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CONTROLLING THE SPREAD OF PLANT INVASIONS: THE IMPORTANCE OF NASCENT FOCI

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SUMMARY

(1) We evaluated through simulation the spatial growth of an invading terrestrial plant population and various strategies for its control. The initial population comprised a single large expanding focus but had the potential for the continual establishment of new foci.

(2) We compared the area occupied through the establishment and expansion of these 'satellite' foci to the area occupied by the initially large or main focus under varying regimens of repeated control, in which either the area of the main focus was reduced or some satellites were destroyed, or both.

(3) Whether varying growth rates for the foci, rates of satellite establishment, the level of reduction of the main focus or the intensity of satellite detection and destruction, the overall effectiveness of control measures was greatly improved by destroying even 30% of the satellites.

(4) These predictions contrast with much current practice in the control of alien plants, where large or otherwise conspicuous infestations are often treated at the expense of eradicating isolated populations while they still remain small. As supported by empirical precedents, consistent implementation of the general strategy suggested by our model should improve the control of alien plants.

INTRODUCTION

The sheer magnitude of trans-oceanic commerce in the last 500 years has ensured that many terrestrial plants have been either accidentally or deliberately introduced far beyond their home ranges. Most soon die without cultivation (Theellung 1912; Hayward & Druce 1919; Mühlenbach 1979; Suominen 1979) but some of those that become naturalized swiftly occupy a vast new range, e.g. *Opuntia aurantiaca* in Australia and South Africa, *Bromus tectorum* in North America and *Lantana camara* in tropical Oceania (Thaman 1974; Mack 1981; Auld, Hosking & McFadyen 1982–83). Although such invasions produce much environmental and economic damage, the results of world-wide efforts to stem these invaders are decidedly mixed (Dodd 1940; Burdon, Groves & Cullen 1981; Eplee 1981; Watson 1985).

Skellam (1951) characterized the rate of spread of such a terrestrial invader as a linear function of the square root of its new range through time, i.e. range expansion is envisioned as a single, expanding focus. This general pattern for portraying the spatial spread of terrestrial invasions has been invoked repeatedly (e.g. Okubo 1980 and references therein; Williamson & Brown 1987), but most invasions do not proceed strictly along one radiating wave front. Instead, invaders usually radiate from multiple, disjunct foci originating from independent introductions from the home range, or through the

dispersal and repeated establishment of the alien from a founder population, or both (e.g. Salisbury 1933; Bannister 1965; Stuckey & Phillips 1970; Baker 1986).

Regardless of their origins, these foci can differ enormously in size because of their different dates of establishment, the configuration of invadable adjacent habitat and the extreme stochasticity operating in small populations (Cavers & Harper 1967; Turner 1974; Mack 1981). As a result, the early stages of an invasion are often characterized by one or a few foci that are much larger than all the others (Hanson & Rudd 1933; Tisdale & Zappettini 1953; Mack 1981; Mooney, Hamburg & Drake 1986), and simply because these new foci are large, they are most easily detected. The predilection in weed control is to deal first with that area in which the intruder is most conspicuous or causing crop loss. As a result, large foci become the first and perhaps the only subject for control (Devine 1977; Fenn 1980).

Such a control strategy, however, overlooks the role that small but expanding foci eventually play in an invasion. If the initial area of a single large focus and the initial collective area of many small foci are equal and all foci grow at the same constant rate, the small foci will collectively occupy space much faster than the single large focus (Auld, Menz & Monaghan 1978–79; Mack 1985). Rapid radiation of an alien from many small foci may account for the acceleration in range expansion often witnessed in terrestrial plant invasions (Salisbury 1961; Auld, Hosking & McFadyen 1982–83; Mack 1985; Forcella 1985; Ewel 1986). We hypothesized that the difficulty in successfully contending with a regional invasion might stem from insufficient attention to curbing the growth of small nascent foci. We investigated this and related hypotheses in two simple simulation models.

A SIMPLE GEOMETRIC MODEL FOR ONE-TIME CONTROL

A simple geometric model illustrates the importance of multiple initially small foci to the spread of an invader, especially if the control to any focus is applied only once. Using this first model, we compare the efficacy of controlling either a main focus or isolated satellites, but not both simultaneously. For this and the next model, foci of growth are considered as expanding non-overlapping circles on a two-dimensional plane. We assume (i) an absence of abiotic and biotic restrictions on the invader, (ii) uniform density within the foci, (iii) no extinction through stochastic fluctuations of the environment and (iv) no threshold effects.

Let an invading population initially consist of a large focus (area = πR_0^2) and $N \geq 1$ non-overlapping 'satellite' foci (each satellite's area = πr_0^2). We assume that $\beta \equiv Nr_0^2/R_0^2 \ll 1$; i.e. the total area occupied by the satellites is initially small compared to the area of the large focus. Allow the radii of all foci to increase with time (t) at the constant rate k . The first approach to control resembles common practice: satellites are ignored and a fraction α of the main focus is removed as the outermost annulus. The second approach prescribes the complete elimination of the satellites, while the large focus is ignored. If the population is allowed to expand, then the ratio (ρ) of the total range occupied after implementation of the first approach to the total range occupied after implementation of the second approach is at t :

$$\rho(t) = \frac{(R_0\sqrt{1-\alpha} + kt)^2 + N(r_0 + kt)^2}{(R_0 + kt)^2}.$$

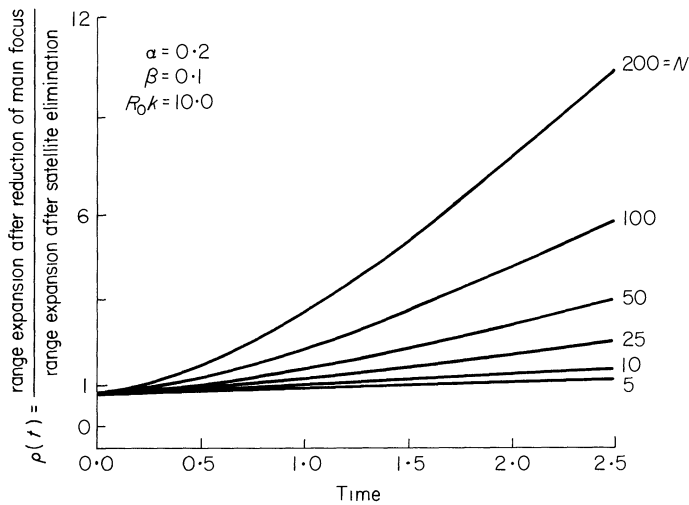


FIG. 1. Ratio of range expansion after reduction of the main focus to the range expansion after satellite elimination with a one-time control effort.

The invader spreads much more rapidly if satellites are ignored (Fig. 1). If $R_0 > r_0$, then $d\rho/dt > 0$. Consequently, the relative area is strictly increasing. Because $\rho(t) \sim N + 1$ as $t \rightarrow \infty$, the ultimate gain or advantage in eradicating the satellites is nearly in proportion to their number. If the satellites grow with rate c , then $\rho(t) \sim 1 + N(c/k)^2$ as $t \rightarrow \infty$; unless $c \ll k$, the qualitative advantage of satellite elimination is maintained.

Any advantage conferred by controlling the main focus of the invasion while ignoring satellites is soon lost. With the satellites initially small (i.e. $Nr_0^2 \ll R_0^2$), $\rho(0) = \sqrt{1 - \alpha + Nr_0^2}/R_0^2 < 1$. Hence, during the initial growth of the foci, the ratio ρ will be less than 1. This gain nevertheless diminishes with time: for $t > t^*$ where t^* is the unique positive root of $\rho(t) = 1$, the ratio ρ exceeds 1 and the satellites occupy more area than the main focus. Even for moderate values of N , t^* is quite small and the advantage of satellite elimination becomes apparent. Only a substantially lower growth rate for the satellites compared to the growth of the main focus would alter this qualitative outcome. Continual removal of new foci (and monitoring the sites of old foci for re-emergence) would enhance control.

THE REPEATED CONTROL OF AN INVADING POPULATION WITH NASCENT FOCI

Structure of the model

We expand our first model to incorporate more realistic aspects of invasions: the establishment of nascent foci, their growth and detection, and the repeated control on foci of different sizes. The invasion consists of the main focus and two categories of satellites. For a satellite to be detected and possibly destroyed, it must reach a *critical age*, i.e. it has grown through a_{crit} intervals of time. Growing, but as yet undetected, satellites are termed *subcritical*; detectable satellites are termed *supercritical*. In this model, a critical age equates directly to a critical size.

At time $t = 0$, we assume the radius of the main focus is R_0 , and the radii of all nascent

satellites equal r_0 . For our simulations, we have taken the ratio R_0/r_0 as 100:1, so that the initial area of the main focus is 10 000 fold greater than the area of a newly formed satellite. We make the simplifying assumptions that the radius of the main focus expands at the constant rate r_m and that the radii of the satellites increase at the constant rates of r_{sub} and r_{sup} for sub- and supercritical satellites, respectively. In addition, we allow r_{sub} and r_{sup} to vary independently on the assumption that foci of different ages could have different rates of spatial expansion. We expect that a_{crit} and r_{sub} would be negatively correlated: the faster small foci grow, the sooner they are likely to be detected.

We assume the population arose from a single introduction and that new subcritical satellites are established in any time interval according to a logistic growth law based on the cumulative area already occupied. The number of new satellites appearing in each time interval is n_{new} (a function of area); we assume $n_{\text{min}} \leq n_{\text{new}} \leq n_{\text{max}}$, according to the requirements of the logistic equation. Thus, at least $n_{\text{min}} > 0$ new satellites will be founded during each interval of time, but never more than n_{max} . To complete the description of the establishment of new foci, we denote by μ the intrinsic rate of generation of new foci per unit area of coverage. We assume that this rate is constant. This assumption ignores differences in the rate of establishment of new foci due to variation in size or other characteristics. Figure 2 displays n_{new} as a function of area for the various parameters used in our simulations.

We incorporated control efforts into our model during the same discrete intervals of time in which satellites were established and grew. In each time interval, a fraction e_{sat} of supercritical satellites are destroyed in descending order of size. We refer to e_{sat} as the efficiency of attack upon these satellites. Many alternative models of control could be employed; we use this particular approach because it is severe — eliminating 50% of the satellites according to our prescription will eliminate more than 50% of the total area covered by the satellites.

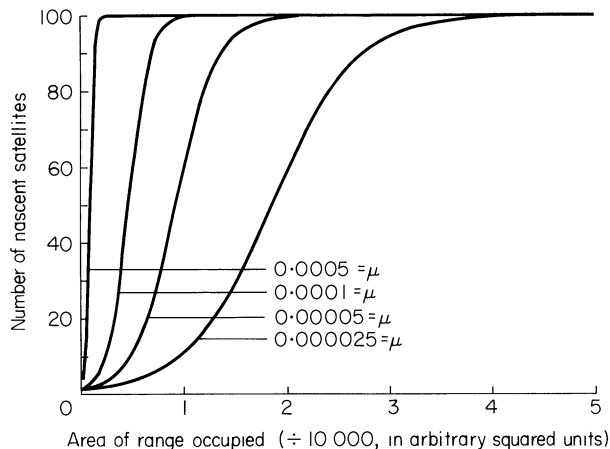


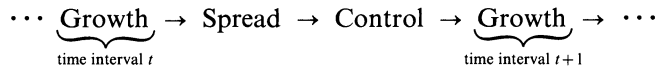
FIG. 2. The number of new satellites created in each time interval (n_{new}) as a function of the total area of range occupied. The curve follows a logistic law, as given by:

$$n_{\text{new}} = n_{\text{max}} \left[1 + \frac{n_{\text{max}} - n_{\text{min}}}{n_{\text{min}}} e^{-\mu \cdot \text{area}} \right]^{-1},$$

where n_{min} and n_{max} are the minimum and maximum number of satellites created (set respectively to 1 and 100 in our simulations).

In any time interval, the area of the main focus is decreased by the fraction ε_m , the efficiency of attack upon the main focus. Any prescribed reduction in the area of the main focus is accomplished by removing an outer annulus of growth. Reduction of the main focus in this manner retards regrowth most effectively; control outward from the centre is usually futile (see Appendix 1).

Growth and control in this model begin with the population consisting only of the main focus and each of the parameters described above set to prescribed values. The order of effects as implemented into a numerical description of the model is:



The total area occupied by the invader is assessed after each time interval. Our choice of units for time and area is not intended to correspond in any precise sense to the situation prevailing in any specific invasion. The time intervals could correspond to a month, a year, or a generation; the areas of the foci could equally well apply to either m^2 or km^2 , etc. We have evaluated the outcome from each combination of parameters in terms of *crossover* time, $\tau_{s/m}$, the number of elapsed time intervals until the cumulative area occupied by both types of satellites exceeds the area of the main focus. If the crossover time is short (i.e. $\tau_{s/m} < 50$), control efforts directed at the satellites would be warranted; if this time becomes long, the main focus should be the principal object of control.

RESULTS

An exhaustive analysis of simulations with the model is not practical due to the large number of variables employed. Consequently, we have chosen examples that are likely to correspond to biologically meaningful situations from more than 10 000 simulations. Tables 1–3 show the crossover times for fixed values of r_m , r_{sub} , r_{sup} and ε_m as a function of the efficiency of attack upon the satellites and the critical age. Boldface entries in the tables correspond to crossover times that do not exceed 50 time intervals.

Several factors emerge as crucial to the containment of an invasion. Foremost is the ability to detect and destroy a large fraction ($\geq 15\%$) of the satellite foci in each time interval. Ideally, these satellites must be detected soon after they form, i.e. their critical age must be low. For any fixed efficiency of attack upon the satellites, the crossover time decreases as the critical age increases. For a fixed critical age, as the attack efficiency on the satellites increases, the crossover time also increases. If all other parameters remain constant, increasing the rate of growth of the subcritical satellites generally decreases the crossover time, especially if the critical age is large. Crossover times generally decrease if the intrinsic rate of generation of new foci (μ) is increased, as we would expect.

Removing a larger fraction of the main focus generally decreases the crossover time because crossover time is defined in terms of the relative area. Whenever the satellites have a total area larger than that of the main focus, they are a greater problem than the more conspicuous main focus. However, unless the actual areas involved are large, neither the satellites nor the main focus may constitute a threat worthy of control. Consequently, we have attempted to present only simulations in which $\tau_{s/m}$ represents an ‘absolute’ compared to a relative problem in the sense that the total areas involved are large.

In Table 1a all foci grow slowly (i.e. the radius of each focus including the main focus, expands by 1% in each time interval) while 10% of the main focus is removed in each time

interval. The crossover time occurs in less than 50 time intervals when attack efficiency on supercritical satellites is 5% or less, regardless of the critical age. Even when 10% or more of the satellites are removed in each time interval, the crossover time usually occurs in 100 time intervals or less for these slowly growing satellites. Unless the satellites are detected early (i.e. critical age is 1 or 2) and the efficiency of attack on satellites is severe ($\geq 30\%$), the combined areas of the satellites are greater than the area of the main focus in less than 100 time intervals.

Using the same rates of growth but removing 30% of the area of the main focus in each time interval results in lower crossover times (Table 1b). This decrease reflects the short time period necessary for the combined areas of growing satellites to exceed the area of a

TABLE 1. Tables 1–3 report the crossover times (i.e. the first time interval in which the accumulative area of satellites exceeds the area of the main focus) for prescribed combinations of critical age (a_{crit}) and attack efficiency (e_{sat}). Crossover times of 50 or less are in boldface; an asterisk * indicates crossover times > 100 . The intrinsic rate of generation of new foci is $\mu = 0.0001$ in each of these simulations. (a) All foci including the main focus grow slowly and 10% of the main focus is removed in each time interval ($r_{sub} = 0.01$, $r_{sup} = 0.01$, $r_m = 0.01$, $\epsilon_m = 0.1$). (b) All foci grow slowly but 30% of the main focus is removed in each time interval ($r_{sub} = 0.01$, $r_{sup} = 0.01$, $r_m = 0.01$, $\epsilon_m = 0.3$).

		Critical age					
Attack efficiency		1	2	3	4	5	10
(a)	0.01	35	35	35	35	35	35
	0.05	50	50	49	48	47	42
	0.10	69	69	66	63	61	53
	0.15	80	80	75	72	69	58
	0.30	*	*	95	86	80	63
(b)	0.01	16	16	16	16	16	17
	0.05	16	16	16	16	16	17
	0.10	19	18	18	18	18	17
	0.15	21	20	20	20	19	17
	0.30	24	24	23	22	21	19

TABLE 2. (a) Subcritical satellites grow twice as fast as the supercritical satellites and the main focus. In each time interval 10% of the main focus is removed ($r_{sub} = 0.02$, $r_{sup} = 0.01$, $r_m = 0.01$, $\epsilon_m = 0.1$). (b) Subcritical satellites grow rapidly and 30% of the main focus is removed in each time interval ($r_{sub} = 0.02$, $r_{sup} = 0.01$, $r_m = 0.01$, $\epsilon_m = 0.3$).

		Critical age					
Attack efficiency		1	2	3	4	5	10
(a)	0.01	35	35	35	34	34	32
	0.05	50	49	47	45	43	36
	0.10	69	67	63	59	56	45
	0.15	80	77	71	66	62	49
	0.30	*	*	87	78	72	55
(b)	0.01	16	15	15	15	15	14
	0.05	16	15	15	15	15	14
	0.10	18	18	17	16	16	14
	0.15	20	20	19	18	17	14
	0.30	24	23	21	20	19	15

TABLE 3. (a) In this example, all foci experience rapid growth. Even when the main focus grows without any control, the satellites collectively occupy more area if the attack efficiency is low ($r_{sub}=0.1, r_{sup}=0.1, r_m=0.1, \epsilon_m=0.0$). (b) Rapid growth of all foci and 10% of the main focus is removed in each time interval ($r_{sub}=0.1, r_{sup}=0.1, r_m=0.1, \epsilon_m=0.1$)

		Critical age					
Attack efficiency		1	2	3	4	5	10
(a)	0.01	37	37	37	37	37	37
	0.05	*	*	*	*	65	57
	0.10	*	*	*	*	*	*
	0.15	*	*	*	*	*	*
	0.30	*	*	*	*	*	*
	0.01	19	19	19	19	19	19
	0.05	19	19	19	19	19	19
	0.10	82	82	58	47	40	21
	0.15	*	*	*	*	82	31
	0.30	*	*	*	*	*	47

shrinking main focus. This qualitative result is nearly independent of the efficacy of attack upon the satellites and the threshold age of detection. The crossover time occurs in less than 25 time intervals even if the fraction of satellites removed equals the proportion of area removed from the main focus. Removing 30% of the satellites only briefly delays the crossover time. As this case illustrates, any apparent gain from a substantial reduction of the main focus is soon offset by proliferation and eventual growth of smaller, currently undetected sites of growth.

Doubling the rate of growth for the subcritical satellites (Table 2), increases the number that become supercritical, i.e. detectable, because the rate of satellite establishment is proportional to the total area. With the proportion detected and destroyed remaining fixed, the result, however, is an overall growth in the area occupied by supercritical satellites. Only at high rates of removal for satellites that reach critical age early is the crossover time delayed for more than 100 time intervals. When 5% or less of these satellites are destroyed per time interval, crossover time occurs in less than 50 time intervals. Under these conditions increasing the critical age has little effect on the crossover time.

By having no control on the main focus ($\epsilon_m=0.0$), the crossover time is deferred to more than 100 intervals in our simulations for all parameter combinations. This outcome occurs even when the subcritical satellites' growth rate is twice the rate of growth of the main focus. In other words, all the entries of Tables 1a and 2a become asterisks if ϵ_m is reduced to 0.0.

Combining a rapid growth rate of subcritical satellites with the removal of a substantial part of the main focus exacerbates the relative importance of the satellites (Table 2b). In this general case, crossover time occurs in less than 25 time intervals. Even if satellites are detected early and 30% are removed, crossover time soon occurs. This case corresponds to the most common control practice.

Even when the main focus is allowed to grow unimpeded, satellites can become the paramount problem for eventual control (Table 3a). This result occurs even though the initial area of the main focus is 10 000 fold greater than the area of a nascent focus, and the population initially contains no satellites. Under these circumstances the satellites are weakly attacked or they have a high threshold of detection, or both. If a high proportion

of satellites is destroyed, then it is possible that their cumulative area never exceeds that of the main focus if it is left to expand unimpeded. Furthermore, if the overall rates of growth are higher, then the crossover time is generally reduced (cf. Table 3b with Table 1).

The rates of growth for the satellites and main focus are of comparable magnitude in all the Tables. However, if the main focus expands about an order of magnitude faster than the satellites, then the crossover time is generally prolonged (≥ 100). In contrast, if the satellites expand faster than the main focus, crossover time is usually low (≤ 50), unless attack upon the satellites is severe and the critical age is low.

The main focus does not experience a net reduction for all values of ε_m because it experiences both a cycle of expansion and control during each time interval. If $\rho > (1 - \alpha)^{-1/2} - 1$, then control merely slows the net expansion of the focus (Table 3b), whereas if this inequality is reversed the focus actually shrinks (Tables 1a–3a).

DISCUSSION

Under a wide variety of circumstances, the area occupied through the growth of satellite foci eventually exceeds the range occupied by the spread of a main focus. After the crossover time, the importance of the main focus to the overall invasion will continue to diminish unless severe control is directed at the satellites. But such a belated control effort is likely to be both impractical and ineffective. Furthermore, any benefit derived by reducing the rate of satellite establishment through curbing the expansion of the main focus is generally not as important in curbing the overall invasion as eliminating satellites. This eventually dominant contribution by the satellites to the overall invasion occurs even if the main focus is initially much larger and grows moderately faster than the satellites.

These conclusions arise from models that employ only the geometrical properties of an expanding circle. One useful feature of this approach is the direct correspondence between a focus expanding at a constant rate and the areal spread of a population as influenced by each plant's proximity to the population boundary. Even initially, many small foci have a greater cumulative circumference than a single large focus with the same total area. Consequently, proportionally more parents in small foci occur on or near the boundary and their seeds are more likely to fall into adjacent uninfested areas. In contrast, most disseminules produced within a large focus land inside the boundary of the focus (assuming mean dispersal distance is less than the radius of the focus). Clonal spread would be generally influenced by the same geometrical proportionality. The observation that small foci of aliens can grow faster than large ones may stem from this ability of proportionally more disseminules and rhizomes to reach the radiating front (Selleck, Coupland & Frankton 1962).

Although computationally simple, our models are conceptually related to diffusion models but lack many of the complicating features of these more involved simulations. Our models assume an approximately asymptotically linear increase in the radius of coverage; spatial diffusion models predict the same change (Skellam 1951; Okubo 1980). Perhaps the chief difference between our models and others is our assumption that density remains constant. This simplifying assumption is justified because plant control (such as the aerial application of a herbicide) often involves much the same effort across a wide range of plant densities. If all the infestations in an invasion are considered, the first concern in control would become the total area of range occupation and not the density within that area (Watson 1985).

Incorporating geographical corridors that facilitate spread through diffusion, or

barriers or allowing foci to converge, all increase the mathematical complexity required for a model's construction without a corresponding increase in information (Okubo 1980). Of these complications, converging foci are probably the most likely to occur, especially late in the invasion (e.g. Mack 1981; Usher 1987). We chose instead to emphasize the common early situation in which new foci are established far beyond the main focus through seed dissemination by birds or commerce, because in those cases control is still possible.

Models incorporating the life-history characteristics of the invader (e.g. age structure, survivorship and recruitment) are intuitively attractive alternatives to the models we propose here (Crawley 1987). But with the addition of each characteristic such models become successively more specialized and lack general application. More importantly, they require parameters that are often difficult to measure in the field and yet fail to provide the unambiguous answers to questions arising in the control of an invasion (e.g. 'With resources for control always limiting, what action should be taken first, and second, and so on'). As Murray (1987) cautions in modelling the hypothetical spread of rabies in Britain, 'a model which incorporated all possible aspects of the epidemic would be impossible to use, since nothing would be known about many of the parameters, nor would there be much hope of estimating them with the data available.' This same limitation is likely to influence the structure of practical models of plant invasions for some time to come.

Control of the proliferation and spread of small foci has seldom been given high priority, but these few case histories strongly support the conclusions of our models. *Striga asiatica* (witchweed), a pernicious alien hemiparasite of corn and sorghum, was accidentally introduced into eastern North and South Carolina (U.S.A.) about 30 years ago. Despite the ease with which the plant's small seeds can be disseminated, the alien has not spread because stringent quarantine was soon imposed on counties within the main focus and eradication has been concentrated on the many, still isolated, small foci of the infestation. Control of the main focus has been directed at its perimeter (Eplee 1979, 1981). The virtual eradication of the common barberry (*Berberis vulgaris*) in the U.S., the intermediate host for stem rust, was accomplished early in this century by vigorously searching and eradicating even isolated plants while simultaneously destroying larger foci (Freeman & Melander 1924; Hutton 1927). The two-step strategy of first destroying outlying populations and then methodically reducing the area of the main infestations has been recommended in the control of *Hakea sericea* and *H. gibbosa* in South Africa and *Euphorbia esula* in North America (Fugler 1982; Watson 1985) and is now employed in the control of *Centaurea diffusa* in Canada (Harris & Cranston 1979). The success seen in releasing the agents of biological control on multiple, isolated foci of an infestation may stem in part from the response predicted here (Frick 1974). Given the importance of nascent foci to an invasion, reducing a large focus in an arable field to only a few isolated populations at the perimeter may merely form the isolated foci from which an invasion will inevitably reoccur (Mack 1985).

The overall failure to appreciate the importance of small, but growing, foci to the control of plant invasions perhaps reflects a larger issue. With few exceptions, we find insufficient attention given to developing an effective strategy ('the art of projecting and directing the larger military movements and operations of a campaign') for controlling the spread of alien plants. Instead, current practice emphasizes tactics ('the art of handling forces in battle or in the immediate presence of the enemy,' both definitions from the Compact Edition of the *Oxford English Dictionary*) for controlling invasions locally, i.e.

the specific procedures used to remove alien plants by burning, excavation, herbicides, etc. The effect of this emphasis on tactics has been to assign highest priority in control to the most conspicuous or the *currently* most detrimental foci while neglecting others. Given the outcome of many of the simulations reported here, these priorities should often be reversed.

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APPENDIX 1

The control of large foci is often restricted to the centre of these infestations. We asked whether this common practice is effective compared to control at the focus' expanding boundary, assuming the goal is regional control or even permanent eradication of the invasion as opposed to localized, temporary control. Once again, we considered the large focus as an expanding circle. We contrasted the response of a large focus to two methods of control: (i) removing a fixed fraction of its area as an outer annulus compared to (ii) removing a circular disc from the centre. Let the initial area of a large focus be πR_0^2 , and suppose a fraction α of area is removed; after removal, the radius (radii) of the remaining focus expands at the fixed rate k .

The ratio of the area remaining using method 1 compared to method 2 after t units of time is

$$\xi(t) = \begin{cases} \frac{(R_0\sqrt{1-\alpha} + kt)^2}{(R_0 + kt)^2 - (\sqrt{\alpha}R_0 - kt)^2}, & 0 < t < \sqrt{\alpha}R_0/k \\ \left(\frac{R_0\sqrt{1-\alpha} + kt}{R_0 + kt}\right)^2, & t \geq \sqrt{\alpha}R_0/k. \end{cases}$$

Separate definitions are required because after $\sqrt{\alpha}R_0/k$ units of time have elapsed, the centre removed under the second method has 'filled in.' Observe that $\xi(0) = 1$ (since the same fraction is initially removed under both methods) and that $\xi(t) \sim 1$ as $t \rightarrow \infty$; eventually the two methods have equivalent effects. The ratio ξ decreases, however, from 1 to a minimum value, and thereafter increases asymptotically back to 1 (Fig. 3).

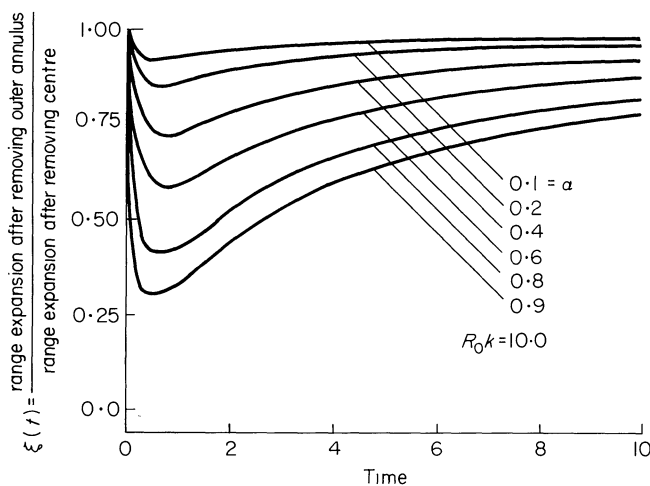


FIG. 3. Ratio of range expansion after removing a prescribed outer annulus to the range expansion after removing a corresponding area from the centre.

Under the conditions described here, removing area from the centre is generally not as advantageous as removing the same area as an outer annulus. The advantage of removing any outer annulus increases with time, the size of the annulus removed, and the frequency of removal. If other assumptions are made (e.g. non-uniform population density as in Menz *et al.* 1980) different conclusions are possible. As long as the main source of propagules for expansion is near the perimeter of the focus our results will hold; if most expansion is due to a high density of plants near the centre of the focus then attack on the centre may be warranted (Menz *et al.* 1980).