Not all disturbances are equal: synthesising the effects of plant demography, natural disturbance and control methods on weed invasions

Yvonne M. Buckley
School of Integrative Biology, University of Queensland, St Lucia, Queensland 4072, Australia and
CSIRO Sustainable Ecosystems, 306 Carmody Road, St Lucia, Queensland 4067, Australia
Email: y.buckley@uq.edu.au

Summary While it is known that disturbance in general is important for weed invasions and that it is a complex process, we have a poorer understanding of the effects of different types and scales of disturbance on both invasion and the management of invasions. Here I synthesise recent methods for the inclusion of disturbance in simple simulation and analytical models and give examples of the important insights that this can give us on the use of biological control, disturbance management and integrated weed management techniques. By understanding the complexity of disturbance we can better predict invasion dynamics.

The level of impact that biocontrol agents need to have to reduce population densities or prevent invasions from spreading depends on the extent and nature of disturbance in the system. Some types of weed control activities can act as disturbances in the system, which may lead to reinvasion by the same or a different weed species if the effects of the control disturbance are not carefully considered. Manipulation of disturbance regimes can make direct control measures more successful and can also be used to restore invaded habitats to a more desirable community composition.

Keywords Invasibility, population dynamics, weed management.

INTRODUCTION

Disturbance is widely regarded as a crucial process in the initial invasion and maintenance of populations of invasive plants (Buckley *et al.* 2007, D'Antonio and Vitousek 1992, Davis *et al.* 2000, Lockwood *et al.* 2007). Models of the effects of disturbance on invasion have demonstrated its role in maintenance of high population densities (Rees and Paynter 1997), the importance of scale (Rees and Hill 2001) and the importance of how different elements of the community are affected (Buckley *et al.* 2007, Buckley *et al.* 2004). These studies have also shown that consideration of the effects of disturbance can fundamentally change the type and intensity of management recommended. It is crucial therefore that disturbance effects are explicitly considered in both integrated weed management experiments and models.

In this paper I synthesise the results of recent work on how disturbance can be incorporated into models of the determinants and management of invasions and how this can affect management recommendations. I define disturbances as events which act to kill or remove plants from a location (which varies in size according to the scale of the disturbance); disturbances can either be intrinsic to the ecosystem (natural disturbance) or extrinsic and imposed as part of weed control strategies (control disturbance). I make an additional assumption that disturbance adapted invaders will always capture disturbed sites if sufficient seeds are available. This is done to include a 'worst case scenario' of a competitively superior, disturbance adapted weed.

MATERIALS AND METHODS

Disturbance is very often a spatial process, with both the scale and arrangement of disturbance events in the landscape important for invasions. For this reason Cellular Automata, lattice and grid-based models are often used to represent space, with each cell in the lattice defined as containing one or a number of plants. Simulations are used to determine the behaviour of the model and by making simplifying assumptions, analytical approximations of the simulation behaviour can be made. This can result in greater understanding of the behaviour of the model, as simulations alone are often too complicated to analyse.

Descriptions of the simulation can be written as one or a series of difference equations describing the change in different vegetation components (e.g. weed, other vegetation) from year to year. The population parameters can include maximum age, age at reproductive maturity, fecundity, seed persistence in the seed bank, germinability and survival, therefore capturing the demographic differences between different species or populations. The population dynamics can be simple or more complex depending on the species and the data available. Disturbance is modelled as a probabilistic process, with each location in the grid having a probability of disturbance which can differ according to the type of vegetation (e.g. Buckley *et al.* 2004, 2007). Disturbances can also be of large or small scale (e.g. Rees and Hill 2001). Disturbances can act to remove above-ground vegetation and/or alter seed parameters; this can occur where fire both kills seed in the seed bank and stimulates germination from the surviving seed (Buckley *et al*. 2004). Disturbances can either be intrinsic to the ecosystem or can be imposed as part of a control strategy. For an example of the latter, weeds may be targeted with herbicide or mechanically removed, introducing significant disturbance into the ecosystem.

A crucial parameter is whether the invasive species can 'self-replace' after an adult senesces naturally. Pioneer species (and some disturbance adapted invaders) may be unable to establish underneath senescent individuals, leaving a site to be recolonised by other vegetation through a natural successional process (Buckley *et al.* 2004).

A very simple example of this type of model is that described in Buckley *et al.* (2007):

$$W_{t+1} = (1 - p_{dW})W_t + p_c[p_{dW}W_t + p_{dU}(1 - W_t)]$$

with more complex versions parameterised for different species given in Rees and Paynter (1997), Rees and Hill (2001) and (Buckley *et al.* 2004). W_{t+1} is the proportion of the area occupied by the weed at time t+1, W_t is the proportion of the area occupied by the weed in the previous year, p_{dW} is the probability of disturbance of weed occupied sites, p_c is the probability that a weed colonises disturbed sites and p_{dU} is the probability of disturbance of non-weed occupied sites. This simple equation can be analysed alone, but the model can also be run as a spatial grid-based simulation, enabling the incorporation of more complex aspects of the life-history of the weed (such as density dependence) and the disturbance regime.

Modifications of this simple model include the addition of weed life-expectancy (Rees and Paynter 1997), probability of self-replacement after senescence (Buckley *et al.* 2004) and different scales of disturbance (Rees and Hill 2001) which are all explored in detail elsewhere.

Analysis of the equations and the simulation model results determines equilibrium levels of weed occupancy in relation to disturbance rates (Rees and Paynter 1997), rate of increase at different weed densities (Buckley *et al.* 2007), critical level of biocontrol agent impact on seed production (Buckley *et al.* 2004), and effects of integrated weed management strategies in relation to disturbance regimes (Buckley *et al.* 2004).

A crucial feature of the simple model presented here is that it can have different disturbance rates between weed occupied and unoccupied sites, with 'disturbance suppressor' weeds having low disturbance of weed occupied sites (low p_{dW}) and 'disturbance promoter' weeds having high disturbance of weed occupied sites (high p_{dW}) relative to disturbance of weed unoccupied sites (p_{dU}). This feature allows representation of scenarios where different disturbance rates occur in weed occupied sites (a site can be a proportion of an area of any size in the analytical version or the area occupied by one plant in the simulation version) than weed unoccupied sites (i.e. areas occupied by other or more desirable vegetation types). These scenarios can occur if natural disturbances affect weeds and other vegetation differently (e.g. livestock grazing) or are imposed by weed managers who explicitly target weeds.

RESULTS

A key feature of the model presented here is that disturbance rates between weed occupied and unoccupied sites can be unequal. The average number of seeds produced by an individual over its lifetime is $R_0 = Fp_{dU}/p_{dW}$; the population will increase from rarity if $R_0>1$. In fact when disturbance rates are equal ($p_{dW} = p_{dU}$), R_0 does not depend at all on disturbance. Disturbance will, however, still affect the equilibrium population density of the weed (see Rees and Paynter 1997), with higher non-weed occupied site disturbance rates leading to higher population densities, except at very high disturbances. The highest population growth rates of the weed will occur when disturbance of non-weed occupied sites is high and disturbance of weed occupied sites is low.

Weed control often involves targeted disturbance of weed occupied patches and can be used to reduce the population growth rate of the weed; however, sometimes even targeted weed control will not lead to the decline of weed populations. Positive population growth rates of the weed can still occur if $p_{dU}>p_{dW}$, that is if disturbance of weed occupied sites is lower than disturbance of non-weed occupied sites. Therefore targeted weed management (p_{dW}) may be a waste of resources if non-weed occupied site disturbance (p_{dU}) remains high.

Where $p_{dW}>p_{dU}$, i.e. high levels of targeted weed control in relation to natural disturbance, population growth rate may also be affected by weed population size. At low weed population densities, control efforts may result in a declining population but the same proportional effort may be ineffective at higher densities. There may also be a threshold density at which control becomes effective. Reductions in fecundity or survival of seedlings, in addition to manipulation of disturbance regimes, may be necessary to achieve declining populations (Buckley *et al.* 2007). This leads to the possibility of scenarios where a seed-feeder may only be effective in combination with disturbance manipulation (increasing targeted weed management and decreasing other sources of disturbance in the ecosystem).

DISCUSSION

Modelling work which decomposes 'disturbance' into components affecting weeds and other vegetation can give us insights into the effectiveness of controlled disturbances (e.g. herbicide or mechanical control) as management techniques. Unequal disturbance rates can determine whether or not a weed population will increase or decline. Management of natural disturbance regimes, in combination with direct management of the weed population through targeted removal (controlled disturbance) or biocontrol (affecting weed demographic parameters), can lead to population declines where targeted weed removal alone may not be sufficient.

While the model presented here is very simple, the concepts introduced can be incorporated into more complex, realistic models (e.g. Buckley *et al.* 2004, Firn *et al.* this volume). Consideration of disturbance regimes may lead to more effective management strategies for invasive plants (Buckley *et al*. 2004, 2007 and Firn *et al*. 2008).

ACKNOWLEDGMENTS

For helpful discussions on this topic I thank Mark Rees, Ben Bolker, Jennifer Firn, Alice Yeates and Ric Colasanti. Queensland Murray Darling Committee, Condamine Alliance and the Australian Research Council provided funding.

REFERENCES

Buckley, Y.M., Bolker, B.M. and Rees, M. (2007). Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters* 10, 809-17.

Buckley, Y.M., Rees, M., Paynter, Q. and Lonsdale, W.M. (2004). Modelling integrated weed management of an invasive shrub in tropical Australia. *Journal of Applied Ecology* 41, 547-60.

D'Antonio, C.M. and Vitousek, P.M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23, 63-87.

Davis, M.A., Grime, J.P. and Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88, 528-34.

Lockwood, J.L., Hoopes, M.F. and Marchetti, M.P. (2007). 'Invasion ecology'. (Blackwell Publishing, Malden, USA).

Rees, M. and Hill, R.L. (2001). Large-scale disturbances, biological control and the dynamics of gorse populations. *Journal of Applied Ecology* 38 364-77.

Rees, M. and Paynter, Q. (1997). Biological control of Scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *Journal of Applied Ecology* 34, 1203-21.