (Fahrig and Paloheimo 1988, Gardner et al. 1991). These results provide firm evidence that simulation models, which use matrices as a spatial framework, need to ensure that the spatial grain of the model is compatible with the spatial processes being modeled. This is supported by recent criticisms that spatial meta-population models often have spatial structures that are inappropriate for the ecological processes being modeled (McCauley et al. 1993). Such inconsistencies may substantially influence predictability, and we consequently recommend that the robustness of spatial models' predictions to changing spatial grain be routinely evaluated as part of sensitivity analysis procedures. The spatial grain of environmental heterogeneity is a related factor that should also influence the selection of the most appropriate spatial grain for a spatial simulation model. This is because environmental heterogeneity can strongly influence invasion dynamics (Bergelson et al. 1993); the spatial grain of the model must therefore be such that it represents

the patterns of environmental heterogeneity that influence the organism's response (Kotliar and Wiens 1990).

CONCLUSIONS

This study has shown that reaction-diffusion models are inadequate building blocks for the modeling of spatial phenomena, a conclusion supported by Vance (1984) but not by Hengeveld (1994). In particular, this paper demonstrates that the failure of the reaction-diffusion model to mimic ecological processes and interactions between these processes reduces the model's predictive ability. The importance of such interactions was demonstrated by a spatially explicit, individual-based simulation model. The importance of interactions between ecological factors and the lack of empirical data on these factors suggest that considerable effort should be devoted to collection of empirical data. The simulation model described here and the results of this study provide clear objectives for such empirical work. On a cautionary note, we have shown that the performance of grid-based spatial simulation models is influenced by spatial scaling artifacts; this suggests that model development requires knowledge of not just the ecological processes of importance, but also of the spatial scale of these processes. In essence this means that the parameter estimation and model development processes must be integrated.

ACKNOWLEDGMENTS

Thanks to Jessica Kemper for comments on early drafts of the manuscript, and to Leanne Scott and Berty van Hensbergen for statistical advice. Donald DeAngelis, Sandra Lavorel, and Marcel Rejmanek are thanked for helpful suggestions and critical comments. This work was supported by the Foundation for Research Development and the Flora Conservation Committee of the Botanical Society of South Africa.

LITERATURE CITED

- Andow, D. A., P. M. Kareiva, S. A. Levin, and A. Okubo. 1990. Spread of invading organisms. *Landscape Ecology* 4:177-188.
- Auld, B. A., and B. G. Coote. 1990. INVADE: towards the simulation of plant spread. *Agriculture, Ecosystems and Environment* 30:212-128.
- Auld, B. A., and B. G. Coote. 1980. A model of a spreading plant population. *Oikos* 34:287-292.
- Benkman, C. W. 1995. Wind dispersal capacity of pine seeds and the evolution of different seed dispersal modes in pines. *Oikos* 73:221-224.
- Bergelson, J., J. A. Newman, and E. M. Floresroux. 1993. Rates of weed spread in spatially heterogenous environments. *Ecology* 74:999-1011.
- Birks, H. J. B. 1989. Holocene isochrone maps and patterns of tree-spreading in the British Isles. *Journal of Biogeography* 16:503-540.
- Bond, W. J., J. Vlok, and M. Viviers. 1984. Variation in seedling recruitment of Cape Proteaceae after fire. *Journal of Ecology* 74:209-221.
- Caswell, H. 1989. Matrix population analysis. Construction, analysis and interpretation. Sinauer, Sunderland, Massachusetts, USA.
- Caswell, H., and A. M. John. 1992. From the individual to the population in demographic models. Pages 36-61 in D. L. DeAngelis and L. J. Gross, editors. Individual-based models and approaches in ecology. Chapman and Hall, New York, New York, USA.
- Costanza, R., and T. Maxwell. 1994. Resolution and predictability: an approach to the scaling problem. *Landscape Ecology* 9:47-57.
- Crawley, M. J. 1983. Herbivory: the dynamics of animal-plant interactions. Blackwell Scientific, Oxford, England.
- Czaran, T., and S. Bartha. 1992. Spatiotemporal dynamic models of plant populations and communities. *Trends in Ecology and Evolution* 7:38-42.
- di Castri, F., A. J. Hansen, and M. Debussche. 1990. Biological invasions in Europe and the Mediterranean basin. Kluwer, Dordrecht, The Netherlands.
- Drake, J. A., H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson. 1989. Biological invasions: a global perspective. John Wiley and Sons, Chichester, England.
- Fahrig, L. 1992. Simulation methods for developing general landscape-level hypotheses of single species dynamics. Pages 417-442 in M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology. Springer-Verlag, New York, New York, USA.
- Fahrig, L., and J. Paloheimo. 1988. Effects of spatial arrangement of habitat patches on local population size. *Ecology* 69:468-475.
- Gardner, R. H., B. T. Milne, M. G. Turner, and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape patterns. *Landscape Ecology* 1:19-28.
- Gardner, R. H., M. G. Turner, R. V. O'Neill, and S. Lavorel. 1991. Simulation of the scale-dependent effects of landscape boundaries on species persistence and dispersal. Pages 76-89 in M. M. Holland, P. G. Risser, and R. J. Naiman, editors. Ecotones—the role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York, New York, USA.
- Goldwasser, L., J. Cook, and E. D. Silverman. 1994. The effects of variability on metapopulation dynamics and rates of invasion. *Ecology* 75:40-47.
- Greene, D. F., and E. A. Johnson. 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* 70:339-347.
- Greene, D. F., and E. A. Johnson. 1995. Long-distance wind dispersal of tree seeds. *Canadian Journal of Botany* 73:1036-1045.
- Groves, R. H., and J. J. Burdon. 1986. Ecology of biological invasions: an Australian perspective. Australian Academy of Science, Canberra, Australia.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, England.
- Hengeveld, R. 1994. Small-step invasion research. *Trends in Ecology and Evolution* 9:339-342.
- Higgins, S. I., and D. M. Richardson. 1996. A review of models of alien plant spread. *Ecological Modelling* 87:249-265.
- Holmes, E. E. 1993. Are diffusion models too simple? A comparison with telegraph models of invasion. *American Naturalist* 142:779-795.
- Holmes, E. E., M. A. Lewis, J. E. Banks, and R. R. Veit. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* 75:17-29.
- Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. *BioScience* 38:682-691.
- Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.
- Kruger, F. J., and R. C. Bigalke. 1984. Fire in fynbos. Pages 67-114 in P. de V. Booysen and N. M. Tainton, editors. Ecological effects of fire in South African ecosystems. Springer-Verlag, Berlin, Germany.

- Lee, W. G., J. B. Wilson, C. D. Meurk, and P. C. Kennedy. 1991. Invasion of the subantarctic islands, New Zealand, by the asterad tree *Olearia lyallii* and its interaction with a resident myrtaceous tree *Metrosideros umbellata*. *Journal of Biogeography* **18**:493–508.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**:1943–1967.
- Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* **8**:133–137.
- Lonsdale, W. M. 1993. Rates of spread of an invading species—*Mimosa pigra* in northern Australia. *Journal of Ecology* **81**:513–521.
- Macdonald, G. M. 1993. Fossil pollen analysis and the reconstruction of plant invasions. *Advances in Ecological Research* **24**:67–110.
- Macdonald, I. A. W., F. J. Kruger, and A. A. Ferrar. 1986. The ecology and management of biological invasions in southern Africa. Oxford University Press, Cape Town, South Africa.
- McCauley, E., W. G. Wilson, and A. M. de Roos. 1993. Dynamics of age-structured and spatially structured predator–prey interactions: individual-based models and population-level formulations. *American Naturalist* **142**:412–442.
- McCune, B. 1988. Ecological diversity in North American pines. *American Journal of Botany* **75**:353–368.
- Montgomery, D. C. 1984. Design and analysis of experiments. John Wiley and Sons, New York, New York, USA.
- Moody, M. E., and R. N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* **25**:1009–1021.
- Mooney, H. A., and J. A. Drake. 1986. Ecology of biological invasions of North America and Hawai'i. Springer-Verlag, New York, New York, USA.
- Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, Berlin, Germany.
- Okubo, A., and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* **70**:329–339.
- Perrins, J., A. Fitter, and M. Williamson. 1993. Population biology and rates of invasion of three introduced *Impatiens* species in the British Isles. *Journal of Biogeography* **20**:33–44.
- Perry, J. N., and J. L. Gonzalez-Andujar. 1993. Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. *Journal of Ecology* **81**:453–463.
- Portnoy, S., and M. F. Willson. 1993. Seed dispersal curves: behaviour of the tail of the distribution. *Evolutionary Ecology* **7**:25–44.
- Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* **77**:1655–1661.
- Richardson, D. M. 1988. Age structure and regeneration after fire in a self-sown *Pinus halepensis* forest on the Cape Peninsula, South Africa. *South African Journal of Botany* **54**:140–144.
- Richardson, D. M., and R. M. Cowling. 1992. Why is mountain fynbos invulnerable and which species invade? Pages 161–181 in B. W. van Wilgen, D. M. Richardson, F. J. Kruger, and H. J. van Hensbergen, editors. Fire in South African mountain fynbos. Springer-Verlag, Berlin, Germany.
- Richardson, D. M., I. A. W., Macdonald, and G. G. Forsyth. 1989. Reductions in plant species richness under stands of alien trees and shrubs in the Fynbos Biome. *South African Journal of Forestry* **149**:1–8.
- Richardson, D. M., I. A. W. Macdonald, P. M. Holmes, and R. M. Cowling. 1992. Plant and animal invasions. Pages 271–308 in R. M. Cowling, editor. The ecology of the fynbos. Oxford University Press, Cape Town, South Africa.
- Richardson, D. M., R. M. Cowling, and D. C. Le Maitre. 1990. Assessing the risk of success in *Pinus* and *Banksia* in South African mountain fynbos. *Journal of Vegetation Science* **1**:629–642.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240–285.
- Shigesada, N., K. Kawasaki, and Y. Takeda. 1995. Modeling stratified diffusion in biological invasions. *American Naturalist* **146**:229–251.
- Silvertown, J., S. Holtier, J. Johnson, and P. Dale. 1992. Cellular automata models of interspecific competition for space—the effect of pattern on process. *Journal of Ecology* **80**:527–534.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196–218.
- Tucker, K. C., and D. M. Richardson. 1995. An expert system for screening potentially invasive alien plants in South African fynbos. *Journal of Environmental Management* **44**:309–338.
- van Wilgen, B. W. 1987. Fire regimes in the fynbos biome. Pages 6–14 in R. M. Cowling, D. C. Le Maitre, B. McKenzie, R. P. Prys-Jones, and B. W. van Wilgen, editors. Disturbance and the dynamics of fynbos biome communities. South African National Scientific Programmes Report 135, Foundation for Research Development, Pretoria, South Africa.
- van Wilgen, B. W., and W. R. Siegfried. 1986. Seed dispersal properties of three pine species as a determinant of invasive potential. *South African Journal of Botany* **52**:546–548.
- Vance, R. R. 1984. The effect of dispersal on population stability in one-species, discrete-space population growth models. *American Naturalist* **123**:230–254.
- Wiener, J. 1981. Dispersal and neighbourhood effects in an annual plant competition model. *Ecological Modelling* **13**:131–147.
- Williamson, M. 1989. Mathematical models of invasion. Pages 329–350 in J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley and Sons, London, England.