

## Weed ecology, biology and spread

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### Summary

Weeds are colonizing plants that commonly dominate early successional stages of vegetation on disturbed land. Ecologically, weeds are mostly competitive ruderals. Each weed has some biological attributes that singly or interactively confer ecological advantage over its neighbour. These biological attributes include seed dormancy, high growth rate, high reproductive output and an ability to disperse widely. Many non-weedy plants have similar attributes, however. When at least some of these ecological and biological attributes interact with human activities that disturb land, such as cropping and pastoralism, then such opportunistic plants are called weeds.

As human activities change so will weed control methods need to be changed. Changes in weed floras are usually considered retrospectively at present. I conclude that sufficient case histories in weed biology have now been accumulated to formulate weed control strategies that are prospective in nature. Therein lies the hope for enhanced weed control based on the results of biological and ecological research.

### Introduction

Weeds are a subset of the plant kingdom that interfere with human activities in some deleterious way. They have long been associated with agriculture - as crop plants were selected from wild populations, weeds co-evolved with them and with the different methods of crop husbandry practised over millennia (4). The medicinal and horticultural values of some plants were also recognized early and selected for by humans; such plants also became weeds subsequently. Closer to the present time, other assemblages of plant

species have become weeds of conservation reserves and other areas of relict vegetation of only indirect economic value (11,13). The latter group of weeds is becoming increasingly significant in many countries as users of conserved land perceive natural values being eroded because of their presence. There thus are different subsets of plants that we now call weeds and each subset may have evolved in response to different selection pressures.

Does an enhanced knowledge of weed ecology and biology help to limit the effects and spread of the subsets of plants we call weeds? In this contribution I shall attempt to answer this question by considering weeds in their ecological and biological contexts. Wherever possible I shall use examples of pairs of weedy and non-weedy congeners in an attempt to narrow an approach that may otherwise be too broad to be useful.

### Weed ecology

Weeds are colonizing plants that commonly dominate early successional stages of vegetation on disturbed land. As such, weed cover may be advantageous in preventing soil erosion and in providing shade under which seedlings of later successional species may establish, e.g., *Solanum mauritianum* Scop. (Solanaceae) in regenerating subtropical rainforest in southern Queensland (22). In most agricultural situations with their high level of disturbance, weeds rapidly colonize bare ground - a response typical of ruderal species. Weeds may dominate the early stages of secondary succession.

Contemporary ecological thinking has moved from the early Clementsian idea of a successional series of species moving inexorably towards a stable state (the 'climax') to incorporate at least three possible pathways (3). Because of continuous disturbance by cultivation and/or herbicide application, the appropriate model of succession for a weedy cropland lies somewhere between the 'tolerance' model applying to secondary succession

and the one Connell and Slatyer (3) termed their 'inhibition' model. The former certainly applies to old-field succession in the absence of further disturbance. The net effect of agricultural operations is to maintain vegetation at an early successional stage to which competitive ruderals are well adapted.

Two other ecological concepts are also relevant to weed ecology. The first concerns the two extremes of adaptation shown by species in the way they allocate resources for survival - the so-called 'r'- and 'K'-selection concept that MacArthur and Wilson (14), first developed for animals and subsequently discussed by Pianka (19). Agricultural weeds are relatively *r*-selected species in that they are typically short-lived occupants of early successional stages of a community that allocate most of their resources to reproduction, usually as seeds. Perennial weeds occupy a position further towards the *K*-selected end of the continuum.

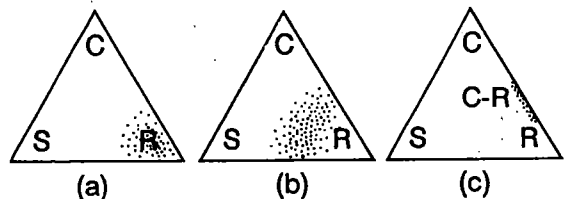
MacArthur and Wilson's one-dimensional model (14) was later extended by Grime (8) to include three extremes - his competitive, stress-tolerant and ruderal groups of plants. As with MacArthur and Wilson's model, most plants lie somewhere between these extremes. Weeds generally are either ruderals or competitive-ruderals (Figure 1). Trees and shrubs tend to be a combination of competitive and stress-tolerant, whereas a group such as lichens are almost entirely stress-tolerant (8). In relatively undisturbed conditions, different types of response may predominate during the course of succession; for instance, in the simplest case, annual ruderals dominate initially, then more competitive perennial herbs become dominant and finally stress-tolerant shrubs and trees predominate. Grime's triangular model is capable of reconciling ecological theory with plant responses as measured in the field; it may be used quantitatively to further distinguish different subsets of weeds and their roles in secondary successional pathways.

How can use of Grime's model (8) help to better understand the ecology of a particular weed? To answer this question, let us consider a grass species widespread throughout Africa, Asia and Australia that has caused crop losses only relatively recently. The species *Diplachne fusca* (L.) Beauv. (Poaceae) is currently a major weed of rice crops in south-

eastern Australia, to which region it is indigenous. It is semi-aquatic with an erect tussock habit and has an annual or short-lived perennial life cycle (16). *Diplachne fusca* occurs naturally in ephemeral wetlands of semi-arid regions where the periods of inundation are irregular, because of unpredictable rainfall. The species is thus well-adapted ecologically to alternating wet-dry cycles of variable length. Rice cultivation provides such conditions along with plenty of areas of bare ground for seedling establishment.

McIntyre (15) used Grime's model (7) to classify the strategy of the established phase of the life-cycle of *D. fusca*. Growth rate (*R* max) and a morphological index (*M* -see 8) were used in an ordination, the results of which classified *D. fusca* as a ruderal species (Figure 1c), though close to the competitive-ruderal region of overlap in the triangle (15, personal communication 1991).

The example of *D. fusca* thus validates the model of Grime (8) for weediness on ecological grounds. I suggest that a more effective test of Grime's model and its relevance to predictive weed ecology would be to use a suite of closely-related species within a genus, to see if it has the power to discriminate between different levels of weedy attributes. This idea has not been tested as far as I can determine; it is time it was. Such a proposal could increase the power of generalizations about weed ecology and prediction of weediness.



**Figure 1** Triangular diagrams representing the positions of (a) annual herbs, (b) biennials, and (c) *Diplachne fusca* (see text), where C = competitive, S = stress-tolerant and R = ruderal plants ((a) and (b) redrawn from Figure 3 of (8) and (c) redrawn from (15)).

### Weed biology

Weeds generally have biological attributes that may be associated, either individually or collectively, with enhanced survival and

dispersal. These attributes were listed and discussed by Baker (2) for examples of both temperate and tropical weeds. In the one species *Eupatorium microstemon* Cass. (Asteraceae) there are weedy and non-weedy populations. The distribution of the latter is confined to upland central America, whereas the weedy taxon is widespread in central and South America and, by 1965, had established in West Africa (2). Biologically, the two *Eupatorium* populations differ, as do a weedy and a non-weedy species of *Ageratum* (Asteraceae) also described by Baker (Table 1). The greater plasticity of the weedy population or species tends to be a general attribute and is what Baker referred to as a 'general purpose genotype'. Baker elaborated further on these differences between weedy and non-weedy congeners of *Eupatorium* and *Ageratum* and some other plant groups to list 14 attributes associated with weediness. No one weedy species has all 14, of course. To Baker's list I would add seed dormancy as an extra attribute associated with weediness in many plant groups.

**Table 1** Comparison of attributes of weedy and non-weedy populations of the one species *Eupatorium microstemon* and a weedy and non-weedy species of *Ageratum* (Tables I and II of (2)).

	Weedy taxon	Non-weedy taxon
1.	plastic	not very plastic
2.	annual	perennial
3.	rapid to flower	slow to flower
4.(a)	photoperiodically neutral ( <i>E. microstemon</i> )	requires short days to flower ( <i>E. microstemon</i> )
4 (b)	flowers at all temps ( <i>Ageratum conyzoides</i> L.)	flowers at low night temps ( <i>A. microcarpum</i> (Benth.) Hemsl.)
5.	self-compatible (autogamous)	self-incompatible
6.	economical of pollen	plentiful pollen produced
	( <i>E. microstemon</i> , n = 4) ( <i>A. conyzoides</i> , n = 20)	( <i>E. microstemon</i> , n = 20) ( <i>A. microcarpum</i> , n = 10)

Newsome and Noble (17) extended this approach of Baker's for the 86 weeds proclaimed as 'noxious' in Victoria (18) to see if there were suites of eco-physiological characters that are associated with success of colonization in Victorian ecosystems. Their list of species was biased towards weeds of agricul-

ture. Newsome and Noble identified ten groups of weeds, of which the main ones were the 'competitors' (29 species) and the 'gap-grabbers' (27 species). The former either shaded their competitors or else extended their root systems further in water- and/or nutrient-limited habitats. Gap-grabbers were species that had high initial growth rates or else formed rosettes that occupied space before those germinating subsequently. The latter group was primarily composed of species that germinate in autumn, over-winter as rosettes and then elongate and flower in spring, e.g., the slender thistles *Carduus pycnocephalus* L. and *C. tenuiflorus* Curtis (Asteraceae). These two groups would seem to lie on the competitor-ruderal axis of Grime (8) - see earlier. A third group, termed 'survivors', comprised species with long-lived individuals resistant to most causes of mortality, such as blackberry (*Rubus* spp., Rosaceae). This third group was numerically less well represented on the list of Victorian noxious plants; it may lie more towards the centre of Grime's C-S-R triangle (Figure 1). Newsome and Noble (17) concluded on the basis of their analysis that most of the Victorian weeds classed as noxious tended to be 'specialists' rather than the 'super generalists' of Baker (2). Their specialists had particular requirements for germination, sometimes had extended vegetative stages and had relatively low levels of environmental plasticity.

In connection with the earlier consideration of the weediness of *D. fusca*, there are three biological attributes of the plant that seem at least as equally important as its ecological status as a competitive-ruderal. Firstly, the species can develop a persistent bank of dormant seeds in the top few centimetres of soil. Secondly, seedling emergence is strongly inhibited by the presence of litter or living pasture plants. Thirdly, the species is summer-growing with a C4-pathway for photosynthesis (16). These three biological attributes pre-adapt this native grass to become a weed in a cultivation system that mimics the natural conditions under which the species has evolved.

I conclude that the concept of a general purpose genotype formulated by Baker (2) is too general to have real predictive value in the assessment of most weedy species. There always seem to be notable exceptions to each

of Baker's generalizations: The combination of biological attributes of a particular weed species or a weedy population of a species may be too individualistic to allow for any useful generalizations significant for control - except perhaps keeping a species out of a region by quarantine. I further conclude that at least in the specific case of *Diplachne fusca* a combination of several biological attributes may, however, be as good a predictor of weediness as a quantitative ecological model such as that proposed by Grime (8).

### Weed spread

Plants disperse and spread around the world by many different means (see e.g., Ridley (20)). Weeds are a subset of plants whose propagules are spread primarily as a result of human activities. In many instances weeds are spread accidentally. In other instances, however, where records are available, the proportion of weed species spread deliberately by humans is surprisingly high - for example, 57% for the introduced flora of South Australia (12). In regions such as eastern Australia (21), California (6) and the Auckland area of New Zealand (5), the number of naturalized species (not necessarily all weeds, however!) is increasing linearly at a rate of from 4 to 6 species per year, and there is as yet no sign of a decrease in this rate of increase, despite all three regions having regulatory quarantine legislation and enforcement. As the number of naturalized species increases so may the diversity in characteristics of spread of those species, some of which we call weeds.

Despite an apparent diversity in the means of spread, most weeds seem to follow a similar pattern of increase in the number of their dispersal units. Initially, after arrival at a new site, there is a latent or lag period, when numbers of propagules of a species may increase but usually only imperceptibly. The latent phase is followed by a period of rapid and detectable increase in the numbers of propagules that may also be called the exponential phase of population increase. A third phase involving a decrease in the size of the population usually follows, either as a result of self-regulation, or as is common in the case of weeds, as a result of application of some control method to limit further population increase. If control is effective and long-lasting, e.g., the effect of a biological control

agent or a competing perennial pasture, then the population usually continues at a low level. It is the task of weed control to get to this final phase as quickly and as economically as possible.

One future task for weed science is to study the factors affecting the first or 'lag' phase in the increase of weed populations. Sometimes it may occur because the propagule initially arrives at a site climatically unfavourable for it. For instance, Mouse-ear hawkweed (*Hieracium pilosella* L., Asteraceae) was first recorded from coastal Timaru in the South Island of New Zealand where it was not weedy. Only when it arrived in the tussock grasslands of the subalpine Mackenzie country did its population commence to increase exponentially and become, at present, the major weed of grazing lands in that region. Was this change because of a different set of climatic conditions that better suited the species to reproduce or was it the effects of a change in land use from roadside vegetation to grazed tussock grasslands? By paying research attention to this early phase of population increase, the study of weed spread may become a more scientific and predictive aspect of weed science and less dependent on botanical anecdote that seems to characterize it at present.

Individual weed species may differentiate genetically into different populations with different responses, for example, to herbicides (10) or to natural enemies (9). Just as the biology of individual opportunistic species may change over evolutionary time, so too does the overall weed flora change over shorter time periods. For instance, major changes in cropping practices for temperate cereals over the last 50 years have been accompanied by a considerably changed weed flora, and especially an increase in grass weeds (1,10). This change may have been predictable. Within the subset of grass weeds in cereals, however, the increase in weediness of the silver grasses (*Vulpia* spp., Poaceae) with the adoption of minimal tillage methods in southern Australia was not predicted. Weed science has so far largely failed to identify potential weeds of changed management systems and will continue to fail to do so until more biological studies are integrated with ecological studies of the ecosystems being invaded.

## Conclusions

From this brief consideration of some aspects of weed ecology, biology and spread I draw the following conclusions.

1. Weeds are not a homogeneous subset of plants about which effective generalizations can be formulated. Rather, they are a diverse group of plants mainly united by their association with human activities and not by common ecological or biological attributes.
2. Prediction of weediness based on ecological status, biological attributes or spread characteristics remains a chancy activity, though it may be becoming less so. An increased input from biologists into this area of weed science seems justified, however, if only in the hope of reducing the high costs of regulating weed populations worldwide and especially in the tropics.
3. Weed control is an on-going and long-term process. Weed science needs to provide a more prospective basis for formulating control programs than is apparent presently. Such a prospective basis will come mainly from studies of weed ecology and biology on a species-by-species basis and how they interact with the ecosystem of which that species is part. A greater attention by weed scientists to the ecosystem, and not just to the weedy species, may make the contributions from weed ecology and biology more relevant to weed control.

## Acknowledgments

I thank Sue McIntyre for permission to use her unpublished information on *Diplachne fusca*, and Jeremy Burdon, Harry Combella, Sue McIntyre, Dick Medd and Dane Panetta for comments on a first draft of this review.

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