A RATIONALE BASED ON BIOLOGICAL CONSIDERATIONS FOR DETERMINING TERRESTRIAL NOXIOUS PLANT CANDIDATES

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Summary. Biological characteristics of particular significance to the determination of noxious weed status include growth rates of seedlings, potential fecundity and a number of both specialized and nonspecialized seed characters which facilitate dispersal over large distances. The necessity for developing approaches to predict which species will become weeds is emphasized and some of the limitations of current predictive techniques are discussed. It is suggested that close examination of the restricted group of species which becomes naturalized following introduction may be the most efficient approach.

INTRODUCTION

Historically, plants which have been declared noxious in Australia have earned this distinction due to suspected effects upon human health, economic losses associated with agricultural production, or invasion and dominance of natural vegetation. Although rigorous documentation of any of these perceived effects has rarely been attempted, this general definition of noxiousness is still a useful one and provides a basis for this paper. While some plants, particularly those which are poisonous to humans or domesticated animals, are 'inherently noxious', others assume noxious weed status through their ability to dominate plant communities. The major criterion for noxiousness in this case, therefore, is invasiveness, since the principal aim of noxious plant legislation is to minimize the economic externalities which arise through the spread of weeds from infested to uninfested land (28). In the following discussion, I will first address the patterns of spread which are demonstrated by weeds and the biological characteristics which facilitate the processes of spread and invasion. I will then describe some recent attempts to predict which plants are likely to be of concern to Australian land managers.

PATTERNS OF WEED SPREAD

Weeds may spread as advancing fronts, scattered isolated colonies or as a combination of these patterns. Generally, species which exhibit a saltatory form of spread extend more rapidly and are more difficult to contain (6, 29). Because of this, biological characteristics which facilitate such quantum displacement are very important. Species which spread more slowly will be easier to contain, presumably with a lower degree of government intervention, but will eventually reach their distributional limits if containment procedures are less than perfect. Forcella (17) has provided evidence that final distributions may, in fact, be broader for weeds which demonstrate high initial rates of spread.

BIOLOGICAL ATTRIBUTES WHICH FACILITATE DISPERSAL

1. Dispersal mediated by humans

By far, the species which tend to move most quickly over the longest distances are those which are transported by humans as they move stock, machinery, fodder or consignments of seeds of crop and pasture species. Various seed coat structures, such as spines and hooks, with or without viscid coatings, facilitate attachment to pelts, hooves, etc. and promote epizoochorous dispersal. Dispersal by ingestion and then excretion by animals (endozoochory) is favoured in hard-seeded species such as occur in the Fabaceae (e.g. *Prosopis*), Amaranthaceae and Chenopodiaceae. Aspects of both forms of animal-mediated dispersal may be quantified, and in the case of endozoochory, additional tests may be made for residual seed viability (40). Presumably, some of the characteristics which facilitate epizoochorous dispersal should also favour attachment to machinery, with the exception that no specialized adaptations are required for seeds to gain adhesion to vehicles through soil or mud (44). The current campaign to prevent the southward spread of *Parthenium hysterophorus* by cleaning harvesting equipment at the Queensland/N.S.W. border has arisen from the recognition of how effective this type of dispersal may be in promoting spread.

For weed seeds to be dispersed in consignments of crop and pasture seed, the habits of parent plants must be such that seeds are presented at an appropriate height to be harvested. Evidence exists that weeds can respond to selection pressure of this sort, e.g. *Picris echioides*, whose ancestral form is a decumbent perennial which grows in open habitats, and has given rise to an annual form with an erect habit which occurs as a weed in wheat fields (8). Weeds whose seeds are retained on the parent plant rather than shedding as they ripen, and whose fruits are resistant to shattering are most likely to be collected during routine harvesting procedures. Of the three varieties of *Echinochloa crus-galli* which coexist in Californian rice-growing regions, for example, only seeds of the latest maturing variety are harvested with the crop to any extent (12). Following harvest, dispersal will be promoted for weeds whose seeds most resemble the seeds of crop or pasture species in terms of size, shape and specific gravity, thereby frustrating attempts at removal by seed cleaning procedures. These seed characters are known or can be determined for desirable species and varieties, so it should not be difficult to evaluate weed species in terms of potential for dispersal in seed lots.

Long-distance dispersal of weeds may take place through mass movements of fodder, as happened in south-eastern Australia during the recent drought-declared periods of 1980 and 1981 (43). Biological pre-requisites for this mode of dispersal are few, namely synchrony of seed production with harvesting activities and the retention of mature propagules by the parent plant. In accordance with this basically non-selective type of dispersal, Forcella (17) found that species with very high rates of spread often have relatively large and heavy seeds.

2. Dispersal by natural vectors

Dispersal by water may displace propagules over considerable distances. Indeed, this has been the major reason for the rapid and inexorable spread of Australia's worst aquatic weeds. For primarily terrestrial weeds, habitat preferences provide a strong indication of the potential for spread by this vector. The ability of propagules to float, inhibition of germination during floating and the retention of germinability after floatation will determine how effectively a species might achieve dispersal in water. An experimental approach to this problem was devised by Staniforth and Cavers (42) to examine dispersal of three *Polygonum* species, and has been used to quantify dispersal and floating ability of dimorphic fruit segments of *Cakile edentula* (36).

Although the majority of wind-dispersed seeds lands within a few metres of the parent plant, small numbers are carried for considerably longer distances. For example, Bakker (10) retrieved propagules of *Tussilago farfara* at a distance of 4 km from their source. Similarly, some remote populations of *Baccharis halimifolia* in Queensland are separated by more than 5 km (34).

These examples serve to illustrate the potential ecological significance of what may be considered to be extreme events. Distances over which plumed seeds and fruits may move are inversely related to their terminal velocities in still air (Table 1), which in turn are determined by such parameters as the ratios between achene weight and pappus weight and between pappus diameter and achene diameter (41). While other features, such as pappus design and the height from which the diaspore is released, are important in determining distances over which propagules may be moved by air currents, the fact remains that all of these features are readily quantifiable and form an empirical basis for comparing the dispersal abilities of newly naturalized weeds.

Table 1. Terminal velocities and resistance coefficients for dispersal units of selected Asteraceae naturalized or weedy in Australia (modified from (41)).

Species	Terminal velocity ($cm\ sec^{-1}$)	Resistance coefficient (cm^{-1})
Cirsium arvense	21.6	2.10
Sonchus arvensis	24.1	1.69
Senecio vulgaris	28.0	1.25
Taraxacum officinale	35.7	0.77
Sonchus oleraceus	35.7	0.77
Hypochaeris radicata	40.5	0.60
Senecio jacobaea	42.1	0.55
Carduus tenuiflorus	78.6	0.16

For the tumbleweeds *Salsola kali* and *Brassica tournefortii* and some grasses, such as *Nassella trichotoma*, medium to long range dispersal may be achieved when inflorescences break off and are moved by wind.

Because so many of the observed patterns of spread are of a probabilistic nature, if follows that more propagules will achieve long-distance dispersal as seed production increases. Using a theoretical approach, Auld and Coote (4) demonstrated that rates of spread increase with increasing population growth rates. Apart from the necessity for joint colonization by individuals of species which are obligate outbreeders (and these probably represent a minority of noxious weeds), the probability of random extinction decreases as the number of colonizing individuals increases (15, 39).

PLANT STRATEGIES RELATED TO INVASIVENESS

It seems to be virtually impossible to nominate a single character, or restricted group of characters, with the largest contribution to success in colonization; a great variety of genetic, physiological and ecological characters have been found to promote the success of colonizing species (9, 11, 33, 39). Bazzaz (13) further differentiates between 'colonizers' that enter unoccupied or sparsely occupied habitats and 'invaders', which are capable of entering relatively intact vegetation and dominating or displacing it altogether. In this regard, a useful conceptual framework for classifying weeds is provided by Grime (20). He defines three primary plant strategies, namely ruderal, stress-tolerating and competitive, according to whether the predominant environmental feature is (a) disturbance, (b) shortage (or excess) of solar energy, water and mineral nutrients, or (c) competitive interactions between plants which occur in productive habitats subjected to low levels of disturbance. Ruderal species, while good colonizers of sparsely vegetated sites, are short-lived weeds of succession (2) and are generally displaced by more competitive species in the absence of continued disturbance. Stress-tolerant species are characteristic of chronically unproductive habitats and are unlikely to contribute many noxious weeds. Competitive species, however, comprise plants which can invade relatively closed communities and attain dominant positions. Responses to disturbance and environmental stress may figure in the secondary competitive strategies, shown by competitive ruderals and stress-tolerant competitors, as described later.

1. Characteristics of competitors

In Grime's (20) scheme, competitors are perennials which are characterized by high growth rates (R) (Table 2) and vigorous growth both above and below ground. The coupling of high R with a large number of growing points enables these plants to alter positions of their resource capturing surfaces, and gain continued access to moisture and nutrients, as well as to avoid shade. Such species often demonstrate lateral spread through vegetative reproduction and respond to defoliation by either renewed growth of damaged parts or by the production of new shoots. It is not uncommon for competitors to form dense, monospecific stands (e.g. *Mimosa pigra*, *Baccharis halimifolia*), and many are characterized by early and continued production of wind-dispersed propagules, which facilitate the colonization of new habitats.

2. Secondary competitive strategies

Competitive ruderal species are common in productive habitats in which dominance by competitors is prevented by disturbance, but where the frequency of disturbance is not sufficient to favour ruderals. Examples of such habitats include grasslands or areas under crop/pasture rotation. Competitive ruderals comprise a variety of life forms (Table 2), and are typified by prolific production of seeds, many of which are wind-dispersed. Important weeds of crops belong to this category, and differ from ruderals *per se* in that growth in the vegetative phase leads to competition with desirable species.

Stress-tolerant competitors are characteristic of habitats with moderate to low productivity and low intensities of disturbance. They occupy sites where stress conditions are experienced during periods of growth, such as soils with low fertility status in Australian coastal regions or in semi-arid rangelands where the predominant form of stress arises through drought. Stress-tolerant competitors differ from competitors by having lower R and leaves with longer life spans. Possible examples from the Australian weed flora include *Hypericum perforatum*, for which the dry weight of seedlings was only three times that of the sown seed after 90 days of growth (14) and *Sclerolaena birchii*, for which R was 0.4 g g^{-1} wk^{-1} between 4 and 8 weeks following germination (3).

PREDICTIONS RELATING TO POTENTIAL NOXIOUS WEEDS

Moore (31) questioned whether noxious weeds legislation has materially affected agricultural production other than by keeping out potential weeds through quarantine regulations. While the quarantine approach can be effective in preventing the ingress of undesirable plants, it is not a simple

Table 2. Relative growth rates of plants scheduled as noxious weeds, declared or pest plants.

Species	States where declared	Life-form[a]	Strategy[b]	Relative growth rate[c] ($g\ g^{-1}\ wk^{-1}$)	Plant age when measured (wks)	Reference
Parthenium hysterophorus	all	A	CR	0.96	3–4	48
Xanthium occidentale	V, T, SA, Q, NT, WA	A	CR	0.72	4–8	25
Carduus nutans	V, T, NSW	A or B	CR	1.12	2–5	26
Cirsium vulgare	T, SA, NSW	B	CR	0.89	2–5	20
Centaurea nigra	V	HP	CR	1.13	2–5	20
Ageratina adenophora	NSW, Q	HP	CR	1.43	2–4	5
Rumex obtusifolius	T, WA	HP	CR	1.49	2–5	20
Senecio jacobaea	V, T, SA, NSW, WA	HP	CR	1.24	2–5	20
Rubus fruticosus	V, T, SA, NSW, WA	HP	C	0.73	not given	1
Chrysanthemoides monilifera	V, SA, Q, WA	WP	C	0.80	4–?	46
Baccharis halimifolia	NSW, Q, NT	WP	C	1.30	2–4	34
Ulex europaeus	V, T, SA, NSW, WA	WP	C	0.74	2–5	20

[a] A = annual; B = biennial; HP = herbaceous perennial; WP = woody perennial
[b] C = competitor; CR = competitive ruderal
[c] Relative growth rates (R) of greater than 1 $g\ g^{-1}\ wk^{-1}$ indicate more than a doubling of dry weight over 7 days. Values of R decrease naturally as plant age increases.

matter to predict which species are likely to achieve noxious weed status under Australian conditions. A degree of success has been obtained with the use of correspondence analysis to determine the most likely source regions for potential Australian weeds in the thistle genera *Carduus*, *Centaurea* and *Onopordum* (18) and in *Echium* (19). Similarly, a bioclimatic predictive approach has been partially successful in matching presumably vulnerable areas within Australia to South African source regions of *Chrysanthemoides monilifera* (23, 24).

For species which are relatively recent arrivals to Australia, Moore (32) suggested that perhaps only those which are newly introduced, established in areas of less than 40-50 ha and with 'characteristics likely to make them weeds' should be proclaimed noxious, considering the rather abysmal record of dealing with more widespread weeds. This raises the question of the likely final distribution of a newly introduced weed, and the approach adopted by a number of Australian authors has been to attempt to predict the extent to which uncolonized areas are at risk of invasion (16, 23, 27, 35, 38, 48). The necessity for gaining such a predictive capacity arises from the practical difficulties which are associated with attempts to eradicate, or even contain, weedy species once they have become established over more than a strictly limited area.

The use of correlative models (23, 24, 35) for the purposes of predicting areas which are at risk of invasion has distinct disadvantages when factors other than climatic (e.g. competing species and predators) have a limiting influence on the distribution of a species in its native range. In addition, particular forms of management may have a marked influence on the range of environmental conditions over which a species may be weedy (see (45) for a discussion related to the native and introduced ranges of *Chondrilla juncea*, a species which is currently spreading in areas of Western Australia which are climatically distinct from its range of occurrence in south-eastern Australia (35)). Michael (30) lists a number of weeds, primarily from Europe and the Mediterranean region, whose Australian distributions are at variance climatically with their native distributions.

Groves (22) has estimated that perhaps only 5% and 1-2% of all plant species introduced in Australia have attained naturalization and weed status, respectively. This implies that highly refined predictive techniques will be required to isolate the very small proportion of accidental and illegal introductions that could eventually obtain noxious weed status. If, indeed, future weeds will be recruited from a pool of naturalized species which corresponds to less than 10% of the total number of introductions, I suggest that it might be most expedient to focus attention upon this restricted group, allowing the environment to act as a 'filter' for less suitable candidates. This approach is strengthened by the fact that even if it were possible to predict with precision the species which would become weeds, new naturalizations appear to be inevitable despite the presence of quarantine services of 'high competence' (23). It is, of course, essential that newly naturalized species are recognized as quickly as possible by land managers and weeds inspectors.

CONCLUSIONS

Experience suggests that the weed species which are most likely to create problems for land managers are those which are able to invade well managed areas (2). This implies that such species have moderate to high competitive ability, an important facet of which is the ability to maintain high growth rates during seedling establishment (Table 2). I suggest that noxious plant candidates may be further distinguished by their ability to accumulate dry matter under conditions of low availabilities of light (5, 34, 37) and nutrients (7), where the competitive ability of more favoured plants may be reduced. Relative growth rate is particularly useful as a criterion of plant performance in that it is an integrative expression of a group of physiological attributes which facilitate the capture of resources (20). As such, it probably provides a more sound basis for the prediction of weed potential than, for example, the speed of germination under laboratory conditions (17, 19). Other plant characteristics such as spininess, lack of palatability, and toxicity, frequently found in weeds which give rise to management problems in grazed areas, will find expression in the competitive balances between weeds and favoured plants. The last characteristic can be readily determined by toxicological investigation if there are any grounds for suspicion (47).

Given that the primary aim of noxious plant legislation is to prevent spread, it is suggested that we should examine systematically the potential fecundities and dispersal characteristics of possible candidates. Some of the most effective types of dispersal and fastest spread are the results of human activities, and may be realized through the possession of nonspecialized characteristics of seeds and their production. Seed cleaning procedures do, however, select for a definable subset of possible seed characters, and restrict the number of species which may be dispersed in seed lots. The potential for less efficient types of dispersal, e.g. dispersal by wind and water, can also be defined.

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