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Simulating the spread and management of alien riparian weeds: are they out of control?

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Summary

1. This paper examines the circumstances under which control programmes may reduce the range of two widespread invasive weeds of riparian habitats: *Impatiens glandulifera* (Himalayan balsam) and *Heracleum mantegazzianum* (giant hogweed).
2. The spread of both species was modelled using MIGRATE, a spatially explicit model that incorporates realistic demographic parameters and multiple dispersal mechanisms. Simulations of a range of control scenarios were run within a geographical information system (GIS) using authentic landscapes based on topographic, hydrological and land cover maps of County Durham, UK. Results were interpreted at both a catchment and a regional scale.
3. Six representative strategies were explored that prioritized control as follows: at random, in relation to human population density, or by the size, age (new and old) or spatial distribution of weed populations. These strategies were assessed at different intensities of management (area treated per year) and for varying efficiencies (proportion of plants destroyed) as well as the timeliness (how long since the species became established) of implementations.
4. Strategies that prioritized control based on weed population and spatial characteristics were most effective, with plant population size and spatial distribution being the key parameters. The reduction in geographical range within a catchment or region following control was always greater for *H. mantegazzianum* than *I. glandulifera* due to its slower rate of spread.
5. Successful control of both species at a regional scale is only possible for strategies based on species distribution data, undertaken at relatively high intensities and efficiencies. The importance of understanding the spatial structure of the population and potential habitat available, as well as being able to monitor the progress of the eradication programme, is highlighted. Tentative conclusions are offered as to the feasibility of eradicating these species at a regional scale.

Key-words: Heracleum mantegazzianum, *Impatiens glandulifera*, invasion dynamics, landscape ecology, seed dispersal, weed management.

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Introduction

Heracleum mantegazzianum Sommier & Levier (giant hogweed) and *Impatiens glandulifera* Royle (Himalayan balsam) were introduced from Asia into the UK over a hundred years ago as garden ornamentals (Tiley, Dodd & Wade 1996; Beerling & Perrins 1993). Having become naturalized following escape from cultivation, both species are now widespread in the British Isles, especially along watercourses. The large plant size, high reproductive output and rapid growth of both species enables them to dominate local vegetation rapidly with a resultant loss in conservation value at some sites (Roblin 1994). Die-back of plants in the autumn exposes bare river banks resulting in increased erosion during high winter flows (Roblin 1994). Furthermore *H. mantegazzianum* poses a risk to public health because its sap contains furanocoumarins, which may cause phytophotodermatitis when in contact with human skin (Tiley, Dodd &

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Wade 1996). Due to these characteristics, legislation under Schedule 9 of the Wildlife and Countryside Act (1981) has made it an 'offence to plant or otherwise cause to grow *H. mantegazzianum* in the wild'. Although *I. glandulifera* is not covered by legislation, considerable interest has been shown in its control.

On confined sites *H. mantegazzianum* can be controlled through livestock management, e.g. sheep grazing (Anderson 1994) and pig farming (Tiley & Philp 1994). Mechanical control is possible but needs to be carefully timed: *H. mantegazzianum* needs to be cut below the apical bud soon after flowering (Dodd *et al.* 1994) and *I. glandulifera* needs to be treated before flowering. Chemical treatment (e.g. glyphosphate) is the most common control method and for both species it is important to treat twice in a season, once before flowering and again later on to treat small plants that sheltered under the original foliage (Caffrey 1994; Lundström & Darby 1994). For many sites the presence of native vegetation and the proximity to water courses restricts the choice of herbicides and methods of application. Reviews of different control methods (including mechanical, chemical and grazing) are available for a number of countries: Ireland (Caffrey 1994), Denmark (Anderson 1994), Sweden (Lundström & Darby 1994) and Scotland (Tiley & Philp 1994). Chemical control is expensive; in 1989/90 in the UK the average cost of materials to treat a hectare of *H. mantegazzianum* was £400 and could reach £1000 ha^{-1} depending on local conditions (Sampson 1994). This expenditure will increase substantially when labour costs are taken into account; in consequence most control efforts are directed at small areas (average 3 ha; Sampson 1994). Given that the resources available for control are limited, it is clearly desirable to develop an explicit strategy for identifying priority areas of control.

The normal recommendation is to tackle upstream populations first and then work downstream, although sometimes the opposite strategy is adopted because vegetative growth starts earlier at lower elevations (Tiley & Philp 1994). Moody & Mack (1988) suggest that it may be best to eradicate small outlying populations first as they contribute most to range expansion (due to their large edge to area ratio). An alternative view is that control should focus on the larger 'source' population(s) that is the principal source(s) of propagules. In practice most control is sporadic and aimed at wherever the problem is perceived to be the greatest, e.g. amenity areas, nature reserves, etc. (Dodd *et al.* 1994). Assessing the relative merits of these different approaches is hindered by the limited data available on efficiency (number of plants completely eradicated) of control efforts or the persistence of their effect following treatment.

Evidently, substantial scope exists to develop management strategies that will improve the effectiveness of control of these two alien species. This study aimed to use simulation models to examine the relative reduction in species range achieved by applying different management strategies, and how this is influenced by the effectiveness of the control methods, the size of the area controlled and plant life history. The simulations assumed the resources to control alien weeds were limited and attempted to determine the most effective way to use available resources. The simulations were also used to assess whether eradication is a feasible goal.

Methods and materials

MODELLING THE SPREAD OF *I. GLANDULIFERA* AND *H. MANTEGAZZIANUM*

Modelling for both species has been carried out using MIGRATE, a cell-based model that is continuous in state but discrete in time and space. The model has been described in detail in earlier papers (Collingham, Hill & Huntley 1996; Collingham, Huntley & Hulme 1997) and so will be described only briefly here. MIGRATE was specifically designed as a flexible and generalized framework to describe the spread of sessile organisms across heterogeneous landscapes, and therefore required little adaptation for use in this study. The environment is represented as a grid of cells each with an associated carrying capacity that determines the maximum number of individuals the cell can support. For all simulations reported here, a cell size of 500×500 m was used, as a smaller cell size would unreasonably prolong simulation run times. The simulations were run in a realistic landscape centred on county Durham in north-east England and incorporated the hydrological network of the River Wear catchment (Bartholomew's data set; CHEST 1993). The catchment scale of the work is therefore roughly equivalent to other contributions to this special issue (Cresser *et al.* 2000; Edwards *et al.* 2000) giving it clear management relevance (Ormerod & Watkinson 2000). Cell suitability was classified separately for each of the two weed species and was based on results from stepwise logistic regression that related the observed plant species distributions with environmental variables (Collingham *et al.* 2000). The logistic regression equation developed from tetrad (2×2 km) species distribution data from *The Flora and Vegetation of County Durham* (Graham 1988) was applied to environmental data sets at a 500×500 m resolution and the resulting 'probability' was used as a substitute for suitability. Field observations suggested that, even where abundant, neither species would ever occupy more that about 1% of a 500×500-m cell. This was used as an upper limit

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for the riparian cells (those which were adjacent to a water course); non-riparian cells were expected to have a much lower plant density (Pyšek & Prach 1994) of 0·01%.

Although multiple introductions of both species were likely to have occurred during the initial phase of colonization of County Durham, the simulations were initiated for both species assuming a single introduction in Durham City (54°46′N, 1°35′W). This assumption was primarily to facilitate comparison between the two species, but the site also corresponds to some of the earliest records for the species in County Durham (Graham 1988). An arbitrary figure of 10 individuals was used for the initial introduction. Values greater than 10 did not increase the rate of spread; values much below 10 merely increased the probability that the founder population would die out rather than spread. The number of individuals in each cell was calculated at the end of each time step of 1 year. For *H. mantegazzianum* an individual survives with a given probability to the next cohort each year and each cohort is represented by different parameters (Table 1). Although *H. mantegazzianum* is monocarpic it can flower at any time between 2 and 5 years after establishment and this is represented in the model by allowing seed production from more than one cohort. For *I. glandulifera* seed production is density dependent (Beerling & Perrins 1993), but for *H. mantegazzianum* a fixed number of seeds per plant is used. The probability that a propagule will reach a suitable cell; the probability that it will then become established; and the probability that it will survive to a cohort capable of producing seeds, were all determined stochastically. Propagules are dispersed using three mechanisms: local dispersal (within a cell), occasional long distance dispersal in a random direction, and occasional long distance dispersal along the river system. To incorporate the directionality inherent in long range dispersal by rivers, the 'flow direction' function available in the ArcInfo geographical information system (GIS) (ESRI 1998) was used to define a downstream direction for each grid cell. Parameter values shown in Table 1 were obtained from the literature (mainly Beerling & Perrins 1993; Tiley, Dodd & Wade 1996) and from field work and experimental manipulations (Willis, Hulme & Huntley 1997). Although the success of the species will vary from year to year depending on the weather (late spring frosts, summer droughts, etc.), there is insufficient quantitative data to allow the parameters to vary with time.

Table 1. Values of reproductive and dispersal parameters used in the simulations reported in this paper. The annual *Impatiens glandulifera* is modelled as a single cohort. Because of the variability in how long it takes *Heracleum mantegazzianum* to mature it is modelled as if it were polycarpic (see text). Root mean squared distances (RMSD) assume a bivariate normal distribution (local dispersal) and half distances assume a negative exponential distribution (long distance and river dispersal). Furthest cell limits are used as a mathematical convenience to counter the problem that both distributions will generate finite probabilities at infinite distances

Parameter	*I. glandulifera*	*H. mantegazzianum*			
Cohort	C1	C1	C2	C3	C4
Maximum plant density (m^{-2})	40*	1·0	1·0	1·0	0·25
Probability seed establishes	0·030†	0·0413‡			
Probability of survival to next cohort	0·0	1·0	1·0	0·995	0·0
Number of seeds/fruit	$1886\,PD^{(-0·367)}$§	0·0	0·0	9820¶	9820
Probability of local dispersal	0·5993			0·5993	0·5993
RMSD local dispersal	1·0m**			5m††	5m
Furthest distance local dispersal	1 cell (500m)			1 cell	1 cell
Probability of dispersal into a river	0·4‡‡			0·4‡‡	0·4
Half distance of dispersal along a river	3 km§§			1 km§§	1 km
Furthest river dispersal	20 km			10 km	10 km
Probability of long distance dispersal	0·0007			0·0007	0·0007
Half distance of long dispersal	1 km			1 km	1 km
Furthest cell for long distance dispersal	20 km			20 km	20 km

*Compromise between 50–70 m^{-2} (Perrins, Fitter & Williamson 1993), 30–40 m^{-2} (Beerling & Perrins 1993) and > 10 m^{-2} (Prach 1994).
†Based on field experiments within the Wear catchment (Willis, Hulme & Huntley 1997).
‡Based on field experiments within the Wear catchment (Willis, Hulme & Huntley 1997).
§PD = plant density; equation from Beerling & Perrins (1993).
¶Seed production simulated in two cohorts because of variability in when fruiting will occur. Seed numbers are also very variable; Tiley, Dodd & Wade (1996) refers to observation of between 1500 and 29000.
**Has been observed spreading at up to 2·47 m $year^{-1}$ (Beerling & Perrins 1993).
††Most seeds and seedlings within 10 m of colony; few more than 50 m away (Caffrey 1994) .
‡‡Based on qualitative observations of typical locations of stands.
§§River and long-distance dispersal parameters are selected to allow dispersal rates similar to those observed.

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A sensitivity analysis was performed on the parameters in Table 1 for both species by running 10 trials with each value changed by ± 50% and using the variation in the mean geographical range after 50 years as the measure of sensitivity. For *I. glandulifera* the most important parameters were the half distance of the long distance dispersal (68%), probability of seed establishing (58%) and probability of long distance dispersal (39%); all other values produced variations of less than 20%. The values for *H. mantegazzianum* were slightly different. Because seed production is not density dependent (as it is for *I. glandulifera*), plant density and number of seeds per plant were relatively more important (40%). The probability of long distance dispersal was less important (20%), but the half distance for long distance dispersal was more important (75%). For both species habitat suitability was by far the most important influence on geographical range, altering the suitability by ± 50% changed the geographical range from zero to over double for both species.

MODELLING DIFFERENT METHODS OF CONTROL

Six management strategies were simulated in addition to the 'do nothing' case where no control was undertaken. Two of the strategies, 'random' and 'social', attempted to mimic realistic responses to a perceived problem, such as a local authority responding to complaints or notifications of the species' presence. The random strategy was very simple; cells within the management zone were visited at random until the maximum number of sites had been found and treated. The social strategy systematically treated infested cells that had the highest human population density first, assuming more people equates to more frequent human–plant interactions.

The 'population' strategy attempted to focus control where the species was most prevalent (based upon the size of the plant population); priorities for control were derived from the number of plants in the cell. If the species had been established for more than a few decades this strategy was equivalent to one of treating first those areas with the most suitable habitat. Two strategies based on age were evaluated; 'age (old)' prioritized those cells that had been occupied longest as control targets, and 'age (new)' targeted cells most recently colonized. When a species is well established, the length of time a cell has been occupied depends upon its suitability and its invasibility (spatial relationship to other suitable and occupied cells). The 'upstream' strategy attempted to limit the impact of dispersal along rivers by tackling upstream populations first: removing sources towards the top of the catchment should reduce the ability of the species to colonize downstream cells. Cells were ranked based on distance from the bottom of the catchment along the river network.

Simulations were run separately for each plant species as they occupy subtly different habitats and do not appear to compete directly. Species were allowed to spread unchecked from the initial site of introduction, usually for a period of 25 years. Control was then applied annually, at an appropriate intensity, expressed as the number of cells treated. In addition to examining the sensitivity of control strategies to variations in their intensity and in the lag period before control measures were applied, the efficiency of control (proportion of plants within a cell that are completely destroyed) was varied between 90% and 100%. The success of each control strategy was assessed as the proportional reduction in the number of cells occupied compared with when management started. Once begun, control measures were applied with the same efficiency and intensity throughout the remainder of the simulation. When relevant, it was also assumed that both the location of potential habitats and the distribution of each species was known and that all cells were accessible for the application of control measures. For *H. mantegazzianum* the efficiency of control was assumed not to vary between cohorts.

In addition to the initial series of simulations, in which the priorities for application of control measures were determined using information for the species within the Wear catchment alone, a further series of simulations was made using data for the whole of County Durham. Comparison of the results from the two series of simulations allowed the relative effectiveness of defining priorities for control at regional as opposed to catchment scales to be assessed.

Results

WITHIN CATCHMENT DYNAMICS

Species spread in the absence of control

The simulated temporal trajectories for the spread of *I. glandulifera and H. mantegazzianum* within the Wear catchment are depicted in Fig. 1. The lack of historical records of the spread of these two species within County Durham precluded any comparison between observed and simulated trajectories. However, MIGRATE has been shown to model successfully the observed rate and spatial pattern of spread of *I. glandulifera* at a national scale (Collingham, Huntley & Hulme 1997). For both species, a lag was apparent between initial introduction and subsequent spread; this was followed by a period of exponential increase that ended asymptotically when all suitable cells had been colonized. Comparing the trajectories for the two species revealed *H. mantegazzianum* to have a longer lag phase (anything up to 25 years) as well as a lower rate of increase (3·5

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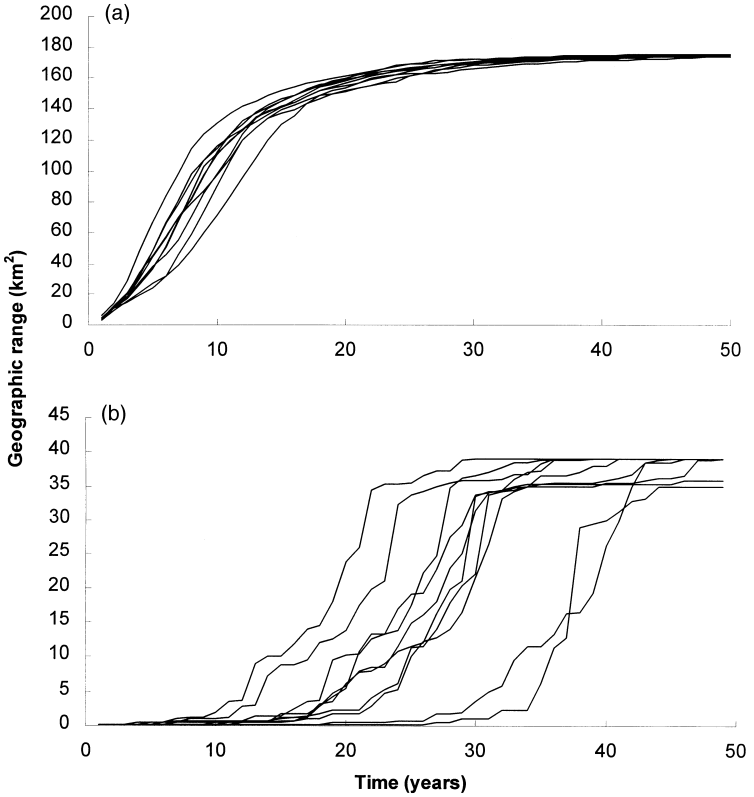


Fig. 1. Ten simulations of the increase in area occupied (km^2) within the Wear catchment of (a) *Impatiens glandulifera*, and (b) *Heracleum mantegazzianum* in the absence of any control management. All simulations start with a single introduction (Durham City).

vs. 10 km^2 $year^{-1}$) and that fewer cells were suitable for its colonization (160 vs. 705). In addition, there was greater variation between individual simulations for *H. mantegazzianum* than those for *I. glandulifera*. These differences were attributable to the lower rate of increase and more limited river dispersal of *H. mantegazzianum* (Table 1) and highlighted the importance of these parameters, rather than absolute fecundity, in determining rates of spread.

Effectiveness of the control strategies

The extents to which the six control strategies, when applied at varying intensities, were able to reduce the number of occupied cells of *I. glandulifera and H. mantegazzianum* are recorded in Table 2. Intuitively, as a larger proportion of invaded cells was controlled each year, there would be a greater reduction in the species' range and more rapid eradication. The simulations emphasized that this can be achieved either by increasing the control intensity or by commencing control earlier, before the species is so widespread. For *I. glandulifera,* none of the strategies achieved eradication unless at least 100 cells were treated annually. This is because the species is already widespread 25 years after introduction (Fig. 1a); implementing control after that time requires annual treatment of *c.* 14% of cells susceptible to invasion if even the most successful strategy is to be effective. In contrast, *H. mantegazzianum* is still relatively localized within the Wear catchment after 25 years. Consequently, a control intensity involving as few as 100 cells per annum effectively controlled *H. mantegazzianum;* at this intensity any strategy can bring about rapid eradication (Table 2). Nevertheless, this represents a relatively intense campaign.

Notwithstanding these interspecific differences in the intensity of control required, the rank order of effectiveness of the six strategies was similar but subtly different. The age (new) and age (old) strategies were universally poor and worse than the random strategy. The upstream and social strategies, which led to relatively large contiguous areas where control was applied, performed better. The population strategy was much better for *H. mantegazzianum* than for *I. glandulifera* and appeared to reflect differences between annual and perennial life-history strategies. The relative success of the social strategy was a result of urban environments being particularly susceptible to invasion by the two species (Collingham *et al.* 2000) as well as of human settlements tending to be clustered across the landscape so that

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Table 2. Percentage reduction in range (cells occupied) after 25 years of management compared with the range when management started for *Impatiens glandulifera* and *Heracleum mantegazzianum* within the River Wear catchment. Values are means from 10 simulations. Three different intensities of management are shown, all implemented with 100% efficiency. Where the species is completely eradicated, the time taken is shown in parentheses

	Intensity of management		
I. glandulifera			
Strategy	100 (14%)	200 (28%)	500 (71%)
Age (new)	3%	81%	89%
Age (old)	48%	100% (6 years)	100% (3 years)
Population	18%	100% (6 years)	100% (2 years)
Random	100% (20 years)	100% (6 years)	100% (2 years)
Social	100% (8 years)	100% (4 years)	100% (2 years)
Upstream	100% (8 years)	100% (4 years)	100% (2 years)
H. mantegazzianum			
Strategy	25 (16%)	50 (31%)	100 (63%)
Age (new)	12%	31%	61%
Age (old)	38%	26%	64%
Random	27%	92%	100% (4 years)
Social	0%	100% (6 years)	100% (4 years)
Upstream	31%	100% (6 years)	100% (4 years)
Population	41%	100% (6 years)	100% (4 years)

control measures were applied synchronously to contiguous areas. Nevertheless, complete eradication within a catchment would be impossible if non-urban cells remained uncontrolled. The upstream strategy was also effective at reducing the occurrence of the species. However, if species became established in non-riparian habitats, then complete eradication was once again impossible. This may help explain why the upstream strategy was more effective for *I. glandulifera* than *H. mantegazzianum*. The age and population strategies require detailed information of the species' distribution; the age (old) strategy requires knowledge of the period of persistence of population, and the age (new) on where new outbreaks are, whereas the population strategy requires only an estimate of present population size. Not only is the latter easier to assess, but the population strategy results in greater control.

Effect of variation in the efficiency of control

The simulations indicated that, once *I. glandulifera* is widespread, efficiency of control must be very high in order to be effective in reducing its range (Fig. 2a). Applying the most effective strategy with an efficiency of 99% (at an intensity of 500 cells per annum) failed to eradicate the species. Interestingly, this may partly be due to the density-dependent seed production of *I. glandulifera* resulting in compensatory seed production as population sizes are reduced. If seed production was fixed per adult, eradication could be achieved with less than 100% efficiency of control. The less widespread occurrence and slower rate of spread of *H. mantegazzianum* led to less stringent efficiency requirements; however, very high efficiencies were still required in order to control the species in a reasonable time (Fig. 2b).

REGIONAL DYNAMICS

Species spread in the absence of control

In contrast to the relative uniformity of the simulated within-catchment temporal trajectories, dynamics of *I. glandulifera* invasion at a regional scale were considerably more variable (Fig. 3a). Rather than the simple sequence of a lag phase followed by exponential expansion and a single asymptote, the dynamics were more complex, reflecting spread within and between several catchments. Steps in the trajectories corresponded to catchment colonization events (to the Tees in the south and Tyne to the north) and were typical of invasions of riparian landscapes by alien weeds (Mack 1985; Pyšek 1994). Note also that the asymptote in Fig. 3a is higher than the 'first' asymptote in Fig. 1a; this is due to the boundary between the Wear and the coastal plain being indistinct. The timing of these stochastic colonization events accounted for much of the variation between simulations, differing by as much as 60 years between simulations (Fig. 3a). Steps in the trajectory were less evident for *H. mantegazzianum* (Fig. 3b), the general temporal trajectory being similar to the within-catchment pattern (Fig. 2a). Significantly, however, whereas the asymptote for *H. mantegazzianum* in the regional simulations was almost twice that for the within-catchment simulations, the rate of spread was about half as fast. This probably reflects the greater tendency for this species to colonize non-riparian cells (Pyšek 1994;

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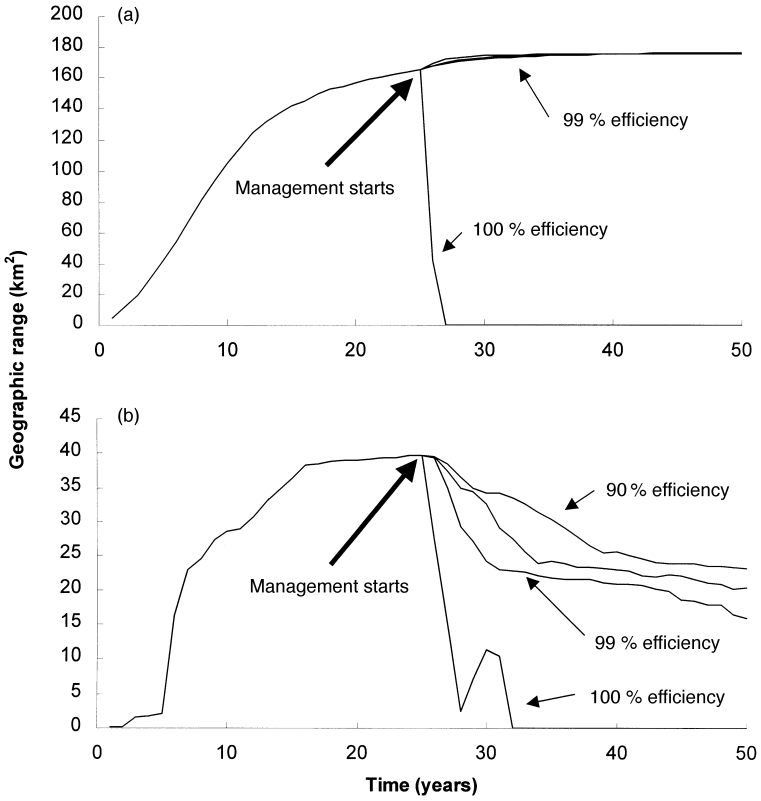


Fig. 2. Median values (from 10 simulations) of the reduction in area occupied (km^2) within the Wear catchment of (a) *Impatiens glandulifera* and (b) *Heracleum mantegazzianum* in relation to different levels of efficiency for the 'upstream' control strategy initiated 25 years after the start of the invasion. Intensity of 500 cells per year (*Impatiens glandulifera*) and 25 cells per year (*Heracleum mantegazzianum*). Efficiencies of 100%, 99%, 95% and 90% were simulated.

Collingham *et al.* 2000) from which subsequent dispersal is less effective. Nonetheless, a number of the simulations revealed a step-like pattern after about 70 years as a neighbouring catchment was colonized.

Effectiveness of the control strategies

The relative effectiveness of the six control strategies was broadly similar at a regional scale to that found for the Wear catchment (Table 3). As might be expected, a given intensity of control gave a reduced probability of species eradication at a regional than at a catchment scale; where eradication was achieved it also took longer to accomplish. Despite the reduced probability of eradication, the proportional range reduction was often higher at the regional scale. This counter-intuitive finding reflects the success with which relatively low intensity control efforts, although insufficient to eradicate the species, are able to reduce the probability of colonization of neighbouring catchments. When the range that might be occupied in the absence of control was compared with the realized range when between-catchment colonization was impeded (Fig. 3), it was apparent that control could have a sizeable impact at the regional scale. That this effect was more marked for *H. mantegazzianum* is consistent with the pattern of spread of this species (Fig. 3).

Effect of variation in the efficiency of control

Regional simulations were also sensitive to small departures from 100% control efficiency (Fig. 4). For *I. glandulifera,* 99% control efficiency was almost as ineffective as no management at all. Although the control efficiency requirements for *H. mantegazzianum* were again less stringent, efficiencies of less than 100% substantially extended the length of time before eradication was accomplished.

The effect of delaying the onset of management can be illustrated with reference to Fig. 5a,b, where management starts 5, 10, 15, 20 and 25 years after establishment. There are some very slight variations in the shape of the declining curves once management starts, but the fact that they are so close to being parallel suggests that the main effect is due to the extent of the population.

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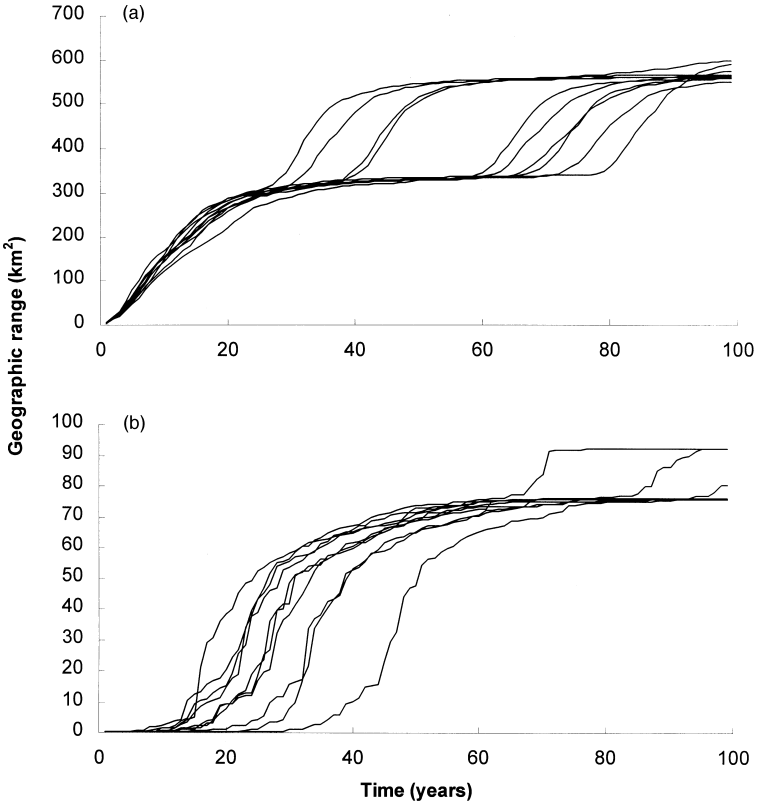


Fig. 3. Ten simulations of the increase in area occupied (km^2) within County Durham of (a) *Impatiens glandulifera* and (b) *Heracleum mantegazzianum* in the absence of any control management. All simulations start with a single introduction (Durham City).

Table 3. Percentage reduction in range (cells occupied) after 25 years of management compared with the range when management started for *Impatiens glandulifera* and *Heracleum mantegazzianum* within County Durham. Values are mean values from 10 simulations. Three different intensities of management are shown, all implemented with 100% efficiency. Where the species is completely eradicated, the time taken is shown in parentheses. Negative values reveal that the species continued to spread despite being managed

	Intensity of management		
I. glandulifera			
Strategy	100 (2%)	200 (4%)	500 (10%)
Age (new)	−13%	−9%	−15%
Age (old)	22%	−7%	100% (10 years)
Population	22%	−7%	100% (3 years)
Random	2%	100% (14 years)	100% (3 years)
Social	100% (20 years)	100% (7 years)	100% (3 years)
Upstream	100% (15 years)	100% (7 years)	100% (3 years)
H. mantegazzianum			
Strategy	25 (3%)	50 (5%)	100 (11%)
Age (new)	−62%	−55%	−36%
Age (old)	14%	37%	3%
Random	9%	11%	78%
Social	−7%	24%	100% (6 years)
Upstream	−2%	36%	100% (6 years)
Population	−10%	100% (10 years)	100% (6 years)

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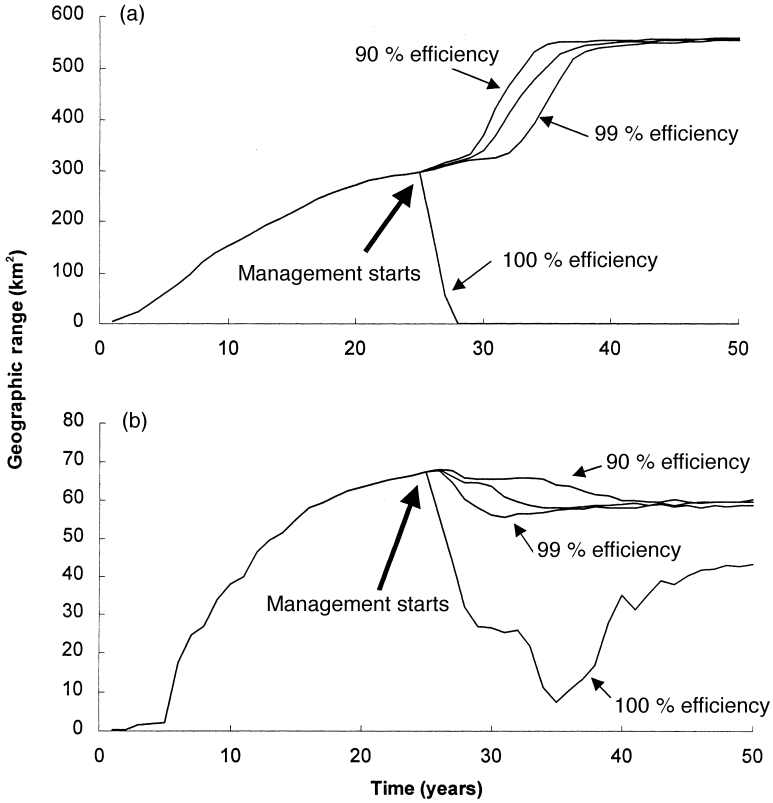


Fig. 4. Mean values (from 10 simulations) of the reduction in area occupied (km^2) within County Durham of (a) *Impatiens glandulifera*, and (b) *Heracleum mantegazzianum* in relation to different levels of efficiency for the 'upstream' control strategy initiated 25 years after the start of the invasion. Intensity of 500 cells per year (*Impatiens glandulifera*) and 50 cells per year (*Heracleum mantegazzianum*). Efficiencies of 100%, 99%, 95% and 90% were simulated.

Discussion

Although MIGRATE incorporates ecological parameters and reflects realistic processes in the spatial spread of species, it is particularly demanding of accurate estimates of dispersal rates and habitat suitability. Whereas predictions of rates of invasion are consistent with what has been observed in County Durham, different values for these parameters would influence both the maximum range and the rate of spread. Furthermore, the temporal trajectories both at the catchment and regional scale are likely to reflect attributes specific to the River Wear and County Durham. These limitations aside, the general insights gained into the effectiveness of different control strategies, the influence of control intensity and efficiency, and the consequences of spatial scale, are likely to be of widespread applicability (for a similar approach see Le Maitre *et al.* 1996).

The reduction in area occupied within a catchment or region following control was always greater for *H. mantegazzianum* than *I. glandulifera*, with eradication achieved sooner at a lower absolute control intensity. The success in controlling this species is partly due to it being less prevalent; within a catchment a similar proportion of the occupied cells have to be controlled to bring about complete eradication. Hence, the intensity of control required for complete eradication will depend upon how widespread the species has become. This reinforces the finding that the sooner control begins following the introduction of an alien plant species, the greater the likelihood of success and the less the effort required.

Control intensity is the prime determinant of its cost, because as the area to be controlled increases so too does the expense of management (Sampson 1994). A single cell within the simulations has an area 25 ha, although only a maximum of 1% of the area is available for colonization. The lowest intensities of control used for each species in the simulations equate to areas of approximately 6 ha for *H. mantegazzianum and* 25 ha for *I. glandulifera*. These estimates are probably conservative, yet are still well above the average area treated in control programmes in the British Isles (Sampson 1994). However, because catchments are not closed systems the occurrence of a species within a catchment will in part relate to its abundance and distribution in neighbouring catchments. Long-term eradication of

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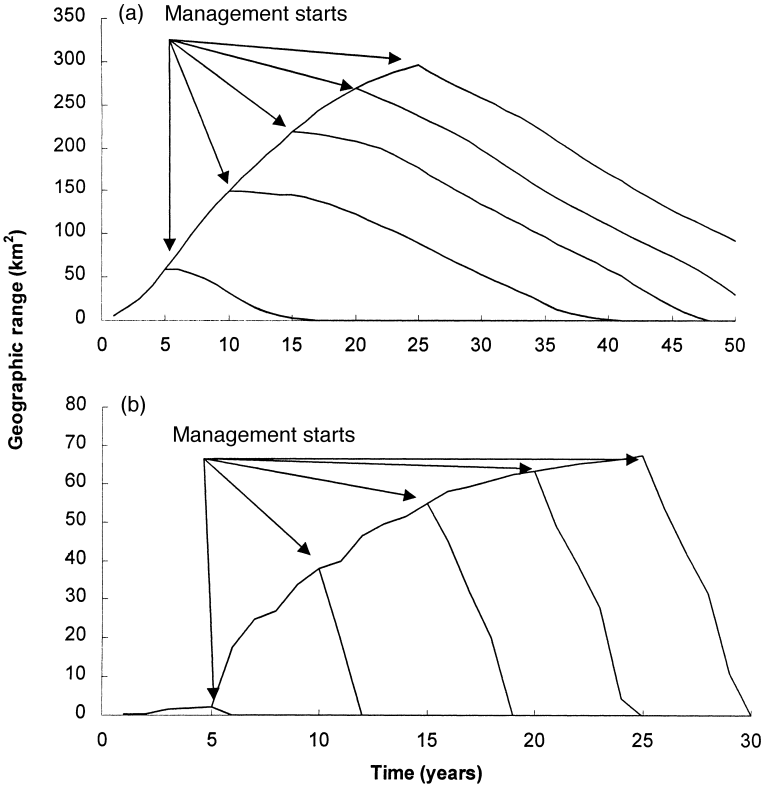


Fig. 5. Mean values (from 10 simulations) of the reduction in area occupied (km^2) within County Durham of (a) *Impatiens glandulifera* and (b) *Heracleum mantegazzianum* in relation to different starts dates for management by the 'upstream' control strategy. Intensity of 100 cells per year (*Impatiens glandulifera*) and 100 cells per year (*Heracleum mantegazzianum*). Start dates of 5, 10, 15, 20 and 25 years after establishment.

a species from a particular catchment may be impossible if neighbouring catchments continue to harbour source populations.

The estimated intensity of control required to eradicate these species suggests that spatially aggregated strategies are the most viable management option. Moody & Mack (1988) used the geometric properties of an expanding circle to model spread where the rate of spread is inversely proportional to the radius of the circle. Thus, many small populations increase the area occupied more rapidly than a single population of equivalent total area. Where the spread of a species is dominated by relatively short range dispersal events, Moody & Mack's (1988) suggestion to prioritize small satellite populations will be a spatially aggregated strategy (they will tend to form a ring around the main population). However, for the two study species the rate of spread is determined primarily by long distance and river dispersal probabilities (which will occur more frequently from larger populations), and controlling satellite populations using strategies like Age (new) are very inefficient.

It is probable that, in the British Isles at least, the majority of control programmes have failed to eradicate either of these two species from even a single catchment (Dodd *et al.* 1994). The few published details of control programmes indicate that most have failed to take the population distribution into account, have directed their efforts at too small a proportion of the plant population, and have focused solely upon a catchment rather than regional scale (Sampson 1994). Rarely is the efficiency of control monitored and the programmes very seldom last for more than 1 year. Successful control of both species at a regional scale is only likely to be possible by adopting strategies based upon species' distribution data, undertaken at relatively high intensities and efficiencies. If eradication is a serious goal of control programmes then they must be co-ordinated at a regional or national scale, involve greater investment, and extend over a longer duration.

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