Theoretical models for weed biocontrol: *Rottboellia cochinchinensis* infection with sterilizing fungi

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Abstract. A basic model similar in form to the Lotka-Volterra predator-prey equations was expanded, in stages, to incorporate a weed seed-bank, a smut spore-bank and density dependence in seed and spore production. The models were parametrised to represent biocontrol of *Rottboellia cochinchinensis* with the head smut *Sporisorium ophiuri*. An analysis of critical points and the model dynamics with time yielded a number of results of practical significance in the development of biocontrol of *R. cochinchinensis* with the head smut: (i) the incorporation of density dependence in both seed- and spore-production did not alter the qualitative outcome, suggesting that the attributes of potential pathogens could be assessed with relatively simple experiments on isolated plants; (ii) times taken to reach equilibrium, after application of smut inoculum were highly dependent on starting conditions, but indicated that it could be many years before any effects on weed density are observed after application of a low dose of smut inoculum; (iii) differences in predicted weed abundance, derived for situations both with and without smut infection, indicated that additional control measures that reduced seed-set or germination rates (e.g. through reduced soil disturbance), or increased *R. cochinchinensis* death rate (e.g. weeding or herbicides), or increased seed-mortality, interacted synergistically with biocontrol; and (iv) control methods that reduced seed-set also interacted synergistically with biocontrol but, in practice, spore production would be reduced as well, so the interaction would be antagonistic.

Introduction

Simple population modelling can be used to help identify the spectrum of possible outcomes in the interactions between a pest, a biocontrol agent and other elements of the system (Waage and Barlow 1993). In many cases, simple models predict a requirement for a substantial reduction in annual seed-set to provide effective long-term control (e.g. Cloutier and Watson 1990) and variation in efficacy of the control agent means that it may be undesirable to rely on it alone. Hence it is also particularly important to investigate biocontrol as part of an integrated package of control measures, and to identify combinations which will complement each other. There have been few attempts to utilize existing models of disease spread or plant-pathogen models in developing weed biocontrol theory. The approach used here is similar to the 'prospective modelling' adopted by Godfray and Waage (1991) for assessing the dynamics of different combinations of biological control agents.

A family of models was developed to represent the essential features of the biology of monocyclic head-smut infection. These models allow comparisons to be made of the effects of biocontrol when sterilizing smuts are used on weeds with different life histories. When the importance of various issues associated with biocontrol of *Rottboellia cochinchinensis* (Lour.) W.D. Clayton were under consideration, parameter values that were estimated for an earlier model were used (Smith and Holt 1995). The various models were used to identify important aspects of the smut and weed life-histories which affect the outcome of biocontrol of *R. cochinchinensis* and thus indicate control options that are likely to interact positively with biocontrol.

Rottboellia cochinchinensis causes serious losses to maize, sorghum, rice and sugar cane crops in the humid tropics. Its prevalence has increased as the practice of maize cropping has intensified. Herbicides used in maize have poor efficacy and the high fecundity of the weed allows populations to increase rapidly (Fisher *et al.* 1985). The head smut, *Sporisorium ophiuri* (P. Henn.) commonly infects the weed in the Old World but has not been introduced

with it to the New World and is therefore a candidate for classical biological control of *R. cochinchinensis* (Ellison 1993).

The host plant becomes infected by the fungus as the seed germinates and the healthy and infected plants compete for resources. The infected plants grow almost normally, but the seed-head becomes a mass of smut teliospores. These teliospores germinate in the soil resulting in sporidia which survive as a yeast-like saprophytic phase. Fusion of the sporidia results in the dikaryotic parasitic stage which infects germinating *R. cochinchinensis* seeds (Ellison 1993).

The models

Derivations.
Model structures are depicted in Fig. 1. The dynamics are considered as a continuous process on a large scale (e.g. district or region). The crop was not included in the model since it is replanted every year by the farmer. As a starting point, the most basic model (1a), is analogous to the Lotka-Volterra predator-prey equation and also analogous to the models of infectious diseases (without immunity) of Anderson and May (1979). In Table 1, X and Y are the numbers of healthy and smutted *R. cochinchinensis*, respectively. Healthy

Table 1. Model equations.

1a. Basic model	1b. Density dependent reproduction added
$\dfrac{dX}{dt} = r_1X - p_1XY - bX$	$\dfrac{dX}{dt} = r_1X\left(1 - \dfrac{X+Y}{K}\right) - p_1XY - bX$
$\dfrac{dY}{dt} = p_1XY - bY$	$\dfrac{dY}{dt} = p_1XY - bY$

2a. Seed bank added	2b. Density dependent seed production added
$\dfrac{dX}{dt} = gU\left(1 - \dfrac{p_2Y}{1+p_2Y}\right) - bX$	$\dfrac{dX}{dt} = gU\left(1 - \dfrac{p_2Y}{1+p_2Y}\right) - bX$
$\dfrac{dY}{dt} = gU\left(\dfrac{p_2Y}{1+p_2Y}\right) - bY$	$\dfrac{dY}{dt} = gU\left(\dfrac{p_2Y}{1+p_2Y}\right) - bY$
$\dfrac{dU}{dt} = r_2X - gU - mU$	$\dfrac{dU}{dt} = r_2X\left(1 - \dfrac{X+Y}{K}\right) - gU - mU$

3a. Smut spore bank added	3b. Density dependent seed and spore production added
$\dfrac{dX}{dt} = gU\left(1 - \dfrac{p_3Z}{1+p_3Z}\right) - bX$	$\dfrac{dX}{dt} = gU\left(1 - \dfrac{p_3Z}{1+p_3Z}\right) - bX$
$\dfrac{dY}{dt} = gU\left(\dfrac{p_3Z}{1+p_3Z}\right) - bY$	$\dfrac{dY}{dt} = gU\left(\dfrac{p_3Z}{1+p_3Z}\right) - bY$
$\dfrac{dU}{dt} = r_2X - gU - mU$	$\dfrac{dU}{dt} = r_2X\left(1 - \dfrac{X+Y}{K}\right) - gU - mU$
$\dfrac{dZ}{dt} = sY - cZ$	$\dfrac{dZ}{dt} = sY\left(1 - \dfrac{X+Y}{K}\right) - cZ$

R. cochinchinensis reproduce at a rate r_1, and a 'contact rate', p_1, between healthy and smutted plants, determines smut infection. Both healthy and smutted plants suffer mortality at rate b, which may, for example, be affected by other control measures such as weeding.

Density dependence was incorporated into weed reproduction through the parameter K which represents the theoretical weed-density at which the reproductive rate would be zero. Reproductive rate is assumed to be affected equally by competition between smutted and unsmutted plants, hence the inclusion of both X and Y in the expression for rate of increase of *R. cochinchinensis* plants $= r_1(1-(X+Y)/K)$. In practice there is also density dependent mortality of seedlings (Thomas 1970). Higher densities are usually observed in irrigated fields (Thomas 1970), hence K varies with environmental conditions. Incorporation of density dependence into weed reproduction (model 1b) creates a structure similar to a continuous form of the Nicholson-Bailey predator-prey model to which some workers have fitted weed-pathogen dynamics (Sheppard 1992).

The incorporation of a seed-bank (models 2a and b), introduces important aspects of the weed/smut interaction, principally that infection takes place during germination, and that a large proportion of the weed population can escape infection as dormant seeds in the soil. In these models, p_2 is the contact rate between germinating seeds and the smutted plants. The
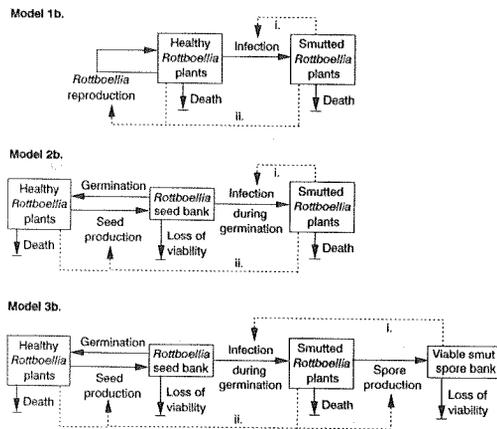

Fig. 1. The family of *R. cochinchinensis*/smut models. Boxes indicate densities of healthy or smutted *R. cochinchinensis* plants, or viable seeds or smut spores. Solid arrows indicate flows between these variables. Dashed arrows indicate influences of healthy- or smutted-plant or seed- or spore-densities on these flows. i - infection rate dependent upon inoculum availability; ii - seed and, or, spore production dependent on total weed density (they decline as density increases and in models 1a, 2a and 3a no such constraint is shown).

infection rate was bounded between 0 and 1 using a simple hyperbolic function (proportion of germinating seeds becoming infected $= p_2Y(1+p_2Y)$). This effectively accounts for multiple infections in a similar way to the multiple infection transformation (Gregory 1948).

The longevity of spores in the soil is unknown, but in models 3a and b, the importance of spore production rate, s, and the rate of loss of spore viability, c, can be examined. The infection parameter, p_3, now represents a contact rate between weed seeds and smut spores. The parameter s also incorporates spore losses because the majority of spores produced are unlikely to reach a possible infection site, and such losses are assumed to be a constant proportion of the spores produced.

Parameter estimates (Table 2) for *R. cochinchinensis* came from the literature, from field observations (R. Reeder unpublished), and from analyses of all these data in other models (M.C. Smith, R. Reeder, and M.B. Thomas unpublished). Those for the smut were derived from the literature (Table 2). No information was available for spore mortality-rate so the parameter was initially given the same value as the mortality rate of *R. cochinchinensis* seeds.

Analyses of weed densities with and without biocontrol

Critical points were derived algebraically or by numerical analysis (model 3b). In most cases, the

Table 2. Parameter definitions, and initial values used in the models.

Symbol	Meaning	Units	Values	Source of parameter estimate
r_1	Maximum rate of increase of *R. cochinchinensis* plants	Proportion/year	16	Annual proportion of seed bank germinating x annual seed production per plant surviving until next season. (0.2x80). Various references.
r_2	Maximum weed fecundity	Seeds incorporated into seed bank/plant/year	80	Modelling of *R. cochinchinensis* population dynamics (M.C. Smith, R. Reeder, M.B. Thomas; unpublished) suggest this is the number of seed production per plant which survives until the next season.
K	Weed density at which fecundity drops to zero	No m^{-2}	200	Various observations e.g. Fisher (1985), Thomas (1970) suggest maximum populations of mature plants of 200-300 m^{-2}.
p_1	Contact rate between smutted and unsmutted plants	Proportion of healthy plants infected/smutted plant/year	0.125	Chosen so that model 1a has the same total *R. cochinchinensis* density as model 3a under default conditions.
p_2	Contact rate between germinating seeds and smutted plants	Proportion of germinating seeds infected/smutted plant/year	0.125	Chosen so that model 2a has the same total *R. cochinchinensis* density as model 3a under default conditions.
p_3	Infection rate of germinating seeds	Proportion of germinating seeds infected x 10^6/ spore/year	5×10^{-4}	Calculations were made on infection data (Ellison 1993) assuming that the probability of infection follows a Poisson distribution.
b	Weed death rate	Proportion/year	1	Assumes one crop per year
s	Maximum production rate of viable spores	No x 10^{-6} incorporated into soil/smutted plant/year	200	Mwijage (1994) estimated 10^8 spores per spike (probably a gross under-estimate). Assuming 20 spikes per plant. This gives 2×10^9 spores per plant, however only a proportion of these survive to cause infection, say 10%.
c	Spore mortality rate	Proportion/year	0.8	This is unknown. It was assumed initially to be similar to seed mortality rate.
g	Seed germination rate	Proportion/year	0.2	Thomas (1970) found that 12% of seeds emerged after one cultivation in the following summer. Bridgemohan and Brathwaite (1989) estimated that 32% of seeds germinated after two cultivations.
m	Seed mortality rate	Proportion/year	0.8	Observations suggest seed bank survives for ~ 3 years (Thomas and Allison 1975)

critical points are also the long-term equilibrium values of the variables. In model 1a which continues to oscillate at constant amplitude over time, the critical points represent long-term mean values. Both healthy and smutted plants cause damage through competition with the crop. It is the total weed abundance (both smutted and unsmutted plants) therefore which is of interest when assessing the efficacy of control measures (Table 3).

For model 1a, weed abundance was proportional to weed reproductive rate, r, and inversely proportional to the infection parameter, p_1. All three models, which allow potentially unlimited *R. cochinchinensis* increase (1a, 2a, 3a), indicate that smut effectiveness is directly proportional to infection parameters, p_1, p_2 or p_3, and inversely proportional to spore mortality rate, c, and smut reproductive rate, s, where these parameters are included. This suggests trade-offs which can be made when selecting suitable smut strains. In the absence of density dependent constraints to weed population growth (models 1a, 2a and 3a), total weed abundance continued to rise exponentially in the absence of smut infection and these models are unrealistic in this respect. Adding the spore bank Z, makes very little difference to total equilibrium density when there is no density dependence (model 2a compared to model 3a) as p_2 in model 2a becomes equivalent to $c/p_3 s$ in model 3a.

Table 3. Equilibrium densities of the total *R. cochinchinensis* populations, with and without smut infection in the weed population.

Model	With smut infection absent	With some plants infected with smut
1a	∞	$\dfrac{r}{p_1}$
1b	$\dfrac{K(r_1 - b)}{r_1}$	$\dfrac{Kr_1}{r_1 + Kp_1}$
2a	∞	$\dfrac{gr_2}{(g + m)bp_2}$
2b	$K\left(1 - \dfrac{b(g + m)}{gr_2}\right)$	$\dfrac{gKr_2}{gr_2 + (g + m)bKp_2}$
3a	∞	$\dfrac{cgr_2}{(g + m)bp_3 s}$
3b	As 2b.	As 3a.

Analyses of density dependence

When density dependence was incorporated in both the seed and spore production (model 3b), K did not appear in the solution, giving an identical outcome to that for model 3a. The simplicity of the solution for the equilibrium abundance with smut in model 3b offers some encouragement for the appraisal of potential biocontrol agents. Rather than having to consider the impact of intra-specific competition on seed-production and spore-production rates, simple field observations of isolated plants may be sufficient to assess these parameters.

The 'cancelling-out' of density dependent effects, found above, was critically linked to the use of exactly the same form of density dependent relationship for both seed and spore production. When density dependence was incorporated in weed reproduction only (model 1b) or seed production only (model 2b), the carrying-capacity parameter, K, appeared in the expressions for equilibrium abundance. In the absence of smut, K is simply a scaling factor. With smut infection, total equilibrium density follows a rectangular hyperbola with increasing K, with an asymptote given by the equivalent equation for model 1a or 2a.

Although inclusion of density dependence does not affect the long-term equilibrium it does exert an influence on model dynamics over time. In models 2b and 3b, *R. cochinchinensis* density decays to equilibrium from the initial conditions given in Fig. 2, whereas model 3a gives damped oscillations, finally reaching equilibrium after about 50 years. It takes over 40 years to reach equilibrium according to model 3b, compared to about 10 according to model 2b. The oscillatory behaviour of model 2a is highly damped, reaching equilibrium after about 20 generations. Times taken to reach equilibrium are highly dependent on starting conditions, but model 3b predicts that it could be many years before any results are observed after application of a low dose of smut inoculum.

Analyses of biocontrol in conjunction with other control practices

Comparison of the equilibrium densities of the total *R. cochinchinensis* population, with and without smut infection, while changing individual parameter values (Fig. 3) allows the potential effectiveness of the smut in conjunction with other control measures to be explored. For example, weeding or herbicide use might be represented by an increase in *b* from the standard
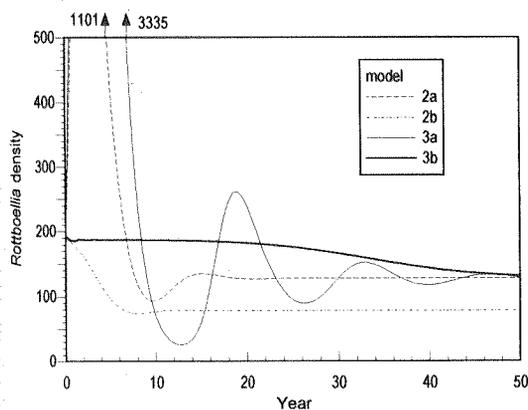
Fig. 2. Total *R. cochinchinensis* density over time for models 2a, 2b, 3a, and 3b. Parameters are as given in Table 2. Initial densities were X = 187.5, U = 837.5 (the equilibrium densities for 2b and 3b without smut in the system) and Y = 5, Z = 0 (representing a small addition of smut inoculum).
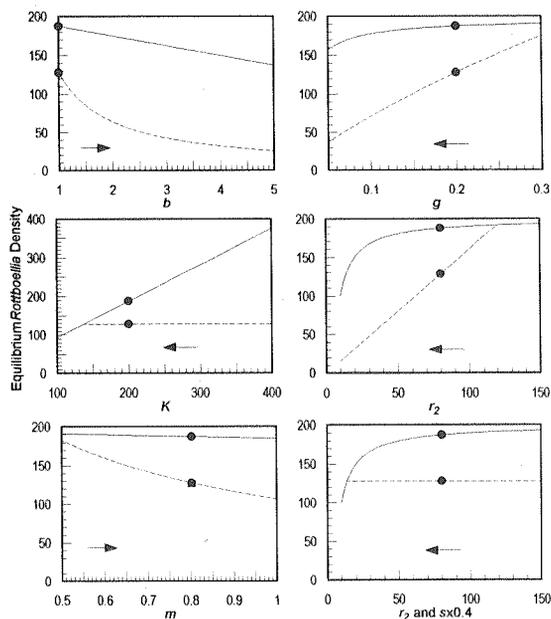

Fig. 3. Predicted interaction of biocontrol with other control measures for model 3b. Equilibrium *R. cochinchinensis* density with (broken lines) and without (unbroken lines) smut infection when individual parameters are varied. In each case, symbols indicate the values obtained with the standard parameter set (Table 2), and arrows, the direction in which control measures would alter parameter values (see text for details).

value given in Table 2 (which represents the natural mortality rate in the absence of control measures). Thus, increasing weed death rate, b, from one to two per year increases the difference between the solid and dashed lines in Fig. 3, indicating that the smut may be more effective under such conditions. Divergence of the lines with increasing impact of control indicates that biocontrol and the other control method interact synergistically. This is the case with measures which increase b, but the graph also suggests diminishing returns from further increases in weed death rate. Convergence of lines with increasing impact of another control method indicates that the other measure decreases the efficacy of biocontrol (i.e. they are antagonistic), and parallel lines indicate that the two effects are simply additive.

Decreasing weed germination rate, g, through reduced tillage, had a synergistic interaction with the smut. Control methods which increase seed mortality (m) or decrease the maximum rate of seed production (r_2) also have a synergistic interaction with the smut. Increasing m has very little affect on weed density with the parameter estimates used here, when used as the sole means of weed control. However control methods which affect both r_2 and s equally (e.g. through early harvest of the crop and weed) give no advantage over using the smut alone. Decreasing the maximum weed population density which can be supported, K (e.g. through reduced water and other nutrient availability), has an antagonistic effect since the equilibrium density with smut is independent of K. On the other hand, this

suggests that the smut may be particularly effective under environmental conditions resulting in a particularly high *R. cochinchinensis* carrying-capacity.

The use of a family of models provides insights into the effect of model assumptions on results. The addition of U (models 2a, 2b, 3a and 3b) results in the weed death-rate, b, being incorporated into the denominator of the equations for total weed equilibrium density in the presence of the smut. Control actions, such as hand-weeding, which have an impact on b, would therefore fail to offer any improvements in long-term weed suppression over biological control alone, according to models 1a and 1b. Increasing the complexity of the model, however, alters this conclusion. This also indicates differences in the interaction with weeding which could occur if the models are parametrised for biocontrol of other weeds with sterilizing smuts.

Simulation of the various control measures in the absence of biocontrol (solid lines in Fig. 3) suggested that they would be relatively ineffective unless they have a major impact on the parameter concerned. The importance of high efficiency in control measures,

particularly those directed at reducing seed production, has been highlighted by a number of authors (Fisher *et al.* 1985; Cloutier and Watson 1990; Smith *et al.* 1993).

Discussion

Although these simple analytical models cannot cope with the complexity that can be incorporated into simulation models, they can be easily interpreted and provide an understanding of the importance of the smut and weed parameters and interactions with other control practices. Parametrisation, particularly for the smut, is not accurate enough to provide an assessment of whether or not biological control is likely to succeed, and more complex simulations may not be more useful at this stage. The equations for critical points, which can be derived from them, may be relatively simple and provide an insight into the factors affecting the success of biocontrol.

This paper illustrates the ease with which these models can be used to investigate weed biological control problems and has demonstrated the following points which will be of practical significance in plans for introducing biocontrol agents: (i) comparisons of models with and without density dependence in spore- and seed-production indicate that simple field observations of isolated plants may provide sufficient information for equilibrium densities of the weed to be estimated after application of the smut; (ii) equilibrium weed densities also depend on the ratio of the smut parameters c/p_3s (models 3a and 3b), and this suggests potential trade-offs when selecting suitable smut strains; (iii) equations of critical points for model 3b, without smut, suggest that control measures will not be effective in reducing *R. cochinchinensis* populations unless the measures have a major impact on the parameter concerned; (iv) the critical points also indicate which of these control methods would interact synergistically with biocontrol; and (v) times taken to reach equilibrium, after application of smut inoculum, were highly dependent on starting conditions, but model 3b predicted that it could be many years before any effects on weed density are observed after application of a low dose of smut inoculum.

Analysis of model 3b suggests that biocontrol with the smut would be effective in conjunction with control methods which reduce g or r_2 or increase b or m. In practice it may be difficult to reduce r_2 selectively without reducing s, because this would require the control method to affect unsmutted plants selectively and, therefore, these control methods would be

antagonistic to biocontrol. A single control practice might affect several parameters, so interactions with the smut may be more complex than the models suggest. For example, the use of cover crops or a more competitive crop might affect r_2, s, K and g. The use of herbicides or weeding, assumed here to increase b, may also reduce r_2 and s, because these values vary according to the time of weed emergence relative to the crop. However, existing conclusions would be unaltered if these parameters changed by similar proportions.

One major simplification arises from representation of the system using differential equations: *R. cochinchinensis* population growth and the smut infection are effectively considered as continuous processes. This makes no sense for individual fields but it may be reasonable, provided that the model is considered as representative of processes on a sufficiently-large spatial scale. Another simplification is in the representation of the smut life-history since the smut has a saprophytic phase in the soil as well as the parasitic phase on *R. cochinchinensis*.

In model 3b, the total weed density affects the production of spores and the production of seeds in the same way. The competitive ability of smutted and healthy plants was therefore assumed to be identical. Nothing is known about their relative competitive ability, although Ellison (1993) found that smutted plants in pots produced significantly fewer tillers. Experiments on other weeds have found the effects of disease on plant growth to depend heavily on host-plant density (e.g. Lively *et al.* 1995). The representation of competition used in model 3b was found to be unsuitable for investigating differential competition between smutted and unsmutted plants. These effects are being investigated elsewhere using a modified formulation of the model.

Acknowledgements

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