MODELLING TO PREDICT THE FATE OF INVADING PLANTS

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Despite the enormous worldwide effort expended in contending with plant invasions, control -- much less eradication -- is infrequent. We hypothesized that more effective control (and even eradication) of alien plants would be achieved by recognizing the importance of new foci in an invasion. We based our hypothesis on two observations: 1) The time course for invasions by terrestrial plants follows a logistic curve: a phase in which the new range is invaded slowly is followed by a phase of rapid range expansion. 2) Length of the initial phase of slow spread may be inversely dependent on the number of initial foci. Dividing a focus into many isolated foci will enormously increase the rate of new range occupation, assuming the same expansion rate for all foci (Mack 1985).

We formalized our hypothesis in a simple model in which each expanding focus is represented as an expanding circle on a two-dimensional plane. We compared the efficacy of a one-time control of a large or primary focus while neglecting small "satellite" foci, with control of small satellites while neglecting the large focus. Let a population initially consist of a primary focus (area $= \pi R_0^2$) and $N \geq 1$ non-overlapping satellite foci (the area of each satelite $= \pi r_0^2$). We assume that $\beta = Nr_0^2/R_0^2 << 1$, *i.e.*, the total area occupied by the satellites is initially negligible compared to the area of the primary focus. Allow the radii of all foci to increase with time (t) at the constant rate k. In the first strategy, satellites are ignored and the outermost annulus of the primary focus with area $\alpha \pi R_0^2$ is removed. The second strategy prescribes elimination of the satellites, and the primary focus is ignored. If the population is allowed to expand, then the ratio (ρ) at t of the total area infested after implementation of the first strategy versus the area infested after implementation of the second strategy is:

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

A simple calculation shows that $d\rho/dt > 0$ (if $R_o > r_o$), so that the relative area is strictly increasing. Because $\rho(t) \sim N + 1$ as $t \to \infty$, the ultimate gain or advantage in eradicating the satellites is in proportion to their number. The gain depends on the ratio of the initial area of the primary focus to the growth rate k. In Figure 1, $R_o k = 10$, and in Figure 2 $R_o k = 2$. In both Figures 1 and 2, $\alpha = 0.2$ (20% reduction of the primary focus), and $Nr_o^2 / R_o^2 = 0.1$ (satellites are initially 10% of the area of the primary focus). The model assumes that the density of the invader is uniform and that no extinction occurs through stochastic fluctuations in the environment. (For a more detailed account of this and other models of spread through the growth of foci, see Moody and Mack 1988.)

Our model shows that any gain achieved by ignoring small foci is short term and is disadvantageous in proportion to the number of foci. Continual removal of new foci (and monitoring the sites of old foci for reemergence) would enhance control.

A successful control effort for a plant invasion with spatial conditions strikingly similar to those prescribed in our model substantiates our recommendations. Witchweed (*Striga asiatica*), an aggressive hemiparasite on corn (*Zea mays*) and sorghum (*Sorghum vulgare*), was accidentally introduced 30 years ago in the southeastern United States. The alien has nonetheless been confined to the eastern Carolinas by prohibiting the plant's further transport and concentrating eradication efforts on satellite infestations in counties peripheral to the primary focus (Eplee 1979, 1981).

Our model incorporates no properties restricted to organisms, but the importance of the foci's circumferences to plant spread is nonetheless clear. For large foci, most disseminules land inside the boundary of the focus. For smaller foci, proportionally more parents occur on or near the circumference; their seeds are more likely to fall into the adjacent uninfested area, thus affecting spread.

Most current practice in alien plant control appears to emphasize the tactics ("the art of handling forces in battle or in the immediate presence of the enemy") of controlling the invasion, *i.e.*, the specific procedures used locally to remove alien plants by burning, excavation, herbicide application, etc. Based on the predictions emergent from this model, we believe much more effort should be exerted in developing an effective strategy ("the art of projecting and directing the larger military movements and operations of a campaign") (Anonymous 1971) for controlling the spread of alien plants.

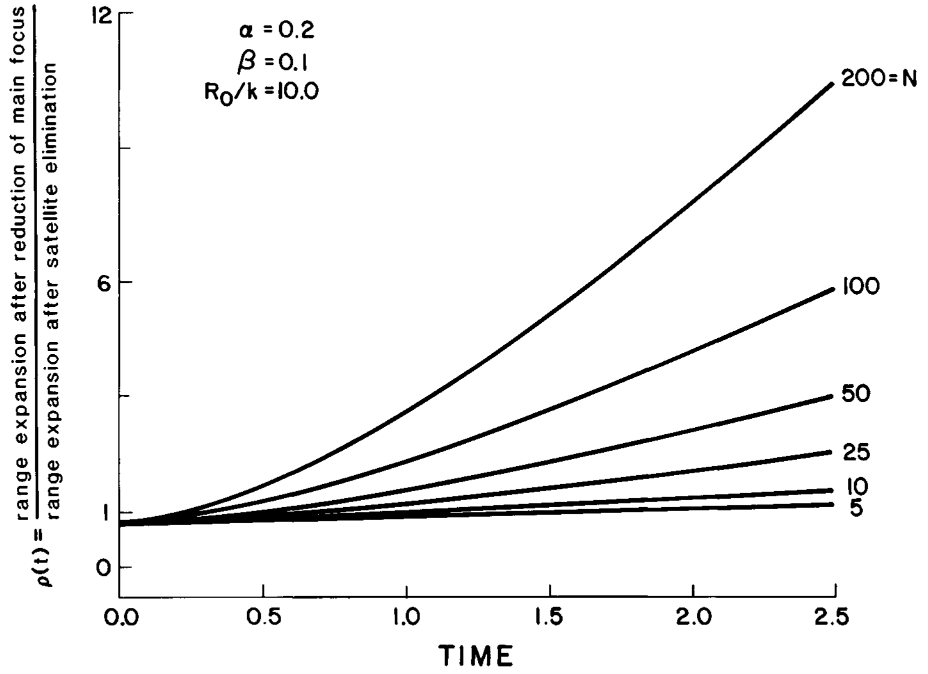

Figure 1. Comparison of the efficacy of two alternative approaches for halting the spread of an alien population of terrestrial plants. R_0 k = 10, = 0.2 (20% reduction of the primary focus) and ß = 0.1 (satellites are 10% of the area of the primary focus).

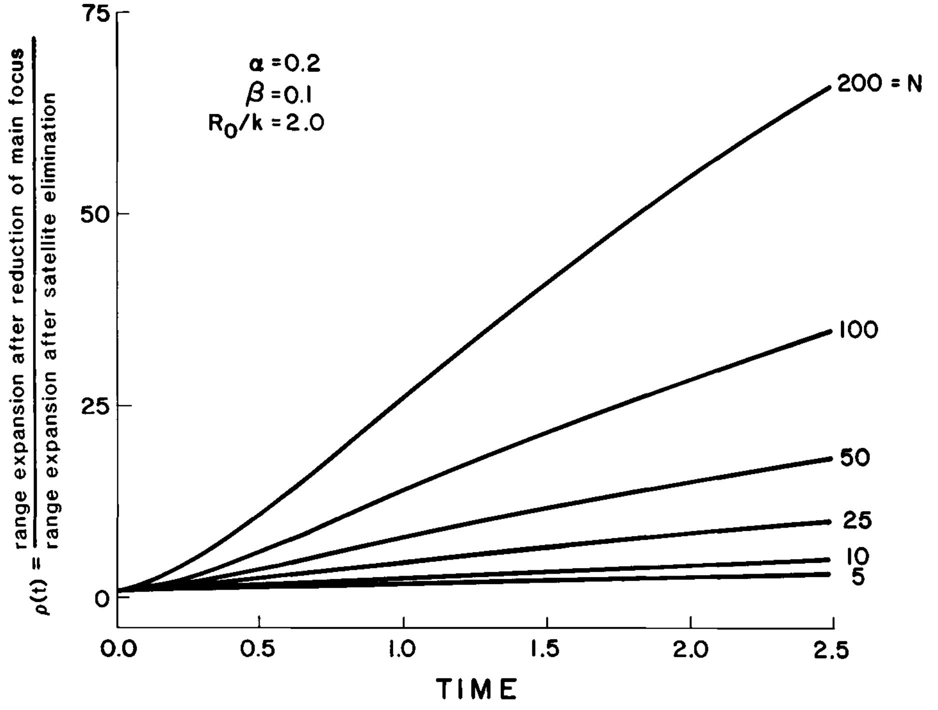

Figure 2. Comparison of the efficacy of two alternative approaches for halting the spread of an alien population of terrestrial plants. R_0k = 2, = 0.2 (20% reduction of the primary focus) and ß = 0.1 (satellites are 10% of the area of the primary focus).

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